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Patterns of elevational beta diversity in micro- and macroorganisms

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ABSTRACT

Aim While ecologists have long been interested in diversity in mountain regions, elevational patterns in beta diversity are still rarely studied across different life forms ranging from micro- to macroorganisms. Also, it is not known whether the patterns in turnover among organism groups are affected by the degree to which the environment is modified by human activities.

Location Laojun Mountain, Yunnan Province, China.

Methods The beta diversity patterns of benthic microorganisms (i.e. diatoms and bacteria) and macroorganisms (i.e. macroinvertebrates) in a stony stream were simultaneously investigated between elevations of 1820 and 4050 m. Data were analysed by using a distance-based approach and variation partitioning based on canonical redundancy analysis.

Results Analyses of community dissimilarities between adjacent sampling sites showed comparable small-scale beta diversity along the elevational gradient for the organism groups. However, bacteria clearly showed the lowest elevational turnover when analyses were conducted simultaneously for all pairwise sites. Variation partitioning indicated that species turnover was mostly related to environmental heterogeneity and spatial gradients including horizontal distance and elevation, while purely human impacts were shown to be less important.

Main conclusions The elevational beta diversity at large scales was lower for bacteria than for eukaryotic microorganisms or macroorganisms, perhaps indicative of high dispersal ability and good adaptability of bacteria to harsh environmental conditions. However, the small-scale beta diversity did not differ among the groups. Elevation was the major driver for the turnover of eukaryotic organisms, while the turnover of bacteria was correlated more with environmental variation.

Keywords
Bacteria, beta diversity, beta-sim, China, diatoms, elevational gradient, human activities, macroinvertebrates, species turnover, streams.

INTRODUCTION

Over two centuries ago, Linnaeus and many of his contemporaries documented that there is a compressed and very orderly succession of climate, vegetative zones and animal communities along elevational gradients (Lomolino, 2001). A century ago, the Jaccard metric (Jaccard, 1912) was invented to measure the changes in species composition (i.e. beta diversity; Whittaker, 1972) in the alpine zone. However, compared with the well-known elevational patterns of species richness (Rahbek, 1995, 2005; Sanders, 2002), the elevational patterns of beta diversity have received very little attention. This lack of attention is unwarranted because the variation in alpha and beta diversity may result from different ecological and biogeographical processes (Wilson & Shmida, 1984; Loreau, 2000; Kessler *et al.*, 2009), and beta diversity may capture the dynamic nature of diversity regulation better than a simple measure of species richness alone.

Beta diversity is central to many ecological and evolutionary topics, such as the processes shaping the distribution of species, the systematic design of biodiversity reserves and the development of ecological theories (Condit *et al.*, 2002; McKnight *et al.*,

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2007; Soininen *et al.*, 2007a; Wang *et al.*, 2008, and references therein). Yet, the elevational patterns of beta diversity have been examined mostly among macroorganisms (e.g. higher plant and animal taxa) (e.g. Jaccard, 1912; Brehm *et al.*, 2003; Mena & Vázquez-Domínguez, 2005; Crausbay & Hotchkiss, 2010), while patterns for microorganisms have been left understudied. To the best of our knowledge, only one study to date has examined the beta diversity of terrestrial bacteria on mountainsides (Bryant *et al.*, 2008), and we do not know of any studies of elevational beta diversity among microbes in aquatic environments.

Patterns in microorganisms are, however, extremely interesting, as one widely debated topic for microbial ecologists is that of the fundamental rules underlying microbial biogeography in the light of the observations made for macroorganisms (e.g. species–area relationship) (Martiny *et al.*, 2006; Prosser *et al.*, 2007). Many studies have emphasized that microorganisms do show biogeographical patterns, which is in contrast with Baas-Becking's view of a cosmopolitan distribution of microbes (Prosser *et al.*, 2007). However, given the high dispersal ability and high population densities of microorganisms, the spatial structure is expected to be lower for microbes than for macroorganisms in many environments (Green *et al.*, 2004; Green & Bohannan, 2006; Prosser *et al.*, 2007). Even though the elevational gradient usually covers only a small spatial extent with relatively high connectivity among sites, macroorganisms perhaps exhibit a higher species turnover along elevational gradients than microorganisms (Bryant *et al.*, 2008). This is because macroorganisms may have a lower ability to adapt in different environmental conditions than microbes (along the steep environmental gradients of mountainsides, for instance), and have lower dispersal ability (Green *et al.*, 2004; Green & Bohannan, 2006; Prosser *et al.*, 2007). This should result in stronger segregation of metazoan communities along elevational gradients, and thus higher beta diversity.

Elevational beta diversity is not, however, only affected by historical processes and natural environmental heterogeneity, but can also be influenced by the strength of human activities. Overall, human impact is suggested to be stronger at lower elevations and often decreases monotonically with increasing elevation (Nogués-Bravo *et al.*, 2008). Across the globe, mountain regions are becoming more urbanized with increasing settlements and transport networks (Price, 2006). For mountain streams, for instance, human activities may result in the degradation of biogeographical barriers, thereby altering patterns of alpha and beta diversity among localities (Ward, 1998; Allan, 2004; Allan & Castillo, 2007; Passy & Blanchet, 2007; Donohue *et al.*, 2009). We also emphasize that human activities may frequently increase productivity in aquatic ecosystems because of higher nutrient input. This may result in increased beta diversity among sites (Chase & Leibold, 2002).

Here, the beta diversity of benthic microorganisms (i.e. diatoms and bacteria) and macroorganisms (i.e. macroinvertebrates) was simultaneously investigated between the elevations of 1820 and 4050 m in a stony stream in China. We compared the patterns in beta diversity along the elevational gradient among the three organism groups to test the prediction of higher beta diversity for macroorganisms than for microorganisms. Then we assessed the relative importance of human-related, spatial and environmental factors in accounting for community variation along the elevational gradient among the three organism groups.

MATERIALS AND METHODS

Field sampling, chemical and biological analyses

The detailed sampling scheme and physicochemical/biological analyses were described in Wang *et al.* (2011). We explain here all analyses in brief. In October–November 2009, we picked 26 sampling sites at approximately every 89 m change in elevation along a stony stream located in Laojun Mountain, Yunnan Province, China (latitude 26°44″ N; longitude 99°48″ E). The stream section started from the top of the mountain and ended in a valley where the elevation did not substantially decrease. The stream above the elevation of 2580 m was in a pristine state and almost inaccessible to humans. The sampling sites extended from 1820 to 4050 m in elevation and spanned a geographic distance of 33.5 km.

Each study site was divided into five or ten cross-sections, depending on the stream width. For diatoms and bacteria, 10 stones were selected randomly from riffle/run habitats along these transects. Biofilm was scraped off the stones for subsamples from a pre-defined area (9 cm^2) using a toothbrush (for diatoms) or a sterilized sponge (for bacteria). The subsamples were subsequently pooled into a composite sample from each site. The samples for bacteria were frozen at −18 °C immediately after sampling. We collected four kick-net samples of macroinvertebrates from stony riffle/run habitats (40 cm net length and 500 μm mesh size). These samples were pooled at each site and stored in 70% ethanol in the field. Water samples and filtered water samples (0.45 μm) were preserved at −18 °C until the chemical analyses could be conducted.

We used a simple measure of population number to indicate the anthropogenic activities along the stream (see, e.g., Mora *et al.*, 2011). The population of each village was obtained from government documents or the local inhabitants. Based on this information, we calculated the *cumulative population*, which measures the number of people upstream from each site (within a band of 1 km along the stream). It should be noted that the variable presented here may not be equal to the exact population number at each site as this tends to vary in time. Some other variables related to anthropogenic activities, such as the number of livestock, were not available. However, the estimated cumulative population probably well reflects the trends of anthropogenic impacts on the stream ecosystem. We stress that cumulative population was not very strongly related to the water chemistry variables summarized by the first two principal components (see details below) in these data (for PC1 $r^2 = 0.189$, $P < 0.05$ and for PC2 $r^2 = 0.002$, $P =$ n.s.). The cumulative human population, however, was related to elevation ($r^2 = 0.299$, $P < 0.01$).

More than 50 physicochemical characteristics were measured *in situ* or in the laboratory (see Wang *et al.*, 2011 for details). Biofilm characteristics, such as net photosynthetic production (NPP), biofilm community respiration (CR) and chlorophyll *a*, were measured in the laboratory. Macroinvertebrates were identified to the species level when possible following the standard keys (Morse *et al.*, 1994) (see Wang *et al.*, 2011, for details). Because we basically found only insect larvae that have flying adult stages (except for the three non-flying taxa), we treated all identified taxa as a group in the following analyses, rather than separating them into subgroups based on flying ability. Diatoms were identified to the species level according to Krammer & Lange-Bertalot (1986–1991) and Metzeltin *et al.* (2009). The bacterial community was analysed using a standard fingerprinting method (denaturing gradient gel electrophoresis; Muyzer *et al.*, 1993) (see Wang *et al.*, 2011, for details).

Statistical analyses

Three kinds of data matrices were constructed: biological matrices for three organism groups, environmental matrices and spatial matrices (longitude, latitude and elevation). All environmental variables, except pH, were log-transformed [by $\log(X + 1)$ or $\log(1000X + 1)$]. We calculated the dissimilarities based on presence–absence data using the Simpson dissimilarity index (beta-sim, or β-sim) to examine the dissimilarity in community composition between pairwise sites for the three taxa. The Beta-sim dissimilarity index was first proposed by Simpson (1943) and later introduced by Lennon *et al.* (2001) as

$$\text{beta-sim} = \min(b, c)/[a + \min(b, c)],$$

where a is the number of species present in both samples and b and c are the numbers of species occurring in only one sample or the other sample. Beta-sim ranges from 0 to 1, representing the highest similarity and lowest similarity, respectively. We chose beta-sim as a metric here because there were clear species richness gradients along the studied elevational gradient for all three taxonomic groups (Wang *et al.*, 2011) and beta-sim is independent of species richness (Lennon *et al.*, 2001; Koleff *et al.*, 2003; Baselga, 2010). We used presence–absence data in our analyses because the beta-sim metric is intended for such data and because abundance data for bacteria are perhaps not as accurate as the data for other organism groups.

To study the patterns of elevational beta diversity, we first calculated the beta-sim between adjacent sites separately for all three taxa. Calculations of dissimilarities between adjacent sites were done to examine small-scale beta diversity (i.e. turnover between sites closest to each other) in the stream. These beta-sim dissimilarities were plotted against elevation and the elevational trends were analysed by a linear or quadratic model with the lowest Akaike information criterion. We used analysis of variance (ANOVA) to test for possible among-group differences in small-scale beta diversity.

Second, we quantified the variation in beta diversity using a distance-based approach (Tuomisto & Ruokolainen, 2006; Soininen *et al.*, 2007b; Wang *et al.*, 2008). That is, the variations in beta diversity were plotted against changes in elevation, horizontal spatial distance or environmental distance. This distance–decay relationship (which measures how dissimilarity decays with increasing distance between pairwise sites) was analysed using a Gaussian generalized linear model, and the significance was determined using Mantel tests (Pearson's correlation) on 9999 permutations. Environmental distance was measured as Euclidean distance using all the environmental variables standardized to have a mean of zero and a standard deviation of one without a log-transformation. As we found that the log-transformed elevational or horizontal spatial distances were less correlated with the community similarity matrices than the raw distances (data not shown), and former studies also used the changes along linear distances rather than log-transformed ones (Bryant *et al.*, 2008), we used here changes in elevation or horizontal spatial distance without log-transformation. We used the analysis of covariance (ANCOVA) to test the hypothesis that the regression slopes do not differ among the three organism groups. Further, we used partial Mantel tests to tease apart the pure effects of elevation, space and environment on biological matrices, and the significance was assessed using 9999 permutations, as described elsewhere (Jones *et al.*, 2006). For instance, the environmental or spatial distance matrix was the explanatory matrix, and the other one was the partial matrix. Partial Mantel tests examine, for example, the influence of environmental distance on biotic distance while controlling for geographical distance, and vice versa.

Third, we partitioned beta diversity into spatial (including elevation and horizontal distance), environmental and anthropogenic components (human impact) using canonical redundancy analysis (RDA) following the procedures described in Legendre *et al.* (2005, 2009). We thus used both the distance-based approach and the raw data approach in the paper as they may give additional insights into the data, reflecting different aspects of beta diversity (Tuomisto & Ruokolainen, 2006). Principal coordinates of neighbour matrices (PCNM; Borcard & Legendre, 2002) eigenvectors were computed across the two spatial factors: the vertical (elevation) and the relative horizontal locations. PCNM quantifies spatial trends across a range of scales and is based on eigenvalue decomposition of a truncated matrix of geographic distances among sampling sites. PCNM eigenvectors can be considered as spatial variables in a canonical analysis. The cumulative population was used to represent the human impacts. By performing principal components analysis (PCA), electronic conductivity, alkalinity and dissolved ions [Si, Cl^-, SO_4^{2-}, K, Na, Ca, Mg, Ba, Sr, As, Al, Fe, Mn, Zn, Cr, Cu, Pb, Ni, PO_4^{3-}, NH_4^+, NO_2^-, NO_3^-, dissolved inorganic carbon (DIC), HCO_3^- and CO_3^{2-}] were reduced to the first two principal components (PC1 and PC2) as explanatory variables representing environmental factors (Wang *et al.*, 2011). This was done because we wanted to decrease the degrees of freedom below the number of sampled sites. The remaining measured variables, such as chlorophyll *a*, NPP, CR, riparian shading, stream width, water depth, water velocity, median for substratum particle size, chromophoric dissolved organic matter, dissolved organic

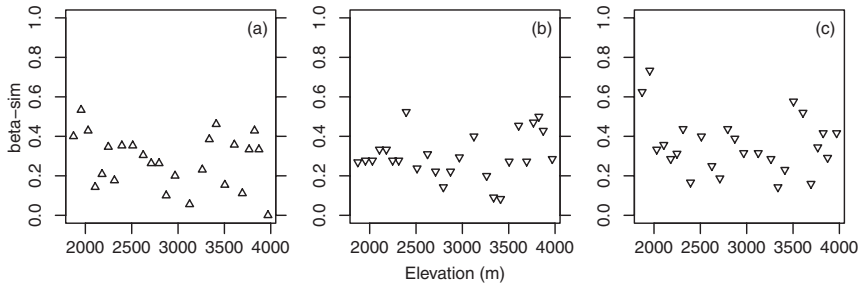

Figure 1 Beta-sim dissimilarity between adjacent sampling sites along the elevational gradient for the three organism groups: (a) macroinvertebrates ($n = 25$); (b) diatoms ($n = 25$); (c) bacteria ($n = 25$). Small-scale beta diversity did not show significant differences among the three organism groups ($P > 0.1$).

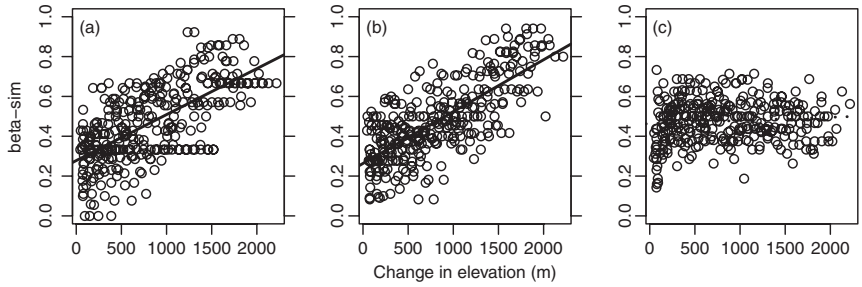

Figure 2 The relationships between the community beta-sim dissimilarity and elevational change: (a) macroinvertebrates (slope = 0.23 km^{-1}, $r^2 = 0.43$, $P < 0.001$); (b) diatoms (slope = 0.26 km^{-1}, $r^2 = 0.55$, $P < 0.001$); (c) bacteria ($r^2 = 0.01$, $P = 0.145$). The regression slopes of the linear relationships based on Gaussian generalized linear model are shown with solid or dotted (statistically non-significant) lines. The relationships were statistically significant according to the Mantel test (9999 permutations, $P < 0.05$) except for the bacterial communities.

carbon, total nitrogen (TN), total phosphorus (TP) and the molecular ratio of TN and TP, were used as environmental variables without a PCA step (Wang *et al.*, 2011). All significant PCNM eigenvectors, environmental variables and cumulative population were selected by forward selection against the Hellinger-transformed abundance species data with 9999 permutations for all three taxa. All statistical analyses were conducted in the R environment (http://www.r-project.org) using additional packages, such as 'vegan', 'spacemakeR' and 'packfor '.

RESULTS

Analyses of small-scale beta diversity did not show any significant linear or quadratic patterns along elevation for any of the studied groups (all $P > 0.05$) (Fig. 1). The degree of small-scale turnover was also equal among sampled organism groups (ANOVA, $P > 0.05$). On average, dissimilarity between adjacent sites was 0.277 ± 0.136 for macroinvertebrates ($n = 25$, Fig. 1a), 0.298 ± 0.115 for diatoms ($n = 25$, Fig. 1b) and 0.357 ± 0.146 for bacteria ($n = 25$, Fig. 1c).

The pairwise compositional dissimilarities across the whole elevational gradient significantly increased with the corresponding changes in elevation for macroinvertebrates (Fig. 2a) and diatoms (Fig. 2b) ($P < 0.001$). There was no significant difference between the turnover rates in these eukaryotic groups (ANCOVA, $P > 0.05$) (Table 1). However, bacteria did not show a significant elevational distance-decay ($P > 0.05$) (Fig. 2c).

The community dissimilarities significantly increased with horizontal spatial distance (Fig. S1a–c in Supporting Information, Table 1) and environmental distance (Fig. S1d–f, Table 1) for all organism groups. However, bacteria showed consistently the lowest turnover rate among three organism groups (Figs 2 & S1, Table 1). According to the partial Mantel tests, the pure effects of elevation or horizontal spatial distance were non-significant for bacteria, while these effects were stronger for diatoms and macroinvertebrates (Table 1). For bacteria, environmental distance represented the only significant pure effect (Table 1).

According to RDA, the pure effect of space (including elevation) accounted for larger parts of the variability in assemblage composition than the pure effect of environment (Fig. 3). Much of the variation in assemblage composition that was explained by the environmental variables was spatially structured as indicated by the joint effect of environment and space for all groups (see also Fig. S2). The pure effects of human impacts were low (or even absent for bacteria) for all groups. For diatoms, the joint effect of human impact, environment and space was largest (21%) among the three organism groups (Fig. 3). The fraction that was left unexplained was high, especially for bacteria (79%) and for macroinvertebrates (63%).

Table 1 Mantel and partial Mantel tests for the correlation between the community similarity (beta-sim dissimilarity) and the explanatory distances (elevational, horizontal spatial and environmental distance) for macroinvertebrates, diatoms and bacteria sampled from a stony stream in Laojun Mountain, China.

							Elevational				Horizontal				Environmental			
	Elevational*		Horizontal*		Environmental*		Horizontal		Environmental		Environmental		Elevational		Elevational		Horizontal	
Effect of controlling for	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Macroinvertebrates	0.66	0.000	0.65	0.000	0.63	0.000	0.33	0.000	0.38	0.000	0.41	0.000	0.31	0.003	0.28	0.004	0.35	0.000
Diatoms	0.74	0.000	0.48	0.000	0.62	0.000	0.66	0.000	0.54	0.000	0.13	0.151	–0.19	0.936	0.17	0.083	0.45	0.000
Bacteria	0.08	0.096	0.14	0.035	0.17	0.013	–0.04	0.717	–0.06	0.829	0.04	0.315	0.12	0.090	0.16	0.023	0.10	0.107

*Elevational, change in elevation; Horizontal, horizontal spatial distance; Environmental, environmental distance (Euclidean distance).
The *P*-values were obtained by 9999 Monte Carlo permutations.

DISCUSSION

One of the longstanding tasks in ecology is to explain the large-scale distribution patterns of species, and the causes underlying these patterns. Compared with the studies along latitudinal gradients with great historical influence in explaining diversity across long distances, the studies of biotic patterns along elevational gradients offer a powerful macroecological method for exploring species distribution along steep environmental gradients (e.g. temperature and moisture) within a small spatial extent. In mountain regions, beta diversity is typically higher than at lower elevations (McKnight *et al.*, 2007) due to the elevational specialization of species. However, beta diversity on mountainsides has been left largely understudied, especially for microorganisms. To our knowledge, we have presented the first study to examine the elevational beta diversity for aquatic microorganisms and to contrast the patterns with those observed for macroscopic organisms. Below, we discuss the results in more detail.

The main aim of our paper was to compare the patterns in beta diversity among the three organism groups – that is macroinvertebrates, diatoms and bacteria – suggested to be highly different in their main characteristics such as body size, dispersal ability and trophic position. This idea was related to the findings that elevational patterns in alpha diversity may be different for micro- and macroorganisms (Bryant *et al.*, 2008; Fierer *et al.*, 2011; Wang *et al.*, 2011). We showed that bacteria exhibited substantially lower large-scale elevational beta diversity than diatoms or macroinvertebrates, as we expected based on the previous macroecological findings for bacteria. This may indicate that bacteria are efficient dispersers and can adapt well to harsh environmental conditions at high elevations. Diatoms and macroinvertebrates in turn showed relatively similar patterns of beta diversity despite the fact that they differ substantially in several important characteristics, such as body size and trophic rank. This finding was rather unexpected, as many studies have shown that microorganisms might be less dispersal-limited than macroorganisms. For instance, smaller *z*-values of species–area relationships were detected for microorganisms than for macroorganisms (Green & Bohannan, 2006; Prosser *et al.*, 2007). Distance-decay patterns for soil microorganisms have also been reported as being relatively weak even across continental scales (Green *et al.*, 2004). We would like to emphasize, however, that the results of partial Mantel tests showed that diatoms were less controlled by pure horizontal distance than macroinvertebrates.

Nonetheless, the finding that the rate of turnover for bacteria was lower than for metazoans (macroinvertebrates) is in line with Bryant *et al.* (2008), where the elevational distance-decay relationship for soil Acidobacteria seemed to be shallower than that of angiosperm communities within an elevational range of 900 m. To facilitate comparison with the study by Bryant *et al.* (2008), we also computed the regressions with Sørensen metric, and found that the resulting slope for bacteria (–0.126 Sørensen per log(m) of elevational change for the whole elevational gradient, $P < 0.001$, Mantel test, 9999 permutations) was similar to the reported turnover rate of acidobacterial compositional simi-

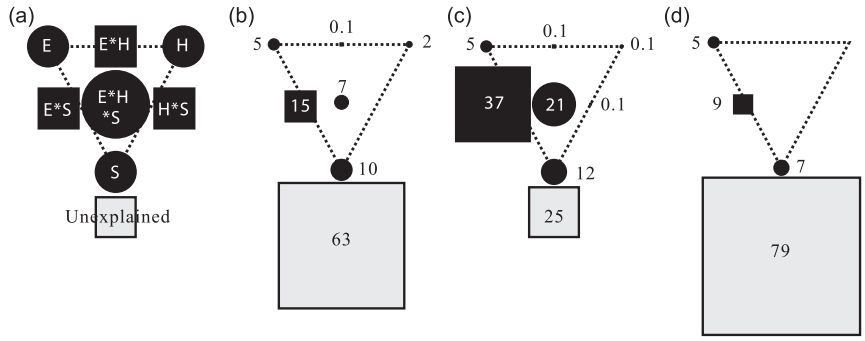

Figure 3 The proportion of the variance in community composition explained by the environmental factors (E), human impacts (H) and spatial variables (S). (a) General outline. Each diagram represents a given biological variation partitioned into the relative effects of each factor or combination of factors, where geometric areas are proportional to the respective percentages of explained variation. The edges of the triangle depict the variation explained by each factor along (i.e. when removing the variation because of other factors). Percentages of variation explained by interactions of two or all factors are indicated on the sides and in the middle of the triangles, respectively. (b) Macroinvertebrates. (c) Diatoms. (d) Bacteria. More details on the selected variables are shown in Table S1. The statistical significance was according to the Monte Carlo permutation test (9999 permutations, $P < 0.01$).

larity (*c.* −0.171 Sørensen per log(m) of elevational change) (Bryant *et al.*, 2008). Our results thus support the notion that bacterial communities may be spatially structured to some degree yet show substantially lower beta diversity than diatoms or macroinvertebrates. However, we stress that this seems to apply only for the patterns in beta diversity among all sampled sites, i.e. at larger spatial scales. When we analysed the degree of beta diversity between the adjacent sites, the groups showed a similar degree of small-scale beta diversity. This disagrees with Soininen *et al.* (2007b) where small-scale beta diversity was shown to be larger for small organisms, and emphasizes the need to examine beta diversity at multiple spatial scales.

According to RDA, human impact emerged as only a weak explanatory variable for biotic communities. One possible explanation is that human disturbance was nonetheless not strong enough to drive the variation in community composition along the elevational gradient and that it covaried with the elevation. Recent studies suggest that harsh 'ecological filters', such as those resulting from strong human disturbance, reduce the importance of stochastic processes in structuring biotic communities and, hence, reduce the compositional heterogeneity of biotic assemblages among sites (Chase, 2007; Passy & Blanchet, 2007). However, the nutrient concentrations measured in our system showed that the nutrient supply, even at low elevations, was probably not high enough to be stressful for the organisms present (Wang *et al.*, 2011). It may well be that the oligotrophic running water from the higher elevation continuously prevented the benthic ecosystems from deterioration, and maintained the environmental heterogeneity for the benthic communities. The second explanation could be that increasing human impact also increased productivity via enhanced nutrient supply, resulting in higher beta diversity among sites (Chase & Leibold, 2002). Several lines of evidence have suggested that beta diversity increases with productivity (see, e.g., Andrew *et al.*, 2012 for butterfly communities). Therefore, the fact that human impact seems not to have a strong effect on communities in this system may be because of these two opposing forces (the homogenizing effect of human impacts versus increased productivity) or due to the fact that human impacts were not stressful enough in this system.

To conclude, we found that elevational beta diversity at large scales is lower for bacteria than for eukaryotic micro- and macroorganisms perhaps showing high dispersal ability and good adaptability towards harsh environmental conditions for bacteria. However, for eukaryotic diatoms and macroinvertebrates, the degree of beta diversity was largely equal. Elevation was the major driver for the turnover of eukaryotic organisms while turnover of bacteria was correlated more with environmental variation. It further seems that human impacts did not affect beta diversity notably for any of the studied groups, which may indicate that impacts were not severe enough to deteriorate the studied stream ecosystem or that there was a trade-off between the two opposing forces (homogenizing effect of human impacts versus increased productivity). As our sampling covered only one stream, we admit that the generality of these findings will be assessed later by other researchers examining elevational gradients in different systems. We also emphasize that researchers should consider scale explicitly in studies of beta diversity, as patterns may change with study scales (Soininen *et al.*, 2007b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 The relationships between the community beta-sim dissimilarity and horizontal spatial distance or environmental distance.

Figure S2 The relationships between the change in elevation, horizontal spatial distance and environmental distance.

Table S1 The environmental, human-related and spatial variables used in the variation partitioning analyses.

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BIOSKETCH

Jianjun Wang is interested in the factors influencing aquatic microbial distributions and in the relationship between microbial biodiversity and its biogeochemical function.

Author contributions: **J.J.W.**, **J. Soininen** and **J. Shen** conceived the ideas; **J.J.W.**, **J. Soininen**, and **Y.Z.** collected the field samples; **J.J.W.** and **Y.Z.** provided bacterial data; **X.D.Y.** helped with diatom pre-treatment; **J. Soininen** provided diatom data; **B.X.W.** provided macroinvertebrate data; **J.J.W.** and **J. Soininen** analysed the data and led the writing. All co-authors contributed to writing and commented on a final version of the manuscript.

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