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#### **ORIGINAL ARTICLE**

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# Elevational patterns and hierarchical determinants of biodiversity across microbial taxonomic scales

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#### Abstract

Microbial biogeography is gaining increasing attention due to recent molecular methodological advance. However, the diversity patterns and their environmental determinants across taxonomic scales are still poorly studied. By sampling along an extensive elevational gradient in subarctic ponds of Finland and Norway, we examined the diversity patterns of aquatic bacteria and fungi from whole community to individual taxa across taxonomic coverage and taxonomic resolutions. We further quantified cross-phylum congruence in multiple biodiversity metrics and evaluated the relative importance of climate, catchment and local pond variables as the hierarchical drivers of biodiversity across taxonomic scales. Bacterial community showed significantly decreasing elevational patterns in species richness and evenness, and U-shaped patterns in local contribution to beta diversity (LCBD). Conversely, no significant species richness and evenness patterns were found for fungal community. Elevational patterns in species richness and LCBD, but not in evenness, were congruent across bacterial phyla. When narrowing down the taxonomic scope towards higher resolutions, bacterial diversity showed weaker and more complex elevational patterns. Taxonomic downscaling also indicated a notable change in the relative importance of biodiversity determinants with stronger local environmental filtering, but decreased importance of climatic variables. This suggested that niche conservatism of temperature preference was phylogenetically deeper than that of water chemistry variables. Our results provide novel perspectives for microbial biogeography and highlight the importance of taxonomic scale dependency and hierarchical drivers when modelling biodiversity and species distribution responses to future climatic scenarios.

#### KEYWORDS

Arctic regions, bacteria, beta diversity, elevational gradient, fungi, species richness, taxonomic coverage, taxonomic resolutions

# 1 | INTRODUCTION

Biodiversity gradient on mountainsides is one of the most historical and frequently documented biogeographical patterns (Lomolino, 2001; Rahbek, 2005). Elevational gradients provide a "natural laboratory" in which climatic conditions vary within a short geographical distance, allowing the investigation of underlying multiscale hierarchical determinants of biodiversity. Over the past two centuries, numerous studies have focused on elevational diversity patterns of macroorganisms and identified some general patterns and potential underlying drivers shaping these patterns (Rahbek, 2005). During recent decades, elevational diversity patterns of microorganisms have also received increasing attention (Bryant et al., 2008; Peay et al., 2017; Shen et al., 2013; Wang et al., 2011, 2017). Nonetheless, the general patterns and driving mechanisms of microorganisms along elevational gradients remain poorly understood.

Microorganisms constitute the most abundant and diverse (ca. 10<sup>11</sup>–10<sup>12</sup> species) group of life on Earth (Locev & Lennon, 2016) and encompass a broad range of phylogenetic clades (Yarza et al., 2014). The history of microbial evolution is probably as old as the history of life itself, and the phylogenetic and physiological diversity of microbial phyla, especially in bacteria, is considerably greater than that among animal and plant phyla (Giovannoni & Stingl, 2005: Prosser et al., 2007). The long evolutionary history of microbes created not only enormous phylogenetic, but also physiological diversity (Yarza et al., 2014). Although microbes are extremely diverse within each phylum and seem to be nearly ubiquitously distributed at the phylum level across habitats, previous studies suggest each member of the same phylum might share general ecological strategies and traits (Martiny, Jones, Lennon, & Martiny, 2015). For instance, Fierer, Bradford, and Jackson (2007) suggested that certain soil bacterial phyla could be differentiated into r- and k-ecological categories. In the case of aquatic bacteria, there are many distinct biogeographical patterns within phyla in freshwater lakes (e.g., Newton, Jones, Eiler, McMahon, & Bertilsson, 2011), and spatial or temporal separation of phyla and other higher taxonomic ranks across freshwater lakes and many other environments. The idea that such biogeographical patterns may reflect ecological coherence at higher taxonomic resolution levels is also partly supported (Abarenkov et al., 2010; Lennon, Aanderud, Lehmkuhl, & Schoolmaster, 2012; Lindström & Langenheder, 2012; Lu et al., 2016; Philippot et al., 2009).

As certain ecological processes may only be evident at particular taxonomic scale, exploring the taxonomic scale dependency of ecological patterns could provide a comprehensive understanding of diversity patterns (Levin, 1992). The taxonomic scale comprises two important aspects: taxonomic resolution (grain) and taxonomic coverage (extent) (Graham, Storch, & Machac, 2018). Since different ecological traits may have different phylogenetic depth, particular ecological trait may be conserved or evident only when examined at certain levels of taxonomic resolution (e.g., at species or genus levels) or among specific taxonomic group (Martiny et al., 2015). In addition, as individual taxa may have specific biotic or abiotic traits along large environmental gradient, changing the taxonomic scope from high to low taxonomic coverage could also affect the potential drivers of biodiversity (Peters et al., 2016). Therefore, incorporating these two perspectives into a theoretical framework might allow more predictive microbial ecology to emerge (e.g., Hurlbert & Stegen, 2014). However, a severe drawback of published studies on microbial elevational biodiversity is that communities have typically been examined only at a single taxonomic scale (e.g., few phylogenetic groups from the same taxonomic resolution level or the whole microbial community). Thus, the question of how diversity patterns could vary with taxonomic coverage and resolution has not been properly addressed in the literature, although such a study might reveal deep insights into biodiversity patterns and

#### **Highlights**

- Elevational patterns in species richness and local contribution to beta diversity, but not in evenness, are congruent across bacterial phyla.
- Taxonomic downscaling significantly changes the elevational patterns of microbes, indicated by weaker and more complex diversity-elevation relationships.
- Bacterial diversity at lower taxonomic resolution levels is predicted well by climatic variables, while those at higher taxonomic resolution levels are more relevant to local environmental filtering.
- Niche conservatism of temperature preference is phylogenetically deeper than that of water chemistry variables.

underlying environmental drivers. For instance, how does the relative importance of environmental determinants for biodiversity patterns change across taxonomic scales?

Biodiversity comprises multiple components such as species richness, species abundance distribution (which is often measured as evenness) and beta diversity (Legendre & De Cáceres, 2013; Magurran, 2013). Species richness measures the total species number at sites, whereas evenness measures how similar the species are in their abundances (Magurran, 2013), being both important facets that describe the biodiversity of local communities. Both of these diversity metrics were found to link with multiple ecosystem processes and ecosystem functioning (Wilsey & Potvin, 2000; Wittebolle et al., 2009). According to a meta-analysis (Soininen, Passy, & Hillebrand, 2012), species richness and evenness often reflect independent components of biodiversity, and therefore, they can potentially provide different insights into elevational diversity patterns (Wang et al., 2017). In addition, beta diversity has long been recognized as an important biodiversity facet to understand how diversity varies in space and time and how it could be maintained (Harte, McCarthy, Taylor, Kinzig, & Fischer, 1999; Jaccard, 1912; Mena & Vázquez-Domínguez, 2005). Interestingly, the relative contributions of sampling sites to beta diversity can also be estimated by a recently introduced metric of local contribution to beta diversity (LCBD; Legendre & De Cáceres, 2013). Considering multiple aspects of biodiversity simultaneously may help to improve our understanding of the general biodiversity patterns and underlying mechanisms.

A comprehensive understanding of biodiversity also requires the investigation of environmental determinants at multiple, often hierarchical, spatial scales (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Levin, 1992; Swenson, Enquist, Pither, Thompson, & Zimmerman, 2006). The hierarchical factors that affect microbial diversity in freshwaters comprise the following: (a) local-scale abiotic factors including pH, nutrients and conductivity, along with biotic WILFY-MOLECULAR ECOLOGY

factors of competition, facilitation and grazing; (b) intermediatescale variables, that is, catchment variables that include terrestrial productivity, bedrock and soil type; and (c) the drivers that operate on large scales such as climate, dispersal and historical factors (Frissell, Liss, Warren, & Hurley, 1986). Some studies suggest that freshwater microbial diversity is determined mostly by local-scale environmental factors such as pH and nutrient concentration (Van der Gucht et al., 2007; Wang et al., 2017), whereas other studies suggest large-scale climatic or catchment properties are also essential (Teittinen, Wang, Strömgård, & Soininen, 2017). However, how the relative importance of these hierarchical environmental factors in shaping biodiversity may vary with taxonomic scales remains understudied.

In this study, we examined elevational biodiversity patterns and their hierarchical drivers for freshwater biofilm microorganisms across taxonomic scales. We considered two aspects of taxonomic scales, that is, taxonomic coverage and taxonomic resolution. With a large number of bacteria and fungi samples collected from the subarctic ponds of northern Finland and Norway, we focused on three specific aims. First, we explored the elevational patterns across 22 microbial phyla and quantified cross-phyla congruence in species richness, evenness and LCBD of bacteria and fungi. Second, we investigated how taxonomic coverage (i.e., the shift from the whole community to individual phylum levels) affected the elevational patterns in biodiversity and the relative importance of hierarchical drivers of local, catchment and climatic factors. Third, we further explored how downscaling to higher taxonomic resolution levels (i.e., the shift from domain to genus) affected the elevational patterns in biodiversity and the relative importance of hierarchical drivers acting on various taxonomic resolution levels.

#### 2 | MATERIALS AND METHODS

#### 2.1 | Field sampling

The detailed sampling scheme and physicochemical/biological analyses were described in Teittinen et al. (2017). Briefly, we sampled 102 ponds in the Kilpisjärvi-Skibotn region and 44 ponds in the Rásttigáisá region in July and August 2015. The study area (68°55' to 69°58'N, 20°02' to 26°25'E) is located in northern Fennoscandia and covers parts of Finland and Norway. The regional climate is characterized by long, cold winters and short, relatively warm, ice-free and light-abundant summers. The annual mean temperature varies from -1.9°C in Kilpisjärvi (Finland) to -0.5°C in Skibotn (Norway). Our sampling covered long climatic and environmental gradients; thus, the sampled ponds were distributed altitudinally across the treeline along an elevational gradient of 10-1,038 m a.s.l. The catchments near sea level are characterized by mixed forests or peatlands, with a transition to a zone that is dominated by mountain birch, and to treeless tundra and barren, rocky catchments with increasing elevation. The majority of the ponds are pristine or close-to-pristine with negligible anthropogenic activity in their catchments.

#### 2.2 | Climate, buffer zone and local variables

Climate variables for each study pond, that is, mean July temperature (MJT), mean annual temperature, mean July precipitation and mean annual precipitation (MAP), were extracted from WorldClim global climate data (ca. 1 km<sup>2</sup> spatial resolution), representative of 1950–2000 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) using ARCGIS (version 10.2.1; ESRI, Redlands, CA, USA). We note that the interpolated climate data may not be truly optimal for relatively small spatial scales considered here and finer climate data might be better for statistical modelling in spatial biodiversity. The used data set is, however, the best climatic data set currently available for the two regions studied, where there is no locally measured climatic data accessible for this large number of ponds.

Normalized Difference Vegetation Index (NDVI) was used as a catchment-scale variable (i.e., buffer zone variable) to indicate terrestrial productivity. Detailed measurement and calculation methods for NDVI are documented previously (Teittinen et al., 2017).

Water temperature, specific conductivity (SPC) and pH were measured in situ. Water samples were collected and analysed later in the laboratory for total nitrogen (TN) according to standard SFS-EN ISO 11905-1, and for Si, Ca, Mg and K concentrations according to standard SFS-EN ISO 11885. The pond areas were measured through digital maps of Finland and Norway.

#### 2.3 | Bacterial and fungal communities

Bacterial analyses were performed according to previously published descriptions (Wang et al., 2017). Briefly, bacterial 16S rRNA genes were amplified in triplicate using bacterial universal primers [515F, 5'-GTGCCAGCMGCCGCGGTAA-3' and 806R, 5'-GGACTACHVGGGTWTCTAAT-3']. Negative controls in PCR were done to ensure valid amplicons. PCR products of triplicate reactions were combined and quantified using PicoGreen (Eugene, OR, USA). PCR products from samples to be sequenced in the same MiSeg run were pooled at equal molality to maximize the even-sequencing effects for all samples. Sample libraries for sequencing were prepared according to the MiSeg 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 (such as sequence length <150 and moving-window (5 bp) quality score <29) were filtered out before demultiplexing based on barcodes. Further, the sequences were clustered into OTUs at 97% pairwise identity with the seed-based UCLUST algorithm (Edgar, 2010). Representative sequences from each OTU were aligned to the Greengenes imputed core reference alignment V.201308 (DeSantis et al., 2006). This took place after chimeras were removed via UCHIME against ChimeraSlayer reference database in the Broad Microbiome Utilities using PyNAST (Caporaso et al., 2010). Identity of each representative sequence was determined using the RDP classifier (Wang, Garrity, Tiedje, & Cole, 2007), and chloroplast and archaeal sequences were removed.

For the identification of fungal communities, an amplicon of ITS2 region was targeted using the primers: gITS7F, 5'-GTGARTCATCGARTCTTTG-3' and ITS4R. 5'-TCCTCCGCTTA TTGATATGC-3'. PCR products were pooled at equal molality and sequenced in the same MiSeg run. Chimeric sequences were removed using de novo chimera detection with USEARCH (Edgar, 2010). ITS2 region was extracted using Fungal ITS Extractor (Nilsson, Bok, Ryberg, Kristiansson, & Hallenberg, 2009), as the conserved flanking regions are known to distort similarity searches, taxonomic assignments and clustering results (Bruns & Shefferson, 2004). The resulting ITS2 reads were clustered to OTUs based on the UCLUST algorithm (Edgar, 2010). with 97% similarity threshold to reference sequences in the UNITE database (Abarenkov et al., 2010), and the OTUs were further identified taxonomically using the RDP classifier (Wang et al., 2007) against the UNITE database (Abarenkov et al., 2010). To ensure that the empirical biodiversity was not biased or confounded by variation in abundance or sampling intensity, the bacterial and fungal sequences were rarefied at 8,000 and 1,000 sequences, respectively. Thus, all the diversity measured in following context described relative instead of absolute diversity.

## 2.4 | Statistical analyses

The MJT, mean annual temperature and mean July precipitation were highly correlated ( $r_s > 0.9$ ); thus, we used MJT to represent the growing season temperature. We used MAP as the long-term measurement for precipitation, which was log10transformed to reduce the skewed distributions. Local variables other than pH (i.e., conductivity [SPC], total nitrogen [TN], Ca, Mg and K) were also log<sub>10</sub>-transformed to reduce their skewed distributions. Statistical dependence between the explanatory variables was assessed using Spearman rank correlation coefficients ( $r_s$ ). Mg and Ca were highly correlated with conductivity ( $r_s = 0.76$ ); thus, they were excluded from further analyses. The maximum NDVI values for 100 and 30 m buffer zones were highly correlated ( $r_s > 0.9$ ). Due to short distances between

**TABLE 1**Abbreviations for thedetected phyla

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some of the ponds, we chose to use the maximum NDVI values calculated using 30 m buffer radius (hereafter NDVI) in forthcoming analyses. All the other pairwise Spearman rank correlations were less than 0.7.

We finally selected 22 microbial phyla, including 18 bacterial phyla and four fungal phyla that were present in more than 60% of the samples (Table 1). The phylum that had the highest number of OTUs across pond biofilm samples was Alphaproteobacteria, followed in descending order by Bacteroidetes, Planctomycetes, Deltaproteobacteria, Cyanobacteria and Chloroflexi, all of which comprised ~55% of the observed OTUs (Table 1). Notably, in the analysis of taxonomic coverage, we divided Proteobacteria phylum into different classes because of the high diversity of Proteobacteria and different ecological functions of these classes.

We estimated OTU richness, evenness and LCBD for all the phyla. Although the decomposition of diversity into truly independent richness and evenness components is mathematically impossible (Jost, 2010), richness and evenness represent clearly differentiated aspects of biodiversity (Magurran, 2013). We used Pielou's evenness (Pielou, 1966) as this is a widely used good measure of distribution of relative abundance in a community (Jost, 2010).

Local contribution to beta diversity enabled the identification of sites that contribute more or less than average to overall beta diversity (Legendre & De Cáceres, 2013). A high LCBD value at a site indicates that the site harbours a unique community composition in the data set and thus comprises many regionally rare species. We computed the LCBD values by using Hellinger-transformed abundance data and the function beta.div in the R code provided by Legendre and De Cáceres (2013). To avoid misleading values, the samples in which the analysed taxa had OTUs number <3 for evenness and <1 for LCBD were omitted. We used a generalized additive model (GAM) to derive the relationship between the different diversity metrics and elevation using the Gaussiantype data family and set the smoothing function to five as dimensionality of the basis expansion (Wood, 2017).

Phyla	Abbrev.	ΟΤυ	Phyla	Abbrev.	ΟΤυ
Acidobacteria	ACI	1068	Gemmatimonadetes	GEM	171
Actinobacteria	ACT	1043	Gammaproteobacteria	GPB	1182
Alphaproteobacteria	APB	3078	Nitrospirae	NIT	113
Armatimonadetes	ARM	323	Planctomycetes	PLA	1567
Bacteroidetes	BAC	1567	TM7	TM7	89
Betaproteobacteria	BPB	898	Verrucomicrobia	VER	536
Chlorobi	CHB	93	WPS-2	WPS	86
Chloroflexi	CHL	1306	Ascomycota	ASC	990
Cyanobacteria	CYA	1308	Basidiomycota	BAS	240
Deltaproteobacteria	DPB	1318	Chytridiomycota	CHY	150
Firmicutes	FIR	524	Zygomycota	ZYG	35

*Note.* We only kept the phyla with the occurrences larger than 60% of all samples. OTU represents the numbers of all OTUs or species presented across all sites for each phylum.

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An approximate significance of smoothing terms was used to test the significance of the fitted trend lines (Wood, 2012). Notably, considering the large sample size collected and the use of robust statistical regression methods, a valid interpretation of elevational pattern could be achieved even without replicate samples (Lennon, 2011). We used the R package MGCV (version 1.8-23) for GAM analysis.

We examined the congruence in biodiversity across phyla and the associations between different phyla and environmental variables using pairwise Spearman rank correlations. We included 22 phyla, elevation and eight different climatic, catchment and local variables (i.e., MJT, MAP, NDVI, TN, K, SPC, pH and area). To visualize the correlations, we generated networks with both significant correlations ( $p \le 0.01$ ) and moderate correlations ( $r_s > 0.35$ ) between all the 31 variables using the R package QGRAPH (version 1.5; Epskamp, Cramer, Waldorp, Schmittmann, & Borsboom, 2012).

The roles of environmental variables in driving bacterial and fungal diversity were analysed by using multimodel inference based on information theory and ordinary least-square regression separately for each variable. We also analysed the environmental variables jointly at three hierarchical scales: climatic, catchment and local variables. The multimodel approach could provide a quantitative measure of the relative importance of each variable through ranking and weighting several models (Burnham, Anderson, & Huyvaert, 2011; Johnson & Omland, 2004). Model averaging of the best model set can not only account for uncertainty in model and parameter selection, but also provide robust parameter estimates for making predictions (Burnham et al., 2011; Johnson & Omland, 2004). To compare the influence of different environmental variables measured at different scales on diversity, all variables were z-transformed to estimate the conditional model-averaged parameter as standardized beta values, that is, beta values were averaged over the models where the parameters appear (Anderson, 2007). The relative importance of each variable was calculated by taking the ratios of absolute values of conditional model-averaged estimates, as it is suggested to provide more informative measures compared with traditional use of sum of AIC weights (Cade, 2015). The R package MUMIN (version 1.15.6) was used for multimodel averaging analyses.

To analyse the elevational patterns in bacterial biodiversity across taxonomic scales of coverage and resolution, and the relative importance of explaining variables, we conducted the comparable multitaxa method as described in Peters et al. (2016), but with some important modifications. The statistical methods including the GAM model and the multimodel influence were similar to that described for the single phylum level above. First (a), we calculated species richness, evenness and LCBD for different taxonomic coverage of phyla (all combinations from 1 to 18 bacterial phyla (N = 262,143) and taxa at different taxonomic resolution levels (from domain to genus). Second (b), we modelled the species richness, evenness and LCBD as a function of elevation using GAMs and calculated the explained deviance and the complexity measure. Complexity was measured by comparing the explained deviance of generalized linear models (EDglm) against the explained deviance of GAMs (EDgam) of biodiversity along elevation, with the formula: complexity = (EDgam - EDglm)/EDgam (Peters et al., 2016). For

the LCBD-elevational relationships, which usually showed U-shaped patterns across phyla and the whole communities (see results section for details), we further used the coefficient of determination (adjusted  $R^2$ ) of guadratic linear model to guantify the strength of U-shaped patterns. The linear or guadratic model was selected based on lower value of Akaike's information criterion (Yamaoka, Nakagawa, & Uno, 1978). Third (c), we ran a multimodel inference analysis with the combination of species richness, evenness or LCBD as the response and all environmental factors as predictor variables using the same analysis as used for single phylum to calculate the standardized beta values and relative importance of variables. Fourth (d), we quantified the relative influence of the environmental variables at three hierarchical scales in explaining biodiversity at each scale. This was done by selecting variables which had the highest absolute standardized beta values at local, catchment or climatic groups in each individual taxon across taxonomic resolution or coverage (i.e., all possible phylum combinations).

## 3 | RESULTS

#### 3.1 | Diversity patterns across taxonomic scales

For species richness, the whole bacterial community showed significant (explained deviance = 22.5%, p < 0.05) monotonically decreasing pattern, but not for fungal community (Figure 1a, Supporting Information Figure S1). Most of the phyla exhibited significant (p < 0.05) elevational patterns (19 out of 22 phyla, Figure 1a, Supporting Information Figure S1). Among these phyla, approximately 60% of bacterial and fungal phyla showed monotonically declining species richness with elevation. The other phyla showed hump-shaped or more complex patterns, especially the fungal phyla. Gradually decreasing bacterial taxonomic coverage from the whole community (18 phyla) to single phyla resulted in lower explained variation (Supporting Information Figure S2a), with increased complexity of species richness patterns across elevation (Supporting Information Figure S2d).

When further examined towards higher taxonomic resolution levels, significant declining patterns were also evident for richnesselevation relationships, constituting the largest proportion (ca. 40%-50%) of individual clades from phylum to order levels. However, at genus level, more than half of the genera exhibited hump-shaped diversity patterns (Figure 1d). The higher taxonomic resolution levels also showed more complex patterns with lower richness-elevation relationships in general (Figure 1d).

The evenness of the whole community exhibited significant linearly declining pattern for bacteria, whereas no significant pattern was detected for fungi (Figure 1b, Supporting Information Figure S1). Bacterial evenness showed strong significant positive relationships (explained deviance = 65.3%, p < 0.05) with species richness (Supporting Information Figure S3), while the relationships were not consistent in phylum level. For phylum level, 13 out of 22 phyla (ca. 60%) showed significant (p < 0.05) elevational patterns in evenness (Figure 1b, Supporting Information Figure S1). Among these patterns, approximately 40% of the phyla showed monotonically declining elevational patterns, whereas the other phyla showed more complex

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**FIGURE 1** Elevational patterns in biodiversity for microbial phyla. Three diversity metrics, that is, species richness (a), evenness (b) and local contribution to beta diversity (LCBD, c), were considered for each bacterial or fungal phylum and their whole community. Generalized additive models were applied to characterize the relationships between elevation and biodiversity. The biodiversity trends of bacterial and fungal whole communities are presented in black solid and dotted lines, respectively, and the trends of phylum biodiversity are shown with coloured solid lines. Species richness and LCBD are scaled as mean = 0 and *SD* = 1 for better visualization. More detailed elevational patterns in biodiversity are shown in Supporting Information Figure S1. The phyla are ordered according to mean species number across sites. The abbreviations of phyla are listed in Table 1. The explained deviance, complexity and relative proportions of different patterns across taxonomic resolution levels from domain to genus level were presented in the lower panels of species richness (d), evenness (e) and LCBD (f). Different colours represent different category of patterns. These patterns were determined based on lower value of Akaike's information criterion. Upper panels indicated the explained deviance of elevation-diversity relationship in GAM model and complexity of patterns across taxonomic resolutions. The error bars indicated the SDs of explained deviance and complexity. The taxonomic resolution levels domain, phylum, class, order, family and genus are shortened as D, P, C, O, F and G, respectively

patterns, such as hump-shaped and bimodal (Supporting Information Figure S1). Decreasing bacterial taxonomic coverage from whole community to individual phyla showed lower explained variation of statistical models of the relationships between evenness and elevation (Supporting Information Figure S2b), and increased complexity in elevational patterns in evenness (Supporting Information Figure S2e). Further taxonomic downscaling greatly weakened the evenness-elevational patterns with more than half of the taxa showing no pattern at higher taxonomic resolution levels (Figure 1e).

For LCBD, the whole bacterial and fungal communities exhibited U-shaped patterns (Figure 1c, Supporting Information Figure S1). Most phyla (18/22) exhibited significant (p < 0.05) elevational LCBD patterns, with ~80% U-shaped and ~20% monotonically declining (Figure 1c, Supporting Information Figure S1). Taxonomic downscaling on coverage

and resolution led to weaker U-shaped relationships between LCBD and elevation (Figure 1f, Supporting Information Figure S2c), but the elevational patterns in LCBD remained complex (Supporting Information Figure S2f). The adjusted  $R^2$  of quadratic linear model for the U-shaped elevational patterns in LCBD decreased with bacterial taxonomic coverage (Supporting Information Figure S2g).

In network analyses for species richness (Figure 2a) and LCBD (Figure 2c), most bacterial phyla were strongly positively intercorrelated, whereas the correlations among fungal phyla were weaker (Figure 2b). The correlations between environmental variables and phylum biodiversity were weaker than the interphyla correlations (Figure 2a,c). The correlations between the evenness of bacterial and fungal phyla were much weaker than for species richness or LCBD (Figure 2b).



**FIGURE 2** Correlation networks for phylum biodiversity and environmental variables. Shown are three biodiversity metrics, that is, species richness (a), evenness (b) and local contribution to beta diversity (LCBD, c). We calculated the pairwise Spearman rank correlations among environmental variables (rectangles), and the biodiversity metrics of bacterial phyla (circles) and fungal phyla (triangles). Green and red lines represent positive and negative significant (p < 0.05) correlations, respectively, and the width of lines shows the strength of correlations. Phylum abbreviations are listed in Table 1

# 3.2 | Underlying determinants of elevational biodiversity

For species richness of the whole bacterial community, temperature was the most important positive predictor, followed by pH and K, showing significantly (p < 0.05) positive and negative effects, respectively (Figure 3a). For individual bacterial phyla, temperature was also the most important climatic variable, with ten positive and two negative significant effects. The catchment level, that is, NDVI, was a poor predictor and was the only significant factor for two phyla. Among the local variables, pH, followed by K, conductivity and TN, was also important for bacterial phyla. When considered jointly, climatic and local variables had dominant effects on bacterial species richness for 50% and 50% of bacterial phyla, respectively. For fungi, pond area was the only variable significantly (p < 0.05) positively correlated with species richness for the whole community and two phyla.

For community evenness, local variables, including K and conductivity, were significant (p < 0.05) factors for the whole bacterial community (Figure 3b). Temperature was also important with positive effects for the most bacterial phyla. At the phylum level, local variables, such as pH, TN, K and conductivity, were typically significant (p < 0.05) for bacteria, but their effects were inconsistent across phyla with both positive and negative effects. No predictor was found to significantly affect the evenness of the whole fungal community.

For LCBD, climatic variables were the strongest predictors with significant positive effects on both the whole community and individual phyla (Figure 3c). NDVI and pH were also important with negative effects on the whole community and most phyla. Among the three variable groups, climate had the most dominant effect on LCBD with 67% of the phyla explained best by climatic variables.

Based on the mean standardized estimates of individual environmental variables (Figure 4a, Supporting Information Figure S4), the mean (Figure 4d) and proportion (Supporting Information Figure

S5) of the highest standardized estimates of environmental variable groups, the joint effects of climatic variables for species richness decreased while decreasing the taxonomic coverage from the whole bacterial community to phylum level, whereas the relative importance of local variables increased. At single phylum level, the effects of local and climatic variables were similar (Figure 4a,d, Supporting Information Figure S5). For community evenness, however, changing taxonomic coverage did not affect the mean (Figure 4e) and proportion (Supporting Information Figure S5) of highest standardized estimates of climatic and local variables, although the later had slightly larger effects at the phylum level (Figure 4b,e). For LCBD, climatic variables had the highest mean (Figure 4f) and largest proportion (Supporting Information Figure S5) of highest standardized estimates across the taxonomic coverage, but decreasing taxonomic coverage greatly reduced the relative importance of climatic variables (Figure 4c,f, Supporting Information Figure S5).

Based on the mean standardized estimates of individual environmental variables (Figure 5a, Supporting Information Figure S7), the mean (Figure 5d, Supporting Information Figure S6) and proportion (Supporting Information Figure S8) of the highest standardized estimates of environmental variable groups, the local variables became relatively more important than climatic ones for species richness when further downscaling the community to higher taxonomic resolution levels (Figure 5a,d, Supporting Information Figure S8). For community evenness, however, taxonomic downscaling did not affect the mean (Figure 5e) and proportion (Supporting Information Figure S8) of highest standardized estimates of climatic and local variables (Figure 5b,e, Supporting Information Figure S8). For LCBD, increasing taxonomic resolutions greatly reduced the mean (Figure 5f) and proportion (Supporting Information Figure S8) of highest standardized estimates of climatic variables, while local variables became more important (Figure 5c,f, Supporting Information Figure S8).



**FIGURE 3** Environmental variables explaining the biodiversity of microbial phyla and whole communities. The lower panels show the standardized parameter estimates, indicated by dot sizes, for the three groups of environmental variables using weighted averaging of parameter estimates over best-fit models in predicting three biodiversity metrics. The numbers of best-fit models are listed in Supporting Information Table S1. The biodiversity metrics are species richness, evenness and local contribution to beta diversity (LCBD). The three groups of explanatory variables are climatic (MJT, mean July temperature; MAP, mean annual precipitation), catchment Normalized Difference Vegetation Index (NDVI) and local variables (pH, TN, conductivity [SPC], K and area). The shaded dots indicate significant (p < 0.05) positive (blue) or negative (red) effects on biodiversity based on multimodel averaging analyses. The upper panels represent the mean values of relative variable importance for all phyla, which is a measure of the absolute ratio of standardized beta. Phylum abbreviations are listed in Table 1. The phyla are ordered according to mean species number

# 4 | DISCUSSION

Despite the increasing attention of elevational biodiversity patterns of microbes in both freshwater and soil ecosystems (Bryant et al., 2008; Wang et al., 2017), the effects of the taxonomic scales on the microbial biodiversity patterns and the relative importance of the hierarchical environmental determinants were previously largely unknown. These results on the elevational patterns and determinants varying with taxonomic coverage and taxonomic resolutions, to the best of our knowledge, are for the first time revealed for microbes. The elevational patterns in species richness and LCBD were congruent across bacterial phyla, but not in evenness. Taxonomic downscaling in both taxonomic coverage and resolution significantly changed the biodiversity patterns and increased the relative importance of local variables on biodiversity patterns while decreased that of climatic variables. This outcome

highlights that the niche conservation with regard to climatic factors is more important for biodiversity for the whole community and the lower taxonomic resolution levels, whereas the effects of environmental filtering by local variables are stronger at the higher resolution levels.

#### 4.1 | Elevational patterns across taxonomic scales

For bacteria, we found that species richness declined with elevation for the whole community and nearly half of the taxa at the phylum to order levels. According to a recent meta-analysis, such a pattern is relatively typical in species richness for both freshwater and soil bacteria communities, with declining patterns in 36.8% and 30.0% of studies, respectively (Wang et al., 2017). However, at higher taxonomic resolution levels, such as genus level, hump-shaped patterns were more dominant, which also led to increased complexity



**FIGURE 4** Relative importance of environmental variables across taxonomic coverage. Individual environmental variables (a-c) and three environmental variable groups (d-f) are considered for three bacterial biodiversity metrics: species richness (a, d), evenness (b, e) and local contribution to beta diversity (LCBD) (c, f). The three environmental variable groups are climatic, catchment and local variables. We calculated the standardized beta values measured with weighted averaging of parameter estimates over best-fit models for biodiversity and environmental variables. The upper row (a-c) shows the relationships between taxonomic coverage and the variation in mean standardized beta values for each phylum combination scenario. The lower row (d-f) shows the relationships between taxonomic coverage and the means of highest absolute standardized beta values (a-c) and the means of the highest absolute standardized beta values (a-c) and the means of the highest absolute standardized beta values (a-c) and the means of the highest absolute standardized beta values (a-c) and the means of the highest absolute standardized beta values (a-c) and the means of the highest absolute standardized beta weights (d-f) indicate the relative importance of examined variables in explaining the observed biodiversity. The error bars indicated the *SD*s for all possible taxa combinations. The box plots for individual environmental variables (a-c) are shown in Supporting Information Figure S4

and weaker diversity-elevation relationships. Various patterns that emerged at phylum level also support different biogeographic patterns observed across bacterial phyla in other habitats, for example, soils (Singh, Takahashi, & Adams, 2012). The increased complexity suggests that the microbial elevational patterns may vary with taxonomic scales, as also being found for macroorganisms (Peters et al., 2016; Weiser et al., 2018). This scaling effect of taxonomic resolutions may explain the general elevational patterns of micro- and macroorganisms (i.e., higher plants and animals). Macroorganisms are usually examined at higher taxonomic level, and only approximately 25% of patterns are declining (Rahbek, 2005). This is consistent with the smaller proportion of declining patterns in microorganisms at higher resolution taxonomic levels. We thus postulate that decreasing taxonomic resolutions may reveal less complex elevational patterns, such as monotonically declining patterns.

Weakly declining trend in evenness for the whole bacterial community was also found by Wang et al. (2017), whereas humpshaped patterns that emerged here frequently at the phylum level have rarely been documented before. Such a trend may be caused by the detected positive relationship between species richness and evenness in the whole community level, while evenness patterns were better explained by local variables compared to species at the phylum level. For LCBD, significant U-shaped patterns indicate that the both ends of the environmental gradient may be occupied with specialized species (Legendre & De Cáceres, 2013). This observation is consistent with the one reported for diatom community along the same elevational gradient (Teittinen et al., 2017). The congruence of these distinct microbial groups suggests that the U-shaped pattern may be a general feature of the microbial beta diversity pattern across environmental gradients. However, the facts that the U-shaped pattern was less evident and nonsignificant patterns were more common at high taxonomic resolution levels imply that the underlying drivers of LCBD may be inconsistent at higher taxonomic resolution levels.

The network analyses revealed that species richness and LCBD had strong biological associations (i.e., intercorrelations) among most of the bacterial phyla, whereas evenness was weaker. Such a result may stem from the following reasons. (a) Firstly, even though the driving variables across the phyla differed, the directions of the responses of species richness and LCBD were mostly consistent across the phyla. This may be caused by the negative effect of temperature, that is, elevation, acting as strong environmental gradient for the lower resolution taxa. Such a strong effect caused the similar responses to temperature across different clades. For evenness, the responses towards environmental drivers were inconsistent and resulted in weak intercorrelations among the phyla. (b) Second, the niche conservatism across the phyla that follow the main environmental gradients is likely to be



**FIGURE 5** Relative importance of environmental variables across taxonomic resolution. Individual environmental variables (a-c) and three environmental variable groups are considered for three bacterial biodiversity metrics: species richness (a, d), evenness (b, e) and local contribution to beta diversity (LCBD; c, f). The three environmental variable groups are climatic, catchment and local variables. We calculated the standardized beta values measured with weighted averaging of parameter estimates over best-fit models for biodiversity and environmental variables. The upper row (a-c) shows the relationships between taxonomic resolution levels and the variation in mean standardized beta values for each phylum combination scenario. The lower row (d-f) shows the relationships between taxonomic resolution levels regarding the three groups of environmental variables. These mean standardized beta values (a-c) and the means of the highest absolute standardized beta weights (d-f) indicate the relative importance of examined variables in explaining the observed biodiversity. For better visualization, the *SDs* were shown for the highest absolute standardized beta weights (d-f). The taxonomic resolution levels domain, phylum, class, order, family and genus are shortened as D, P, C, O, F and G, respectively. The box plots for individual environmental variables (a-c) and environmental variable groups (D-F) are shown in Supporting Information Figures S6 and S7, respectively

more important in determining the occurrence (and thus richness at sites) of species than their abundance. This is because a species' occurrence is temporally more stable than its abundance, whereas a species' abundance, especially that for microbes, is easily affected by daily or seasonal environmental variations due to their fast growth rates and short life cycles. (c) Third, biotic interactions such as facilitation or competition could increase or decrease diversity through changing utilization of limiting resources and resource partitioning (Tilman et al., 2001). This change in overall utilization of resources may lead to the diversity change of the whole bacteria community that could promote the diversity congruency across different phyla (Cardinale, Palmer, & Collins, 2002; Hibbing, Fuqua, Parsek, & Peterson, 2010). However, it remains largely unknown for microbial communities in how biotic interactions affect at the phylum level and how such interactions maintain the diversity.

# 4.2 | Environmental determinants for elevational patterns

We found that temperature was the strongest climatic factor positively affecting overall bacterial species richness, which is congruent with previous studies (Wang, Pan, Soininen, Heino, & Shen, 2016; Zhou et al., 2016). The great importance of temperature suggests direct or indirect temperature-dependent mechanisms, such as a positive effect on metabolisms (Brown, Gillooly, Allen, Savage, & West, 2004; Fuhrman et al., 2008; Wang et al., 2016), productivity (Wang et al., 2016; Wang, Brown, Tang, & Fang, 2009), ecological interactions (Chen, Landry, Huang, & Liu, 2012) and speciation rate (Allen & Gillooly, 2006), for generating and maintaining the aquatic bacterial diversity. Since the climate of the subarctic mountain region is characterized by a relatively warm but short growing season, high growing season temperatures at low elevations may stimulate resource exploitation rate and growth rate that facilitate the high bacteria diversity. It should be noted, however, that temperature may also affect microbial communities indirectly through unmeasured local factors or biogeographical processes that are associated with elevation, such as the concentration of dissolved organic carbon (Karlsson, Jonsson, & Jansson, 2001; Rofner et al., 2017; Wang et al., 2011, 2017) or dispersal effects (Szekely & Langenheder, 2017). Nevertheless, the dominant roles of temperature at broad taxonomic scales (Figure 5a) are also consistent with the finding among macroorganisms showing that temperature is an important driver in the multitaxa community (Peters et al., 2016). Furthermore, our -WILEY-MOLECULAR ECOLOGY

findings of a strong positive relationship between temperature and community uniqueness (LCBD) strengthen the notion of the importance of the climatic variables. Although a recent study found that LCBD was more affected by local environmental filtering associated with anthropogenic influences (Pajunen, Luoto, & Soininen, 2017), our data set suggests that climatic variables play a more important role in pristine freshwater environment. It is probable that harsh and unproductive conditions harbour more unique species composition in high elevations in the study area, but the underlying mechanisms promoting the high uniqueness in low elevations remain uncertain.

Local variables, such as pH. K and conductivity, were also important in explaining bacterial species richness and evenness. The importance of pH in determining bacterial community diversity is also observed in other studies of freshwater and soil bacteria (Fierer & Jackson, 2006; Shen et al., 2013; Wang et al., 2017). However, our results revealed that such pH effects are more prominent at higher resolution taxa. The effect of pH on species richness and LCBD suggested that more acidic ponds may impose stronger environmental filtering for higher resolution taxa, which harbour low species richness but unique composition. It was not surprising that K had significant effects on species richness and evenness, since K strongly correlates with Ca, Mg and conductivity and may indicate the integrated effects of weathering and watershed processes (Soranno et al., 1999). Although some local variables were less important in explaining the biodiversity of the whole bacterial community, they may be essential for the biodiversity of some single taxa. For instance, TN was the strongest factor for the phyla Alphaproteobacteria, Deltaproteobacteria and Gemmatimonadete, which may indicate specific physicochemical preference of these taxa.

Interestingly, narrowing down the taxonomic coverage and resolution reduced the relative importance of climatic variables and increased the importance of local variables. This effect may be explained by the following reasons. First, energy-related variables (e.g., temperature) modulate diversity through controlling population abundance and the stochastic extinction rates (Cardinale, Hillebrand, Harpole, Gross, & Ptacnik, 2009). More broadly defined taxa may be more likely to undergo zero-sum dynamics over such energy constraint (Hurlbert & Stegen, 2014). That is, increase in the abundance of one taxon would reduce that of another taxon. Thus, energy-related factors were more evident at the broad scale of taxonomic community while did not influence much on higher resolution individual taxa. Second, the increasing effects of local variables with taxonomic downscaling may be best explained by the niche conservatism among the different bacterial taxa, that is, different bacterial taxa are conserved in their optimal ecological niche (Philippot et al., 2009). Since different clades tend to retain their own ecological niche space and ecological traits, it is likely that species richness may be phylogenetically constrained by certain local variables that are associated with species physiological tolerance. For instance, pH and TN strongly constrained the species richness of some phyla in our studied ponds. However, the whole community levels encompass a wider portfolio of niches (e.g., pH optima,

N limiting) such that environmental filtering of local variables constraining particular phyla will not necessarily govern the richness patterns of the whole community. Third, the increased relative importance of local variables when downscaling to higher taxonomic resolutions may suggest that the potential niche conservatism with respect to local variables may be phylogenetically shallower, and large-scale climatic variables seem to be more dominant at lower taxonomic resolutions. These findings are in line with the different phylogenetic niche depths of ecological traits observed in microorganisms (Martiny et al., 2015). For instance, the dominant role of temperature at broad taxonomic resolution levels clearly indicates that the niche conservatism of temperature preference is phylogenetically deeper than for local variables such as pH for the pond bacteria. However, this finding is different from the shallow phylogenetic depth for temperature preference for Cyanobacteria, Actinobacteria and Escherichia coli. (Martiny et al., 2015).

Our findings provide direct empirical evidence to support the concept that more taxonomically inclusive clades have stronger effects on species richness-temperature or richness-energy relationships (Hurlbert & Stegen, 2014). A similar association has been reported in an elevational study on plants and animals (Peters et al., 2016). We also found evidence for the similar downscaling effects on LCBD, with decreasing effects of climatic variables towards the phylum level, although LCBD patterns were probably affected by climatic variables rather than catchment and local variables. In evenness, however, local variables tended to be more important than the other variables regardless of taxonomic coverage, which is in line with a study that suggests that bacterial evenness is best explained by local variables (Wang et al., 2017).

#### 4.3 | Elevational patterns in fungal biodiversity

Compared to bacteria, the biodiversity of freshwater fungi has been less explored. In terrestrial habitats, the fungal diversity patterns have been examined at the whole community level (Gai et al., 2011; Pellissier et al., 2014; Tedersoo et al., 2014; Yang et al., 2016) and also at the phylum level (Looby, Maltz, & Treseder, 2016). Although there were no significant elevational patterns in biodiversity of the freshwater fungi at the community level, the significant humpshaped patterns were observed for two fungal phyla. The significant effect of precipitation on these two fungal phyla is consistent with a global-scale study in which fungi are most strongly related to precipitation and local soil variables (Tedersoo et al., 2014). The weak support of pH in explaining whole fungal community suggests that fungi are less sensitive to pH changes than bacteria. Interestingly, fungal species richness scaled positively with pond area, which is consistent with the species-area relationship and suggests that larger pond may serve as a larger colonization pool for fungi. In addition, although environmental drivers changed according to taxonomic scales in bacteria, the taxa number of fungal samples was too low to conduct the similar analyses of taxonomic coverage. In the future, with more intense sampling, the taxonomic scaling effect for fungi could provide a better understanding of their biodiversity patterns and determinants.

# 5 | CONCLUSIONS

Our study revealed that taxonomic downscaling provides new insights into the elevational patterns and their underlying drivers. Although the elevational patterns in biodiversity at finer taxonomic scales were variable and were not necessarily congruent with the biodiversity patterns for the whole microbial communities, we clearly showed that there was a congruence of elevational patterns in species richness and LCBD at bacterial phylum level, but not in evenness. Further, elevational patterns in bacterial species richness and evenness showed increasing complexity towards higher taxonomic resolution levels. These findings reveal that the niche conservatisms of microbial taxa could happen even at the lower taxonomic resolution levels by sharing general ecological strategies and traits for their occurrence in terms of the broad-scale environmental variables, such as climatic factors. This is further supported by comparing different spatial scales of drivers, which showed that taxonomic downscaling increased the relative importance of local variables for biodiversity but decreased the importance of climatic variables. Our results collectively emphasize the ecological coherence across microbial taxonomic scales and provide novel evidence of the importance in considering different biodiversity facets across taxonomic scales and hierarchical drivers.

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#### DATA ACCESSIBILITY

The bacteria and fungi sequences were deposited in MG-RAST database under the Accession no 82476.

#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### AUTHOR CONTRIBUTIONS

The samples were collected by J.W., J.S., A.T. and F.P. The biological data were provided by J.W. Data analyses were performed by C.Y. The first draft version was written by C.Y. The manuscript was finished by J.W. with the contributions from all authors.

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#### SUPPORTING INFORMATION

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