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Ecological processes underlying the community assembly of aquatic microscopic and macroscopic organisms under contrasting climates in the Tibetan Plateau biodiversity hotspot

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Running title: Stream communities under contrasting climates

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Abstract

Understanding the role of climatic variation on biodiversity is of chief importance due to the ongoing biodiversity loss and climate change. Freshwaters, one of the most threatened ecosystems in the world, offer a valuable context to study biodiversity patterns of distinct organism groups in relation to climatic variation. In the Tibetan Plateau biodiversity hotspot, we studied the effects of climate and local physico-chemical factors on stream microorganisms (i.e. bacteria) and macroorganisms (i.e. macroinvertebrates) in two parallel catchments with contrasting precipitation and temperature. Diversities and community structures were better explained by climatic and local environmental variables in the drier and colder catchment and at higher elevations, than in the warmer and wetter conditions and at lower elevations. This suggests that communities may be more strongly assembled by deterministic processes in the former, comparatively harsher conditions, compared to the latter, more benign conditions. Macroinvertebrates were more strongly affected by climatic and local environmental factors compared to bacteria, but the diversities and community structures of the two groups showed spatially similar responses to overall abiotic variation, being especially evident with their community structures' responses to climate. Furthermore, bacterial and macroinvertebrate diversities were positively correlated in the drier and colder catchment, implying that these biologically and ecologically distinct organism groups are likely to be driven by similar processes in areas with such climatic conditions. We conclude that changes in climatic and local environmental conditions may affect the diversity of macroorganisms more strongly than that of microorganisms, at least in subtropical mountainous stream ecosystems studied here, but simultaneous responses of both groups to environmental changes can also be expected.

Key words: assembly processes, bacteria, body size, climate change, elevation, macroinvertebrates

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1. Introduction

Human actions have severely modified the abiotic and biotic conditions on Earth (Butchart et al., 2012; Lewis & Maslin, 2015; Waters et al., 2016), with climate change being one of the most influential threats to biodiversity (IPCC, 2018; Vitousek, 1994). The changing climate can alter ecosystem processes and biodiversity patterns in a variety of ways, many of which are impossible to predict in advance (Cardinale et al., 2012; Forster, Hirst, & Atkinson, 2012; Parmesan, 2006; Woodward, Perkins, & Brown, 2010). Impacts of climate change can cascade through entire ecosystems, alter their functions (Chapin et al., 2000; Frauendorf et al., 2019; Wieczynski et al., 2019) and produce biogeochemical feedback to climate through biological processes, such as those related to carbon and nutrient cycling (Bardgett, Freeman, & Ostle, 2008; Kyupers, Marchant, & Kartal, 2018).

Estimating climate-induced functional changes in ecosystems requires deep understanding of climate change impacts on biodiversity (Bardgett et al., 2008; Bradford et al., 2019). In the face of global change, research themes such as anthropogenic impacts, biological community variation and macroecological pattern-searching approaches have indeed become more common (McCallen et al., 2019). Macroecological contexts are especially useful for studying the relationships between biodiversity and its underlying drivers, as species richness, species distributions and abundances can be statistically linked to surrounding environmental conditions at ecologically meaningful spatial scales (Brown, 1995; Shade et al., 2018).

The key for understanding biodiversity responses to changes in the environment is to detect the degree to which biological communities vary along environmental gradients. The terminology used to discuss and compare environmentally-driven and other types of patterns in biological communities is considerable (Brown, Sokol, Skelton, & Tornwall, 2016). In general, however, a strong relationship between community variation and environmental

variation can be indicative of deterministic assembly processes (cf. niche assembly, Chase & Leibold, 2003; Leibold et al., 2004). When no clear relationships between community variation and abiotic environmental variation exist, then biological communities are typically considered to be shaped by stochastic processes or, alternatively, by biotic interactions. Stochasticity is a term that can refer to, for instance, dispersal processes or ecological drift (Vellend, 2010). The unexplained part of variation in biodiversity-environment models is commonly suggested as evidence of stochastic processes, which are difficult or impossible to account for in practice (Vellend et al., 2014). Acknowledging the relative influences of deterministic and stochastic processes on variation in biodiversity is highly relevant for understanding and estimating possible global change impacts on biodiversity. For example, if communities show deterministic patterns, changes in surrounding environmental conditions will likely alter biodiversity through niche assembly and can thus be somewhat predictable.

Climate is considered to be an important driver of global biodiversity patterns (Gaston, 2000), although temperature-related changes in species distributions also appear at regional scales along latitudinal and elevational gradients (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). In a local context, for instance, changes in precipitation and flow regime are likely to alter stream habitat conditions, resources, biomass and community structures (Frauendorf et al., 2019). Drought was linked to a higher similarity in experimental pond communities, whereas benign, wetter conditions were associated with higher site-to-site community variation, possibly resulting from stochasticity (Chase, 2007). In contrast, deterministic processes dominated in stable, and stochastic processes in dynamic temporary prairie wetlands (Daniel, Gleason, Cottenie, & Rooney, 2019). Factors other than climate usually are more important for biodiversity patterns at regional or local scales (Parmesan & Yohe, 2003). In a regional context, for instance, agricultural land use (Jyrkänkallio-Mikkola et al., 2017), climate, land cover and local water chemistry (Pajunen, Luoto, & Soininen,

2017) have been linked to variation in aquatic microorganism diversity (Besemer, 2015). Local-scale variables such as water chemistry and physical conditions are also important drivers of aquatic macroorganism diversity (Rocha et al., 2018; Sandin & Johnson, 2004). Biodiversity responses to environmental drivers tend to be linked to the spatial scale examined (Azovsky, 2002; Chase et al., 2018; Heino, 2011; Soininen, 2012), as the impact of local environmental factors on community structure generally decreases with increasing spatial extent (Mykrä, Heino, & Muotka, 2007; Parmesan & Yohe, 2003).

The formation of biodiversity patterns in itself is a complex process, but the patterns – largely outcomes of deterministic and stochastic assembly processes – also tend to be linked to the characteristics of the organism groups studied. Body size is a characteristic relevant for understanding the balance how deterministic or stochastic processes dominate community structuring (Farjalla et al., 2012). Ultimately, body size is a feature defining the scale at which the organism operates and perceives its environment. Microbes, for example, may respond to the environment at very small scales (Azovsky, 2002; Zinger et al., 2019). When observing organisms at the border of microscopic and macroscopic worlds, it is generally assumed that smaller organisms are better dispersers than larger ones, at least among passive dispersers and at large spatial scales (Finlay, 2002). A number of recent studies have reported that communities comprising of smaller organisms tend to be more deterministically assembled compared to communities of larger organisms (Beisner, Peres-Neto, Lindström, Barnett, & Lorena Longhi, 2006; Astorga et al., 2012; Zinger et al., 2019). However, other studies have reported the exact opposite, showing that determinism increases with body size (Farjalla et al., 2012; Soininen, Korhonen, & Luoto, 2013). The plethora of earlier findings on the relationship between body size and dominating assembly processes suggests that broad generalizations are premature.

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The scientific community is highly unanimous that due to the ongoing climate change, temperatures will continue to rise worldwide, with some regions witnessing increased precipitation and others suffering drier conditions (e.g. IPCC, 2018). It is thus useful to examine the degree to which climatic and local physico-chemical variables are connected to biodiversity patterns in contrasting climatic conditions. Freshwater ecosystems, with their biodiversity being highly threatened due to climate change, offer an important model system to examine these patterns (Reid et al., 2019; Wiens, 2016; Woodward et al., 2010). Here, we studied aquatic microscopic (i.e. bacteria) and macroscopic (i.e. macroinvertebrates) organisms in two parallel catchments located in the south-eastern part of the Tibetan Plateau, a region harboring very high biodiversity (Antonelli et al., 2018; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). The two surveyed catchments, upper parts of the Salween and Mekong Rivers, differ in climatic conditions, the former study area being significantly wetter and warmer than the latter drier and colder one. The spatial arrangement of our sampling sites allows examining strong latitudinal and elevational gradients, further strengthening climatic variation across the sites (e.g. Sundqvist, Sanders, & Wardle, 2003). Both catchments have similar geological histories, which is an important factor when aiming to detect the effects of climate and other environmental factors to biodiversity patterns (see also Frauendorf et al., 2019; Sanders & Rahbek, 2012). Furthermore, the neighboring catchments likely share the regional species pool, providing an ecologically meaningful spatial scale for this study. Our aim was to compare patterns in biodiversity and community assembly mechanisms between microscopic and macroscopic stream organisms in the contrasting climatic conditions described above. For reaching this goal, we specifically asked the following two questions: 1) Do community structures and diversities differ between the wetter and drier catchments? 2) Are the explanatory powers of

climate and local variables different between the two catchments, elevations and organism groups?

2. Materials and Methods

2.1. Sampling and data processing

The south-eastern part of the Tibetan Plateau (Yunnan, China) is one of the world's biodiversity hotspots (Myers et al., 2000). Along the Hengduan Mountains, three rivers flow parallel to each other (Three Parallel Rivers UNESCO World Heritage Site). In October 2014, we sampled 89 individual streams that flow into two of these parallel rivers. Of these, 52 of the sampled streams flow into the upper parts of the Salween River (*Nujiang* in Chinese) and 37 streams into the upper parts of the Mekong River (*Lancang* in Chinese) (Fig. 1). Although flowing side by side in the surveyed region, the studied parts of the two catchments have significantly contrasting climates: the Salween catchment is wetter (mean annual range 632–1021 mm) and warmer (14.2–22.2°C), and the Mekong catchment is drier (420–718 mm) and colder (11.2–17.6°C) (see Appendix A for more details). Due to simplicity, the Salween catchment is referred to as the "wet" and the Mekong catchment as the "dry" catchment throughout the remaining of this chapter, as well as the Results section.

Each sampling site was divided into five or 10 cross-sections, depending on the width of the stream. Along the transects, 20 stones were randomly collected from riffle or run habitats. Biofilm, comprising of attached microbial cells, was scraped from the surfaces of the stones with a sterilized sponge. The site-specific pooled samples were frozen to -18 °C immediately after the sampling using a portable refrigerator. Four kick-net samples of macroinvertebrates were taken from stony riffle or run habitats. The pooled samples were immediately stored in 70% ethanol in the field.

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At each site, longitude, latitude and elevation were recorded using a GPS device, and stream width, depth, shading percentage, current velocity, substratum particle size, water temperature, pH and conductivity were measured. At each site, water samples were taken and then preserved at -18 °C, until a number of chemical components (e.g. various nutrients and metals; see Appendix A) were analyzed in the laboratory. These physico-chemical variables are referred to as local variables throughout the remaining of the paper. The sampling and laboratory methods followed Wang et al. (2011).

Information on climatic variables for each site was collected from CHELSA Bioclim (http://www.chelsa-climate.org). Mean annual temperature, annual temperature range, annual precipitation and precipitation seasonality were selected to illustrate basic climatic conditions and used as climatic explanatory variables in statistical analyses. The list of explanatory variables included in the analyses is presented in Appendix A along with descriptive statistics.

2.2. Biological analyses

For bacterial communities, we followed the same procedures as indicated in Wang et al. (2017). Briefly, genomic DNA was extracted from biofilm using a phenol chloroform method (Zhou, Bruns, & Tiedje, 1996). Bacterial 16S rRNA genes were amplified in triplicate using bacterial universal primers 515F and 806R targeting the V4 region. Positive PCR products were confirmed by agarose gel electrophoresis. PCR products from samples to be sequenced in the same MiSeq run were pooled at equal molality. The pooled mixture was purified with a QIAquick Gel Extraction Kit (QIAGEN Sciences, Germantown, MD, USA) and requantified with PicoGreen (Eugene, OR, USA). Sample libraries for sequencing were prepared according to the MiSeq Reagent Kit Preparation Guide (Illumina, San Diego, CA, USA). Overlapped paired-end sequences from Miseq were assembled using FLASH (Magoč &

Salzberg, 2011). Poorly overlapped and poor-quality sequences were filtered out before de-multiplexing based on barcodes. Further, the sequences were clustered into OTUs at 97% pairwise identity with the seed-based uclust algorithm (Edgar, 2010). After chimeras were removed via Uchime against ChimeraSlayer reference database in the Broad Microbiome Utilities, representative sequences from each OTU were aligned to the Greengenes imputed core reference alignment V.201308 (DeSantis et al., 2006) using PyNAST (Caporaso et al., 2010). Taxonomic identity of each representative sequence was determined using the RDP Classifier (Wang, Garrity, Tiedje, & Cole, 2007) and chloroplast and archaeal sequences were removed. The bacterial dataset was rarefied to 10,000 sequences.

Macroinvertebrates were first sorted in the laboratory and subsequently identified to the genus level when possible using standard keys (Morse, Yang, & Tian, 1994). Genus level was the target taxonomic level here because there are no sufficient taxonomic keys for finer-level identifications of macroinvertebrates for this region (see also Li et al., 2019). Genus-level information is usually, however, highly congruent with species-level information (e.g. Mueller, Pander, & Geist, 2013).

2.3. Statistical analyses

Prior to statistical analyses, singletons were removed (i.e. taxa occurring only at one site) from the bacterial and macroinvertebrate datasets to reduce noise. Bacterial and macroinvertebrate datasets were analyzed separately.

Permutational analysis of variance (PERMANOVA) and non-metric multidimensional scaling (nMDS) analyses were performed to detect whether communities differed between the wet and dry catchments. Hellinger distances (i.e. Hellinger-transformed abundance data with Euclidean distances) were used in the PERMANOVA analyses and Bonferroni-corrected p-values were used due to examining the differences in community

structures between two groups. Mann-Whitney tests were performed to compare whether Shannon diversity, i.e. a measure of alpha diversity, differed between the two catchments. Community dissimilarity as illustrated by Hellinger distances (e.g. Legendre & De Cáceres, 2013) and Shannon diversity were investigated along the wet and dry elevational study transects using Spearman rank-based Mantel tests and linear models.

Variation partitioning analyses (Anderson & Gribble, 1998; Legendre & Legendre, 2012) were performed to reveal the effects of climatic and local variables on community structure and Shannon diversity. To rule out excessive effects of latitude (i.e. sites that were located very north or very south), only the parts of the catchments that overlapped in latitude were used in the variation partitioning analyses. Based on the mean latitude of the overlapping sampling sites, we formed two elevational bins (low and high). Response and explanatory variable matrices were then subset according to the two catchments (wet and dry) and the two elevational bins. In total, there were nine distinct groupings for both bacterial and macroinvertebrate communities: wet catchment, dry catchment, wet catchment – low elevational bin, wet catchment – high elevational bin, dry catchment – low elevational bin, dry catchment – high elevational bin, both catchments, both catchments – low elevational bin, and both catchments – high elevational bin. Climatic and local variables were used as two separate explanatory variable groups in the models where the catchments were considered separately, and catchment identity (catchment-ID) was added as a third explanatory variable group for models where both catchments were analyzed simultaneously. Adding the catchment-ID variable offered a way to acknowledge possible large-scale spatial patterns, perhaps illustrating differences in catchment-specific processes or dispersal across catchments (e.g. the effect of a mountain range; Dong et al., 2016), in the study area.

Before variation partitioning, principal component analysis (PCA) was performed to reduce the dimensions of measured metal and metalloid concentrations. The first two axes

were used as proxies for these elements. Other local variables (except pH) and climatic variables were log-transformed to better meet normal distributions. The biological abundance matrices were Hellinger-transformed. Local and climatic explanatory variables were selected with a forward selection method using function 'ordistep' in the R package vegan. For cases where no climatic or local variables were selected, annual mean temperature and/or DOC, i.e. the most common climatic and local variables selected, were forced into the models to get a general idea of how variation in the response variables is partitioned according to these rather basic abiotic drivers. For analyses including both catchments at the same time, catchment-ID was forced into the subsequent models. Adjusted R^2 values were considered in the context of the variable selection and variation partitioning analyses (Peres-Neto, Legendre, Dray, & Borcard, 2006).

Spearman correlation tests were performed to analyze the relationship between proportions of explained variations for bacteria and macroinvertebrates. These analyses were conducted only with the pure and shared explanatory powers of climate and local variables, and the total explained variation by these fractions. The original variation partitioning analyses, which included catchment-ID as a third explanatory variable group, were re-analyzed for this purpose with only climate and local environment included, so that the explanatory powers of climate and local variables were better comparable across subsets of response variables. The relationships between bacterial and macroinvertebrate community dissimilarity illustrated by Hellinger distances and Shannon diversity were analyzed with Spearman rank-based Mantel and correlation tests, respectively, using the entire dataset (i.e. also sites that did not overlap in latitude).

All analyses were done in the R statistical environment (R Core Team, 2018) and using packages vegan (Oksanen et al., 2018), ggplot2 (Wickham, 2016) and Scatterplot3d (Ligges & Maechler, 2003).

3. Results

Altogether, 5025 bacterial OTUs and 98 macroinvertebrate taxa were analyzed from the two catchments. NMDS plots illustrated that the community structures of both bacteria and macroinvertebrates differed between the dry and wet catchments (Fig. 2a and b), which was also confirmed by PERMANOVA ($p = 0.001$ for both cases). For both taxonomic groups, community dissimilarity showed increasing trends with increasing elevational distances in both catchments (Fig. 2c and d). Based on Mantel tests, the elevational distance-decay relationships were positive and statistically significant (Mantel rho = 0.419, $p = 0.001$ and Mantel rho = 0.424, $p = 0.001$ for bacteria in the wet and dry catchments, respectively; Mantel rho = 0.137, $p = 0.019$ and Mantel rho = 0.387, $p = 0.001$ for macroinvertebrates in the wet and dry catchments, respectively). There were partly contrasting relationships between Shannon diversity and elevation for the two catchments and the two organism groups, but they were not statistically significant, except for macroinvertebrate diversity and elevation in the wet catchment (adj. $R^2 = 0.060$, $p = 0.044$; Fig. 2e and f). Mann-Whitney test showed that Shannon diversity of bacteria differed between the two catchments ($p < 0.001$), but that was not the case for macroinvertebrate diversity ($p = 0.819$).

The variation partitioning analyses showed that the explanatory variables accounted for 0–61% and 3–26% of variation in Shannon diversity and community structure, respectively (Fig. 3). Much of the explained proportions were linked to pure effects of local and climate variables, and their shared contribution. Pure climate and local fractions generally explained more of variation in community structure and diversity for macroinvertebrates than for bacteria. The catchment-ID usually was not associated with patterns in diversity or community structure of either of the two groups, but for macroinvertebrate Shannon diversity in the high elevational bins, there were notable, pure

catchment-related patterns. In general, the variations in community structures and diversities could be better explained in the higher than the lower elevational bins. When considering the catchments separately, more of the variations in our response variables could be explained in the dry than in the wet catchment. Thus, there were regional differences in the amounts of explained variations in our response variables, and the differences were observed between catchments and elevational bins (i.e. within catchments). Details on selected explanatory variables, and results of variation partitioning and fraction tests are presented in Appendix B.

More of the variations in macroinvertebrate community structures and diversity could be explained than those of bacteria. Sums of explained proportions for community structures were 147.2 and 94.3, and for Shannon diversity 249.2 and 156.6 for macroinvertebrates and bacteria, respectively. Macroinvertebrates were thus more strongly associated with climate, local variables and catchment-ID compared with bacteria. Despite of the different amounts of explained proportions, based on visual inspection, there seemed to be a similar response of the organism groups to the explanatory variables (Fig. 3). When considering only the effects of climate and local variables, the similarity of response was clearest for local variables with Shannon diversity (Spearman rho = 0.304, p = 0.124; Fig. 4a) and for climate with community structure (Spearman rho = 0.584, p = 0.017; Fig. 4b). Total explanatory powers (i.e. pure and shared effects of climatic and local variables) were positively associated with bacteria and macroinvertebrates, being clearer for community structure (Spearman rho = 0.734, p = 0.003) than Shannon diversity (Spearman rho = 0.05, p = 0.552).

Shannon diversity of macroinvertebrates and bacteria were positively correlated with each other across all sites in the dry catchment (Spearman rho = 0.150, p = 0.010), but there was no significant relationship between diversity of the two organism groups in the wet catchment (Fig. 5a). Based on Mantel tests, community dissimilarities of bacteria and

macroinvertebrates were positively correlated in the dry (Mantel rho = 0.178, p = 0.001), but less clearly in the wet catchment (Mantel rho = 0.027, p = 0.028; Fig. 5b).

4. Discussion

The ongoing climate change necessitates increased understanding of the relationship between biodiversity patterns and environmental variation (Bardgett et al., 2008; Bradford et al., 2019; Parmesan, 2006). Simultaneous examinations of microscopic and macroscopic organisms at broad spatial scales provide important insights into biodiversity patterns (Shade et al., 2018). Here, we studied microscopic (i.e. bacteria) and macroscopic (i.e. macroinvertebrates) stream organisms in a setting of two neighboring subtropical catchments with significantly contrasting climatic conditions. The proximity of the two catchments suggests that they share the regional species pools for both biotas, which was evidenced by the fact that we saw no clear signs of catchment or mountain related spatial constraints in our response variables.

For both organism groups, a larger share of variation in Shannon diversity and community structure could be explained in the drier and colder than in the wetter and warmer catchment, and at higher than at lower elevations. If we assume that drier climatic conditions are more challenging for aquatic organisms than wetter ones, the drier catchment can, in this sense, be considered as a comparatively harsh environment (see also Chase, 2007). Furthermore, the drier catchment also has colder temperatures, while the wetter catchment is warmer, strengthening the harsh–benign separation between the two catchments. Likewise, higher elevations tend to have more challenging conditions than lower elevations in terms of stronger current velocity, colder temperatures and decreased water availability due to smaller catchment sizes. Thus, in addition to the dry catchment, the higher elevational bin can also be seen as an example of naturally harsh conditions. However, the meaning of "harshness" varies for different species: some species – be they microscopic or macroscopic – are better

adapted to, for instance, wetter or colder conditions than others. Our findings nevertheless suggest that community diversity in drier and colder conditions was more strongly driven by deterministic environmental filtering processes, while wetter and warmer environments fostered more stochastic events in community assembly. Our findings based on observational field data somewhat agree with the results from an experimental study, where extreme harshness (i.e. drought) was linked to higher similarity in communities and benign (i.e. wetter) conditions were associated with higher site-to-site variation and stochasticity (Chase, 2007). However, a higher influence of determinism in stable wetlands and stochasticity in dynamic wetlands were reported for the impact of hydroperiod to diversity (Daniel et al., 2019). These contrasting results may be due to the different taxonomic groups, biodiversity metrics or environmental contexts, such as the stronger differences in hydrologic conditions in Daniel et al.'s (2019) study compared to this study. Nevertheless, the support from both field observations (this study) and experiments (Chase, 2007) implies that comparatively harsh conditions have the potential to act as strong environmental filters, while there may be more room for random events in more benign conditions (see also Li et al., 2019). It is nevertheless important to keep in mind that any results based on actual field data provide insights that are highly context dependent. Comparative study settings, such as in this study, should be interpreted in the proper spatial context. For instance, "wet" or "warm" conditions in our study region might be something different in another region.

Interestingly, the idea that deterministic processes likely dominate in comparatively harsh (here, drier and colder) conditions is supported by the observed relationships between bacterial and macroinvertebrate Shannon diversities and community structures in the two catchments. For Shannon diversity, bacteria and macroinvertebrates were positively associated only in the drier and colder catchment. For community structure, bacteria and macroinvertebrates were always significantly associated with each other, but their

associations were much stronger in the drier and colder than the wetter and warmer system. Such consistent decoupled biological associations under contrasting climate conditions were further supported by elevational distance-decay relationships of macroinvertebrates, which showed stronger relationships in the comparatively harsher conditions compared to the wetter and warmer conditions. These findings point to the fact that although distance decay is a general phenomenon (Hanson, Fuhrman, Horner-Devine, & Martiny, 2012; Nekola & White, 1999; Soininen, McDonald, & Hillebrand, 2007), its strength may vary across climatic conditions and among biologically distinct organism groups even when the spatial context is the same (see also Astorga et al., 2012; Ma et al., 2017).

Community structures and Shannon diversity of macroinvertebrates were more constrained by the studied environment compared with those of bacteria. Conversely, bacteria showed more unexplained variation, possibly resulting from stochastic processes. Similar findings that smaller organisms show more stochastic and larger organisms more deterministic patterns were also reported across a set of boreal lakes (Soininen et al., 2013) and tropical bromeliad water tank habitats (Farjalla et al., 2012). These earlier studies suggested that faster population dynamics, stronger dispersal and challenges in sampling microbes in the field are possible reasons why smaller organisms show more stochastic patterns than larger organisms. However, larger organisms have been reported to show more stochastic and microbes more deterministic patterns in freshwater and forest soil ecosystems (Astorga et al., 2012; Beisner et al., 2006; Zinger et al., 2019). These contrasting findings may be related to the different spatial contexts examined. Across multiple waterbodies and varying landscapes (Astorga et al., 2012; Beisner et al., 2006), the effect of body size on organisms tracking suitable environmental conditions may be opposite to a more restricted study setting (e.g. mountain streams in two parallel catchments). Also, differences in the spatial scale examined are likely to be another reason for such contrasting findings. For

instance, Zinger et al. (2019) studied a 12 ha forest soil plot, whereas our spatial extent covered thousands of square kilometers. It is thus likely that the relationship between body size and the chief assembly process may also depend on the spatial scale studied: at comparatively large spatial scales (e.g. Soininen et al., 2013; this study), smaller-sized organisms were mainly driven by stochastic events, but at a very small spatial scale, larger-sized organisms showed stronger signs of stochasticity (Zinger et al., 2019). The effect of the spatial scale when inferring assembly processes has gained well-deserved attention in recent years (Heino, 2011; Soininen, 2012; Viana & Chase, 2019), providing further support for the idea that the relationship between body size and the dominating assembly process (determinism vs. stochasticity) is probably dependent on the spatial scale and environmental context of investigation. Ultimately, microscopic organisms live and perceive their environment in a much finer scale than larger organisms (Azovsky, 2002). Thus, when concentrating on microhabitat conditions of the biofilm and stone surfaces, the importance of deterministic processes for microbial community assembly would likely be different compared to our current findings, which were based on broad-scale investigations. Also, the sheer diversity of bacterial OTUs is another possible reason why our models could not explain bacterial diversities and community structures as well as they did for macroinvertebrates, which is a less diverse group of organisms.

Despite the differences in deterministic and stochastic assembly patterns between bacteria and macroinvertebrates, their responses to environmental variables were spatially similar, which the relatively high level of stochasticity in bacterial diversity could not hide. Spatially similar diversity patterns were also recently reported for birds, plants and macroinvertebrates across wetlands with differing hydroperiods (Daniel et al., 2019). The comparatively similar patterns of bacteria and macroinvertebrates were especially evident in the relationships between community structures' responses to climate and, to a lesser degree,

between Shannon diversity and local variables. These findings have two implications. First, congruent responses of community structures of two distinct organism groups suggest that beta diversity (e.g. variation in community structure) is more reliable in describing overall biodiversity-environment relationships than alpha diversity (e.g. Shannon diversity) (Socolar, Gilroy, Kunin, & Edwards, 2015). Second, climatic signal in biological associations is stronger than that of contemporary environments (e.g. "snapshot" local variables). Our results imply that local environments may regulate alpha diversity, but climate controls the spatial turnover of community composition across a region. Furthermore, a recent study revealed that finer taxonomic resolutions showed patterns associated more strongly with local variables and less with climatic variation, suggesting that climatic preferences are evolutionary older than local environmental preferences (Yeh, Soininen, Teittinen, & Wang, 2019). The fact that climate was a rather strong determinant of congruent patterns in bacterial and macroinvertebrate communities indicates that climatic preferences may indeed be evolutionary signals in both organism groups.

We considered two biological groups with different body sizes and two catchments with comparatively contrasting climates. Such parallel, neighboring catchments are rarely found elsewhere. The consistent patterns observed suggest that drier and colder climatic conditions promote deterministic community assembly, macroorganisms are more deterministic than microorganisms, and climatic signal is generally stronger in beta diversity than in alpha diversity. However, our findings are not immune to the limits of our methods and other study-specific decisions, such as unmeasured but important environments, unaccounted biological interactions, and study habitats and organism groups selected. Overall, the high amount of unexplained variation in models, in addition to the possibility of prevalence of stochastic processes, can also indicate that not all relevant environmental variables were measured or that there were unacknowledged biotic interactions (e.g. Vellend

et al., 2014). In our case, the comparatively large set of physico-chemical and climatic variables was likely sufficient and ecologically relevant for both bacteria and macroinvertebrates (cf. Besemer, 2015; Pajunen et al., 2017; Rocha et al., 2018; Sandin & Johnson, 2004). Thus, the unexplained proportions of variations in the response variables probably stemmed more from stochastic processes and less from not-measured explanatory variables. Future studies should incorporate biotic interactions, more organism groups and various types of ecosystems to the assessment of the roles of climatic conditions on biodiversity. Furthermore, due to lack of reliable estimations of anthropogenic land use in our study region, we could not study relationships between anthropogenic land use, climatic conditions and biodiversity (e.g. Peters et al., 2019), leaving another important research avenue for the future.

To conclude, biodiversity in the subtropical region of the Tibetan plateau is likely to be more vulnerable to climatic and climate-driven environmental changes in areas with harsher (i.e. drier and colder) climatic conditions compared to areas with more benign (i.e. wetter and warmer) conditions. Regarding body sizes, communities consisting of larger-sized organisms will likely show stronger responses to climate change in mountain stream ecosystems, possibly leading to altered food web dynamics (e.g. Frauendorf et al., 2019), compared to microscopic organisms. Microscopic and macroscopic organisms, however, may show spatially similar responses to environmental changes, with aquatic communities in general being vulnerable to the effects of the ongoing global change. Overall, future biodiversity in mountain regions will depend on how speciation, dispersal and refugia respond to climate change (Antonelli et al., 2018), and how the interplay between human activities and climatic conditions shapes these ecosystems (Peters et al., 2019).

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Author contributions

JW conceived the idea with contribution from AV. JW conducted field sampling and provided the data. JW performed the bioinformatic analyses. WZ and AV performed the statistical analyses. AV wrote the manuscript with contributions from all authors. All authors contributed to the intellectual development of this study.

Conflict of interest

The authors declare no conflict of interest.

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Supporting information

Appendix A. Descriptive statistics of explanatory variables.

Appendix B. Used explanatory variables and variation partitioning results.

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Data availability

The bacterial sequences have been deposited in MG-RAST database under the accession number 90910.

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Figure captions

Fig. 1. The study area was located in the biodiversity hotspot of south-eastern Tibetan Plateau. In total, 52 sampled streams flow into upper parts of the Salween River, while 37 sampled streams flow into upper parts of the Mekong River. The black dots indicate the sampling sites, which were all close to the main reaches of the Salween and Mekong rivers.

Fig. 2. NMDS plots illustrating differences in bacterial (a) and macroinvertebrate (b) communities across the dry and wet catchments. Bacterial (c) and macroinvertebrate (d) communities showed increasing dissimilarities (Hellinger distance) with increasing elevational distances in both catchments. Shannon diversity of bacteria (e) and macroinvertebrates (f) did not show clear patterns with elevation in the wet and dry catchments. Statistically significant relationships indicated by Mantel tests (c, d; rho) or linear models (e, f; Adj. R^2) are illustrated by solid lines, while dashed lines indicate non-significant relationships.

Fig. 3. Variation partitioning results for Shannon diversity (a) and community structure (b) for different subsets of data. Left panels represent cases where only climate and local variables were included, while right panels represent cases where catchment-ID was included as a third explanatory variable group. Relative contributions illustrate the proportions of variation in the response variables that could be explained by the explanatory variable groups and are based on adjusted R^2 values. Cli = climatic variables, Loc = local variables, Cat = catchment-ID, Dry = dry catchment, Wet = wet catchment, Low = low elevational bin, High = high elevational bin, Whole = both catchments and elevational bins together.

Fig. 4. Comparison of the proportions of explained variation by climatic and local variables between bacterial and macroinvertebrate Shannon diversity (a) and community structure (b).

Statistically significant relationships based on Spearman correlation coefficient (r_s) are indicated by solid lines. Dashed lines indicate non-significant relationships. Cli = climatic variables, Loc = local variables.

Fig. 5. Relationships between bacterial and macroinvertebrate Shannon diversity (a) and community structure (b) in the dry and wet catchments. Solid lines illustrate statistically significant relationships as indicated by Spearman correlation test (r_s) and Mantel test based on Spearman method (rho). Dashed lines indicate non-significant relationships.

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Figures

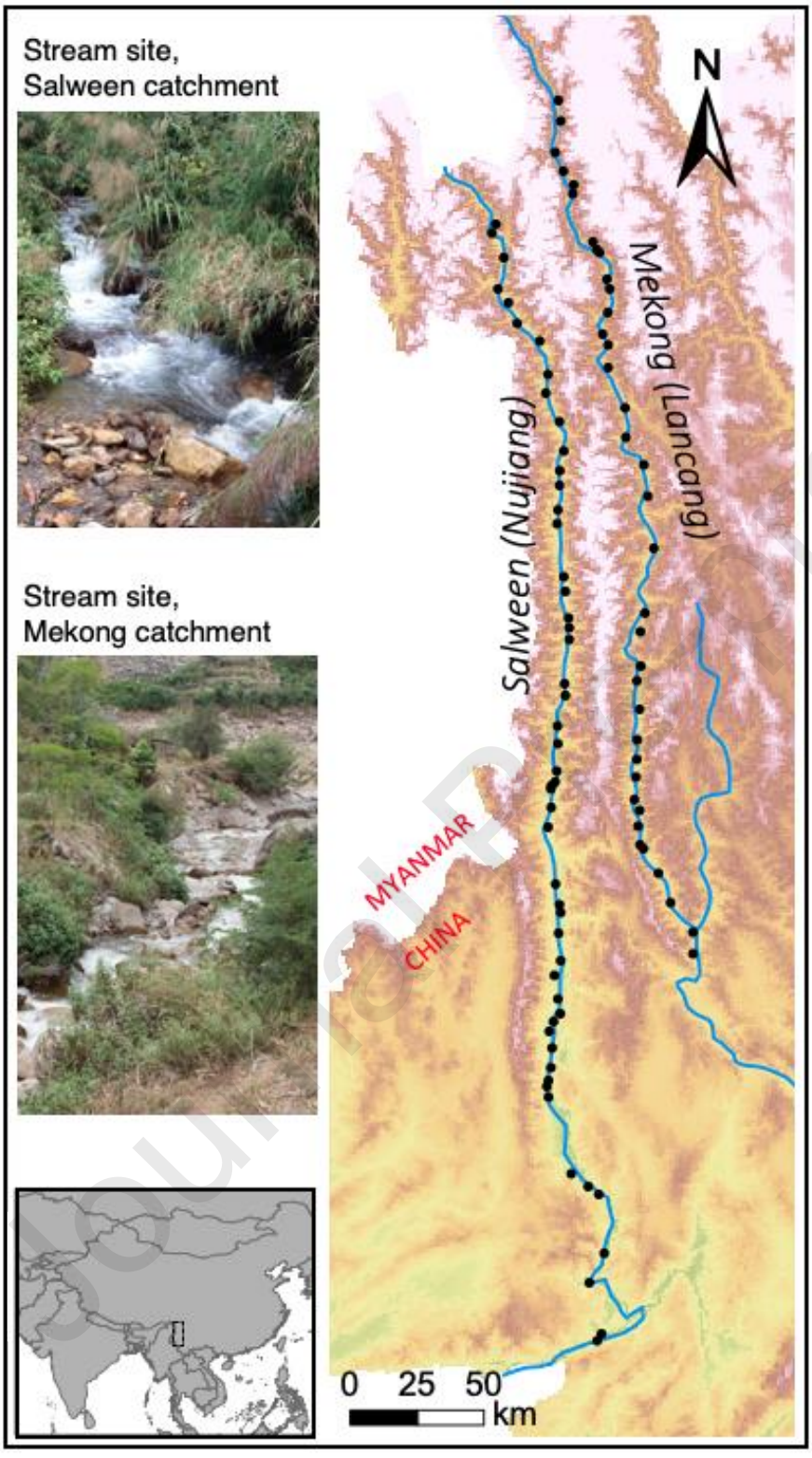


Fig. 1.

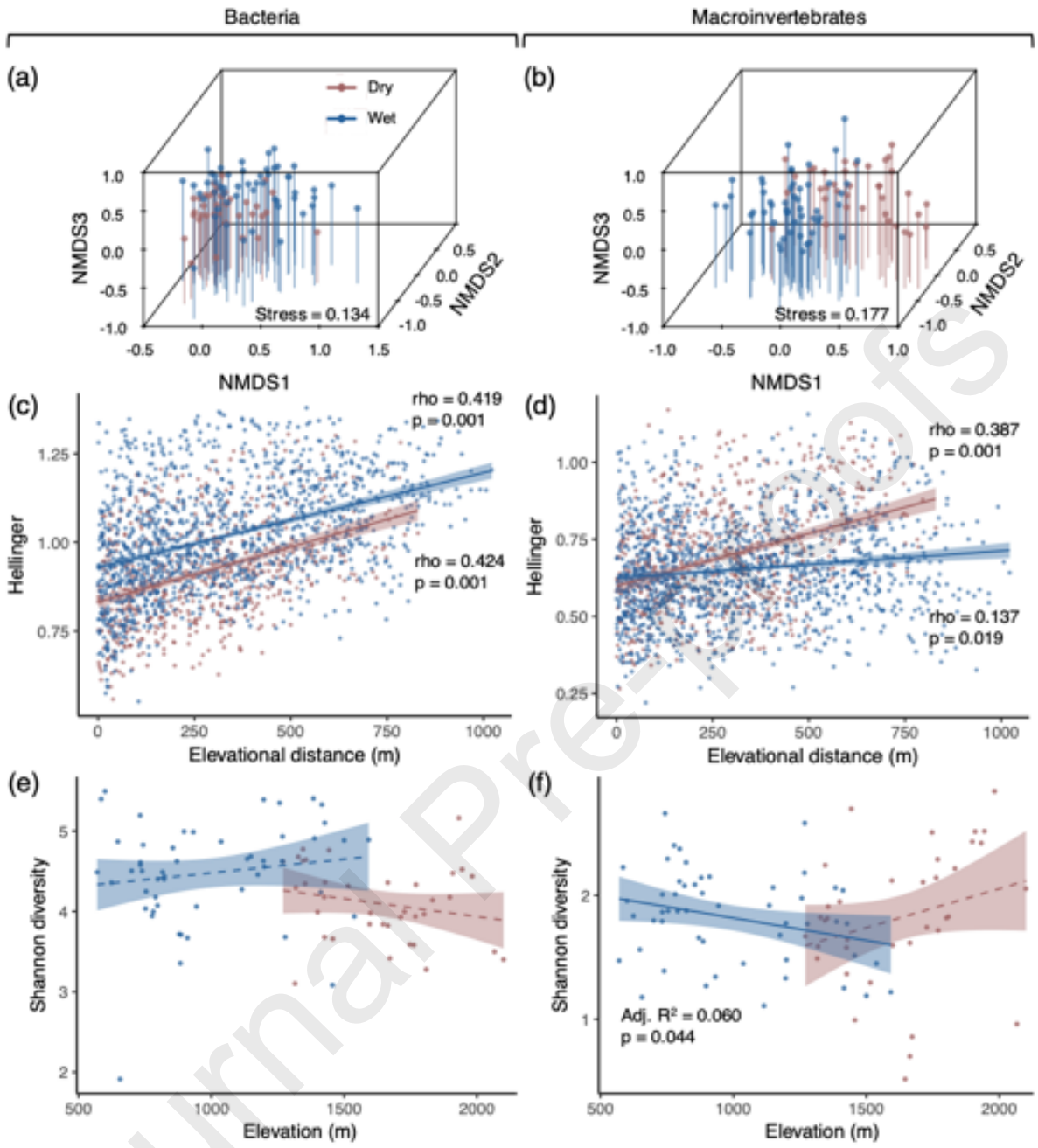


Fig. 2.

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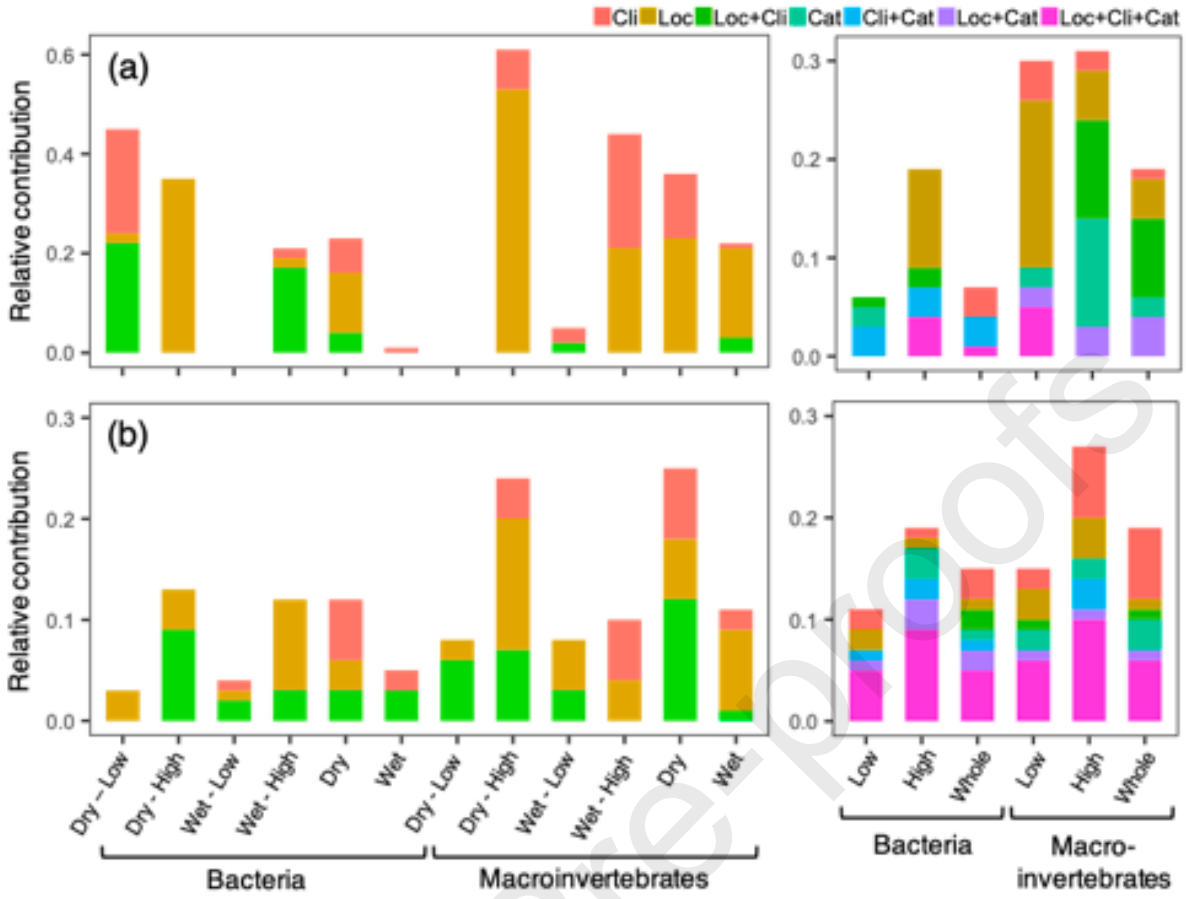


Fig. 3.

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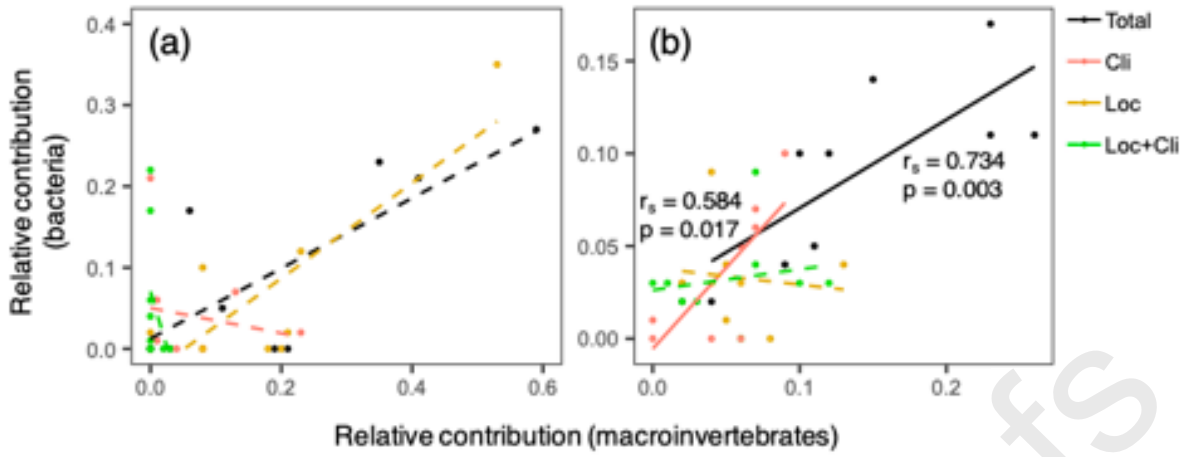


Fig. 4.

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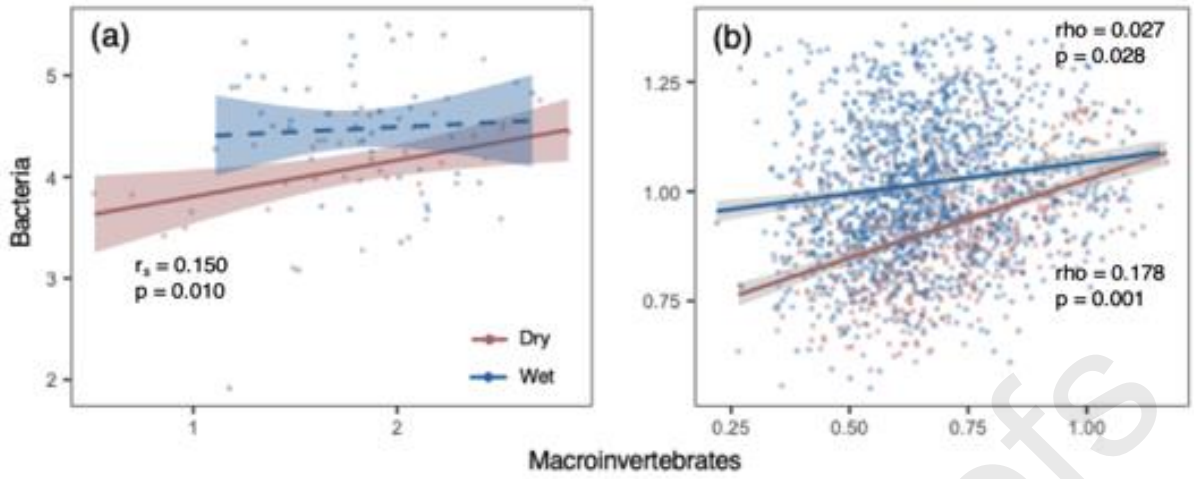
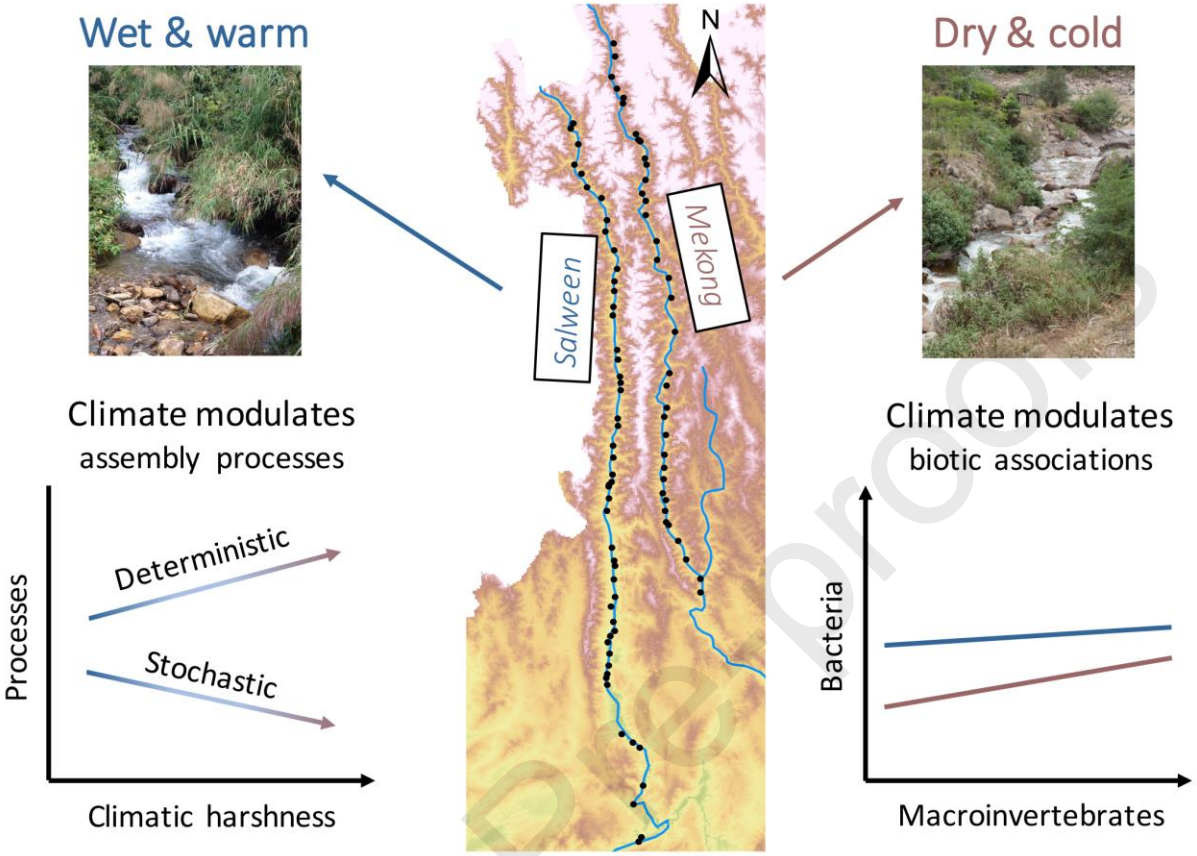


Fig. 5.

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Graphical abstract



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Highlights

(1) The effects of climate and local environment on aquatic microscopic (i.e. bacteria) and macroscopic (i.e. macroinvertebrates) organisms were studied in two parallel catchments with contrasting climates.

(2) In the colder and drier conditions, biodiversity was more strongly associated with deterministic environmental filtering, while in warmer and wetter conditions biodiversity was more strongly driven by stochastic processes.

(3) Although both groups of organisms showed a spatially similar response to climatic and local environmental variation, macroinvertebrates were more constrained by the abiotic environment while bacteria showed more stochastic patterns.

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