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Assembly mechanisms of soil bacterial communities in subalpine coniferous forests on the Loess Plateau, China[§]

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Microbial community assembly is affected by trade-offs between deterministic and stochastic processes. However, the mechanisms underlying the relative influences of the two processes remain elusive. This knowledge gap limits our ability to understand the effects of community assembly processes on microbial community structures and functions. To better understand community assembly mechanisms, the community dynamics of bacterial ecological groups were investigated based on niche breadths in 23 soil plots from subalpine coniferous forests on the Loess Plateau in Shanxi, China. Here, the overall community was divided into the ecological groups that corresponded to habitat generalists, 'other taxa' and specialists. Redundancy analysis based on Bray-Curtis distances (db-RDA) and multiple regression tree (MRT) analysis indicated that soil organic carbon (SOC) was a general descriptor that encompassed the environmental gradients by which the communities responded to, because it can explain more significant variations in community diversity patterns. The three ecological groups exhibited different niche optima and degrees of specialization (i.e., niche breadths) along the SOC gradient, suggesting the presence of a gradient in tolerance for environmental heterogeneity. The inferred community assembly processes varied along the SOC gradient, wherein a transition was observed from homogenizing dispersal to variable selection that reflects increasing deterministic processes. Moreover, the ecological groups were inferred to perform different community functions that varied with community composition, structure. In conclusion, these results contribute to our understanding of the trade-offs between community assembly mechanisms and the responses of community structure and function to environmental gradients.

Keywords: bacterial community, assembly mechanisms, ecological groups, niche breadth

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Introduction

Elucidating the mechanisms that govern community diversity, metabolic function, and biogeography patterns is a central, but controversial, topic in ecology (Zhou and Ning, 2017), particularly in microbial ecology. Deterministic processes comprise ecological selection mechanisms which are imposed by abiotic and biotic factors that then determine the presence or absence and relative abundances of species (Dumbrell *et al.*, 2010; Ofiţeru *et al.*, 2010; Chase and Myers, 2011). In contrast, stochastic processes suggest that community biogeography patterns are simply influenced by stochastic factors, including ecological drift, dispersal, and speciation (Hubbell and BordadeAgua, 2004). In addition, the invocation of stochastic processes assumes that species are all ecologically equivalent (Woodcock *et al.*, 2007). The two types of ecological processes are not mutually exclusive, but rather exist in a continuum (Gravel *et al.*, 2006). However, variation in ecological selection strength and the rates of dispersal can influence the relative roles of deterministic versus stochastic processes across temporal and spatial scales, in addition to within entire ecosystems (Chisholm and Pacala, 2011; Dini-Andreote *et al.*, 2015). Consequently, assembly processes vary based on environmental conditions or the specific characteristics of organisms (Zhou and Ning, 2017).

Different ecological groups, such as generalists and specialists, exhibit different organismal traits. For example, generalists and specialists can differ in richness and have disparate ecological niches. Furthermore, these ecological groups that exhibit different ecological dynamics can be disturbed by various factors (Monard *et al.*, 2016) and may exhibit different responses to varying environmental conditions (Liao *et al.*, 2016). Therefore, the community assembly mechanisms for habitat generalists may differ from those of specialists due to the wider habitat range of the former (Futuyma and Moreno, 1988; Van Tienderen, 1991). Given this supposition, investigating the different biogeographic patterns of ecological guilds will help to deepen our understanding of microbial community assembly processes.

Microbial community composition can vary considerably across spatial or environmental gradients, such as the one that has been observed for ocean water column communities (Sunagawa *et al.*, 2015), or communities along alpine forest soil elevational gradients (Siles and Margesin, 2016). Importantly, this variation can affect ecosystem function (Louca *et al.*, 2016). Moreover, ecological guilds can exhibit different community structures due to varying ecological responses to environmental variation. However, much less is known about variation in the community functions of ecological guilds as a consequence of environmental variation.

Subalpine mountain environments provide a high level of available microbial niches and exhibit correspondingly rich microbial communities (Ren *et al.*, 2017). These environments are characterized by pronounced climatic gradients and climosequences over short distances, thereby leading to high levels of environmental heterogeneity (Siles and Margesin, 2017). Across multiple subalpine mountain environments, habitat specialists and generalists are expected to be identified among bacterial communities due to different niche breadths (Logares *et al.*, 2013). Based on the above environmental characteristics, subalpine systems provide ideal experimental platforms for investigating mechanisms of microbial community assembly.

Soil microbial community assembly, here, in subalpine forests was analyzed by sampling soils from 23 plots within subalpine mountain coniferous forests located on the Loess Plateau in the Shanxi province of China. To identify community composition, bacterial 16S ribosomal RNA genes were analyzed via high-throughput sequencing, and the bacterial communities were divided into generalist and specialist groups based on niche breadths. Based on these data, we investigated (i) the niche optima and degree of specialization for ecological groups along the environmental gradients, (ii) the roles of ecological groups towards overall community function, and (iii) the influence of ecological processes on these properties.

Materials and Methods

Site description and sampling

A total of 23 typical soil plots were sampled (Supplementary data Fig. S1 and Table S1) in August 2016 and 2017. The study sites were located in subalpine mountain coniferous forests between 1,900 m and 3,055 m above the mean sea level. Eight plots were sampled from Wutai Mountain (WT), which exhibited the maximum elevation gradient of the study, ranging between 1,900 m and 3,055 m above the mean sea level. Ten plots were sampled from the Pangquangou Natural Reserve (PQG) that exhibited maximum geographical distances and a moderate elevation gradient ranging from 1,950 m and 2,650 m above mean sea level. Finally, five plots were sampled from Luya Mountain (LY), which exhibited a minimal elevation gradient ranging between 2,200 m and 2,400 m above mean sea level. At each sample site, a 1 m × 1 m sampling plot was established along the elevation gradient. Five soil cores at a depth of 15 cm were taken at each sampling plot and then pooled to form a single independent sample. However, this may result in one library per plot and thus there may also influence the variability of the bacterial communities within each plot. Soil samples were sealed in plastic bags, refrigerated, and immediately transported to the laboratory, where they were then sieved using a 2-mm mesh (germicidal treatment). Soil samples were then stored at -80°C for further analysis.

DNA extraction, PCR amplification, and sequencing

Soil DNA was extracted from 1 g of soil from each sample using the E.Z.N.A. Soil DNA Kit (OMEGA). 16S rRNA genes from each sample were amplified in 25 μl reactions using universal bacterial PCR primers targeting the V3-V4 hypervariable region (341F 5′-ACTCCTACGAGGAGCA-3′ and 805R 5′-TTACCGCGGCTGCTGGCAC-3′) (Tripathi *et al.*, 2018). PCR reactions were conducted with the following thermal cycling parameters: 95°C for 5 min (initial denaturation), 30 cycles of 30 sec at 95°C (denaturation), 62°C for 30 sec (annealing), and 72°C for 30 sec (extension), with a final extension for 7 min at 72°C. PCR products were purified using an Agarose Gel DNA purification kit (TIANGEN). DNA extract quality and quantity were then measured using an Infinite 200 PRO plate reader (TECAN). The DNA purity was assessed by A_{260}/A_{280} absorbance ratios, and only those DNA extracts with absorbance ratios between 1.8–2.0 were used for further analyses. Triplicate DNA samples were extracted from each soil sample and subjected to PCR amplification of 16S rRNA genes, then mixed and followed by pooling for sequencing on the Illumina MiSeq sequencing platform at Shanghai Personal Biotechnology Co., Ltd.

Bioinformatics analysis

16S rRNA gene sequencing data were analyzed using the QIIME (v1.8.0, http://qiime.org/) pipeline (Caporaso *et al.*, 2010). Filtered sequence alignments were denoised using the DeNoiser program (Reeder and Knight, 2010) and then screened for chimeras using the UCHIME algorithm (Edgar *et al.*, 2011). Sequence datasets were subsampled for each sample to an equal sequencing depth set as the minimum number of sequences reads in a sample in order to avoid bias due to differential sequencing depths. Sequences classified as Eukaryota, Archaea, and 'unknown' were then removed. The remaining 16S rRNA gene sequences were clustered into operational taxonomic units (OTUs) at a 90% similarity level using the average neighbor clustering method. The 90% OTU cutoff level was used because it produced OTUs with high abundances for subsequent analyses and circumvents potential taxonomic misclassifications due to sequencing artifacts (Barberán *et al.*, 2012). In addition, the 90% nucleotide identify threshold of 16S rRNA genes corresponds roughly the family level of taxonomic classification (Konstantinidis and Tiedje, 2007; Barberán *et al.*, 2012). OTUs were then assigned taxonomic identities via BLAST searches against the SILVA database using the k-mer searching method as implemented in the MOTHUR software package (Pruesse *et al.*, 2007). Additional information on the 16S rRNA gene sequencing data are provided in Supplementary data Table S2.

Analysis of environmental variables

Soil total carbon (TC), total nitrogen (TN), and total sulfur (TS) were measured using an elemental analyzer (Vario EL/MACRO cube). Nitrate (NO_3^--N), ammonium (NH_4^+-N), and nitrite (NO_2^--N) nitrogen were measured using an Automated Discrete Analysis Instrument (CleverChem 380). Soil pH was measured by shaking a soil: water suspension (1:2.5 mass/volume) for 30 min, followed by measurement with a pH meter (Hl 3221). Finally, soil organic matter was determined using the potassium dichromate volumetric method.

Assignment of habitat specialists and generalists

To investigate differences in the community composition

attributable to habitat specialist and generalist subcommunities, habitat specialization of OTUs was determined using Levin's niche breadth (B value) via the "niche.width" function in the "spaa" package for R (Levins, 1968; Logares *et al.*, 2013). OTUs with low-abundances (mean relative abundances $< 2 \times 10^{-5}$) were removed prior to these analyses (Pandit *et al.*, 2009; Liao *et al.*, 2017). The division of OTUs into ecological groups followed criteria identified in previous investigations (Liao *et al.*, 2016, 2017). Briefly, OTUs with a niche breadth (B) > 17 were defined as generalists, because this value corresponds to an outlier value of the B-value distribution (Liao *et al.*, 2016) (see Supplementary data Fig. S2). OTUs exhibiting B < 1.5 were regarded as specialists, which was selected because it is the smallest possible value for B.

Ecological groups can be categorized into ecologically meaningful units based on niche optima (Fodelianakis *et al.*, 2016). Using these analyses, the responses of ecological groups can be investigated in context of environmental gradients. The Xmax value was considered as the environmental gradient at the sampling plot where an OTU exhibited the highest relative abundance. The average value of Xmax for ecological groups was then considered to be the niche optimum for that group.

Influences of ecological processes

To distinguish the relative importance of deterministic and stochastic processes in community assembly, the *β*-diversity-based null model was used, as previously described (Tucker *et al.*, 2016). The implementation of this model can help to distinguish the relative roles of deterministic and stochastic community assembly processes (Condit *et al.*, 2002; Tuomisto *et al.*, 2003; Gilbert and Levin, 2004). A null deviation near zero suggests that stochastic processes are more important in driving the community, whereas larger positive or negative null deviations suggest that deterministic processes predominate (Tian *et al.*, 2017).

To further investigate the roles and influences of different community assembly processes, additional analyses were used as previously described (Stegen *et al.*, 2012, 2013, 2015). The phylogenetic signal, which describes the relationship between phylogenetic relatedness and ecological similarity, was measured (Kraft *et al.*, 2007; Fine and Kembel, 2011). Determination of the phylogenetic signal was done using the "phylosignal" function in the "picante" R package. In addition, the pairwise phylogenetic turnover between communities was calculated as the mean nearest taxon distance metric (βMNTD; Olivierj, 2008; Fine and Kembel, 2011), using the "comdistnt" function in the "picante" R package.

The difference between observed βMNTD and the mean value of the null distribution is measured in units of standard deviations (of the null distribution) and is referred to as the β-Nearest Taxon Index (βNTI) (Stegen *et al.*, 2013).

For a given community, the relative influences of variable selection or homogeneous selection were evaluated as the fraction of its comparisons with βNTI > +2 or βNTI < -2, respectively. The Bray–Curtis-based Raup–Crick metric (RC_{bray}) was calculated (Stegen *et al.*, 2015). The relative influence of dispersal limitation was estimated as the fraction of a community's $|\beta NTI| < 2$ and $RC_{bray} > 0.95$. The relative influence of homogenizing dispersal was estimated as the fraction of a community's $|\beta NTI| < 2$, and $RC_{bray} < -0.95$. The un-dominated scenario (i.e., ecological drift) was therefore estimated as the fraction of a community's $|\beta NTI| < 2$ and $|RC_{bray}| < 0.95$ (Stegen *et al.*, 2015).

Network analyses

OTU networks were constructed on the basis of the Spearman correlation matrix of OTU abundances using the psych package for R. OTUs are nodes in the network, while the edges connecting the nodes represent correlations between OTUs. Only those connections where correlation coefficients were > 0.6 and $P < 0.05$ were used in the network. Thus, positive correlations indicate co-occurring OTUs based on abundances, whereas negative correlations indicate that the OTUs are mutually exclusive (Barberán *et al.*, 2012). *P*-values were adjusted using the false discovery rate (FDR) to control for the analyses (FDR < 0.05; Ma *et al.*, 2016). Network analyses were conducted in the igraph package for R and visualized in the Gephi software (http://gephi.github.io/).

Functional predictions of communities

The database for the functional annotation of prokaryotic taxa (FAPROTAX) was used to assign functional predictions to OTUS (http://www.zoology.ubc.ca/louca/FAPROTAX/lib/php/index.php). The detailed evaluation of FAPROTAX includes direct comparison with metagenomics and genomic data, as previously described (Louca *et al.*, 2016).

Statistical analyses

We used ANOVA to evaluate the differences in α-diversity indices, soil physicochemical properties and null deviation values among sites using Vegan packages for R. Principal coordinate analysis (PCoA) was used to visually depict the dissimilarity of OTU composition among samples based on Bray-Curtis distances. Ternary plots (Bulgarelli *et al.*, 2015) were used to investigate the relative relationships of inferred community functions that are performed by different ecological groups. We used redundancy analysis based on Bray-Curtis distances (db-RDA; function capscale in package vegan in R) to investigate the correlation between community composition and environmental factors. Furthermore, the significance of each factor is assessed via a step-wise model building (function ordiR2step in package vegan in R). Significance was assessed by Monte Carlo permutations (999 iterations). To evaluate the multicollinearity of environmental attributes, variance inflation factors (VIFs) for each variable (after standardizing the data) were computed. The vif.cca function in the Vegan package for R was used to sequentially exclude variables with VIF > 20. Multivariate regression tree (MRT) analysis was used to identify the relationship between bacterial α-diversity estimates and environmental variables in a visualized tree, and diversity indices were normalized prior to MRT analysis. Species abundance distribution models were fit using the sads package for R (Dumbrell *et al.*, 2010). Finally, analysis of similarities (ANOSIM) tests were conducted to statistically test for significant differences in soil physicochemical properties and bacterial community structure among sites.

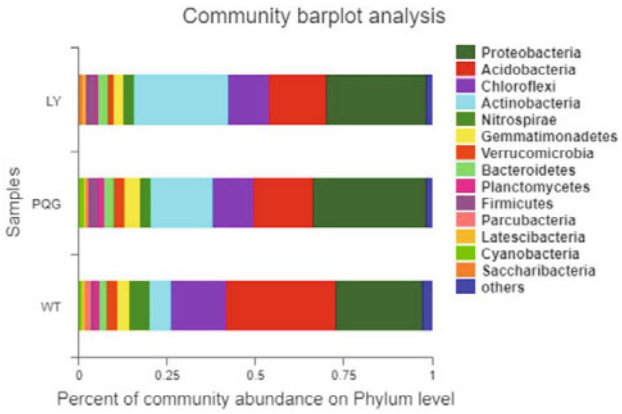

Fig. 1. **Relative abundance of phyla among sites.**

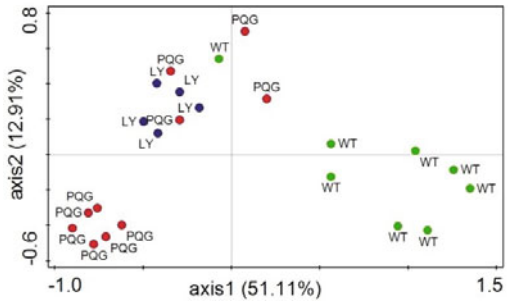

Fig. 2. **PCoA of bacterial community dissimilarities among sampling plots.**

Results

Physicochemical properties of soils

Soil physicochemical properties varied significantly across sampling sites (ANOSIM, R = 0.79, $P < 0.01$) (Supplementary data Figs. S3 and S4). Briefly, NH_4^+-N and NO_2^--N were highest at LY (36.91 and 0.16 mg/kg, respectively) and lowest at WT (17.41 and 0.04 mg/kg, respectively). NO_3^--N (6.45 mg/kg), SOC (70.29 mg/g), TC (6.4%), and TN (0.51%) were all higher at WT than at the other two sites. Variation in pH was significantly associated with sampling sites ($P < 0.05$, mean = 6.21). Finally, there was no significant difference in TS among sites ($P > 0.05$, ranging from 0.06% at LY to 0.09% at PQG).

Community structure, composition, and species abundance distribution modeling of ecological groups : A total of 829 OTUs were identified from 1,062,241 high-quality 16S rRNA gene sequences from 23 soil samples. Good's coverage for the samples ranged from 95.19% to 99.75%, indicating that

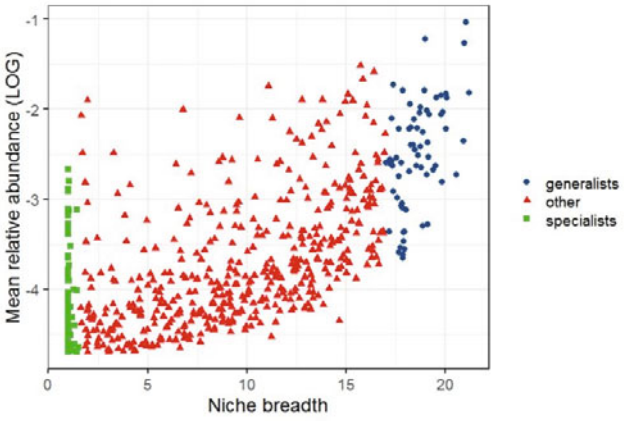

Fig. 3. **Distribution characteristics of ecological groups among sites.** Each point represents an operational taxonomic unit (OTU) specified as a generalist (blue; B > 17), other taxa (red, 1.5 < B <17), or specialist (green; B < 1.5). The y-axis shows mean relative abundance (log transformed) for OTUs, and the x-axis shows OTU niche breadths.

the majority of bacterial diversity in the soils was represented in the datasets. Rarefaction curve analyses yielded generally asymptotic curves (Supplementary data Fig. S5), further indicating that the sampling effort conducted here was sufficient to sample the diversity present in the soils.

Community composition and structure significantly varied among sites (ANOSIM, $R = 0.61$, $P < 0.01$; Fig. 1). For example, the relative abundances of Proteobacteria were the highest at PQG (37.79%), while those of Acidobacteria were the highest at WT (31.03%). PCoA further indicated biogeographic separation patterns of bacterial community composition among sites (Fig. 2). To further investigate community assembly mechanisms, ecological groups were evaluated based on niche breadths.

Communities were divided into specialists, generalists and 'other taxa' to identify differential distribution patterns for each ecological group (Fig. 3). Among all OTUs, 67 were considered as generalists (11.31%), 461 as other taxa (77.87%), and 64 as specialists (10.82%). The specified ecological groups exhibited different community structures and compositions (Fig. 4). Proteobacteria were the most abundant phylum among the three ecological groups (generalists: 16.92%; other: 17.91%; specialists: 21.88%), followed by Chloroflexi (12.15%, 5.97%, 10.94%) and Bacteroidetes (8.46%, 13.43%, 4.69%). Acidobacteria were not detected among the generalist community fraction, while Proteobacteria (21.88%) were more observed in specialists.

Different species abundance distribution models were fit to the different ecological groups (Supplementary data Fig. S6). Specifically, a log-series abundance distribution model was

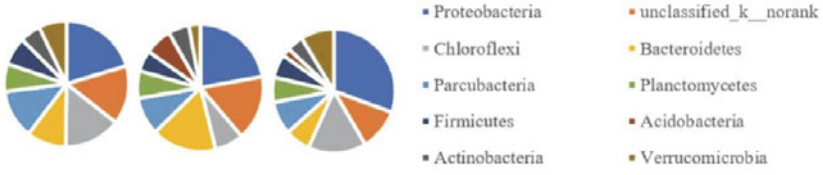

Fig. 4. **Overall relative abundances of taxonomic groups within the three ecological guilds.** The pie charts from left to right represent generalists, other taxa, and specialists, respectively.

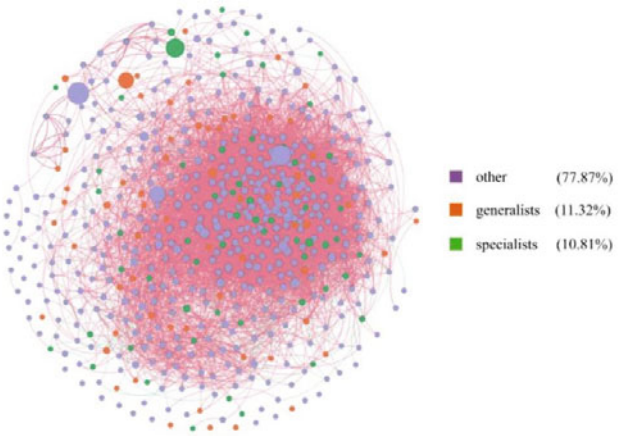

Fig. 5. Network of co-occurring OTUs based on correlational analysis. Connections indicate strong (Spearman's $P > 0.6$) and significant ($P < 0.05$, fdr = 0.05) correlations. Node size is proportional to the betweenness centrality of the node. Green edges connecting nodes indicate exclusion interactions and red edges indicate co-occurrences.

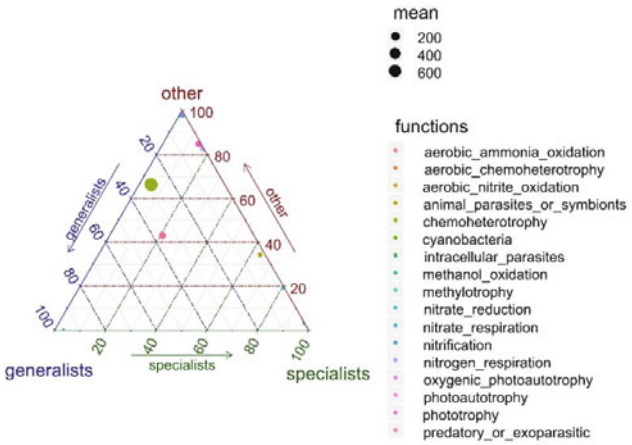

Fig. 6. Distribution of metabolic functions among the three ecological groups. Each point represents one metabolic function, and the size of each circle represents its relative abundance based on inferred functional genes. The position of each point is determined by the contribution of the indicated compartments to the total relative abundance for that function.

the best fit for specialists (AIC = 6622.7, $P < 0.01$), while log-normal models were the best fit for the other two ecological groups (generalists and other taxa) (Supplementary data Table S3).

Network analysis comprised 568 OTU nodes and 11,869 correlation edges (Fig. 5 and Supplementary data Table S4). The average path length of the network was 3.29, and the average diameter was 10. The clustering coefficient for the network was 0.49, and the modularity index was 0.31. A significantly higher number of co-occurrence interactions were identified relative to mutual exclusion interactions in all of the networks, as inferred from positive correlations (11,646 total) relative to negative correlations (223 total).

Metabolic functions of ecological groups

The metabolic functions of the bacterial communities, in terms of the abundances of proxy genes, differed among ecological groups (Fig. 6). Most metabolic functions (9 out of 12) were significantly more represented in the other taxa group compared to specialists and generalists. These functions included aerobic ammonia oxidation (mean abundance = 1,003), aerobic chemo-heterotroph (1,181), aerobic nitrite oxidation (1,137), chemo-heterotroph (1,279), nitrification (2,340), nitrate respiration (69), oxygenic photoautotroph (242), photoautotroph (242), phototroph (240). The abundances of a few metabolic functions (2 out of 12) were higher

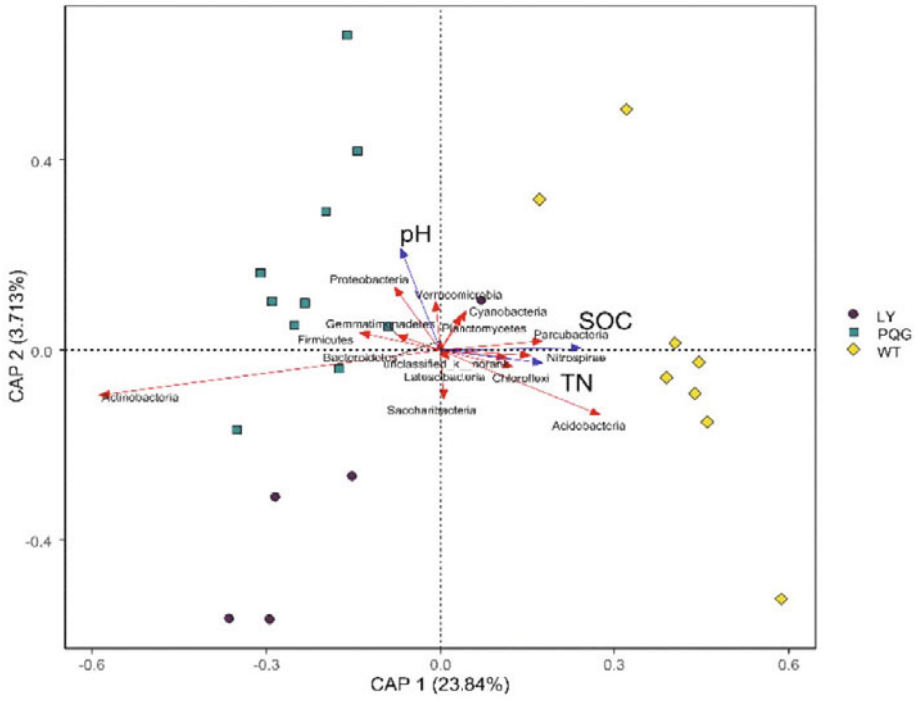

Fig. 7. The db-RDA indicating significant influences of environmental factors on microbial community structure among the sampling sites.

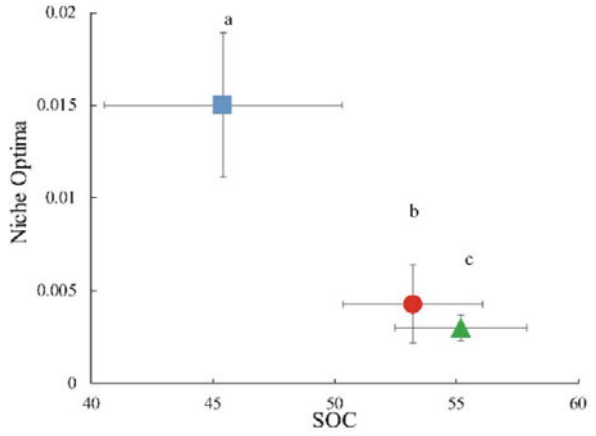

Fig. 8. Niche optima of ecological groups. Points represent the mean relative abundance values of ecological groups along the SOC gradient. The niche optimum is defined as the average SOC value of the sample where the maximum relative abundance of each ecological group was observed. The blue square represents generalists; red dot represents other taxa; green triangle represents specialists. The y-axis error bars represent the standard deviation of the mean relative abundance and x-axis error bars represent the standard deviation of the average niche optimum of each group. Different letters represent significant differences in $P < 0.05$ level.

in the generalist group, including methanol oxidation (36) and methylotrophy (37). Finally, nitrate respiration was most represented (69) in the specialist group populations.

Correlation of environmental factors to different ecological groups

According to results of db-RDA, environmental factors significantly influenced bacterial community structure (permutation test, $P < 0.01$) (Fig. 7). Furthermore, the results of stepwise model demonstrated SOC was the most important factors, follow by TN and pH. Multivariate regression tree analysis (MRT) (Supplementary data Fig. S7) indicated that normalized diversity estimates were mainly attributable to

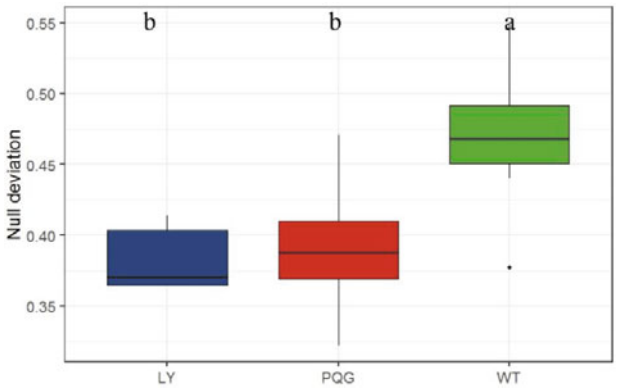

Fig. 9. Null deviation for bacterial communities for the three ecological groups. A null deviation of about zero indicates that stochastic processes are more important in structuring the community, whereas larger positive or negative null deviations suggest that deterministic processes are more important. Different letters represent significant differences at the $P < 0.05$ level between sites.

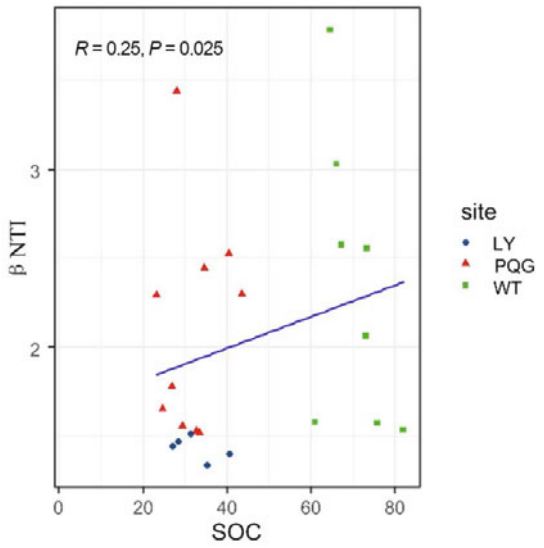

Fig. 10. Effect of SOC on βMNTD of bacterial communities across all sampling plots. Blue line shows a linear regression.

SOC that explained 36.75% of the variation (in the first spilt), followed by pH (6.68%). Given its contribution to explaining community diversity patterns, SOC was further used as a descriptor for environmental gradients.

Along the SOC gradient, the niche optima of ecological groups were significantly differentiated (generalists: 45.41; other: 53.15; specialists: 55.19; $P < 0.05$) (Fig. 8). Following from this observation, SOC can be inferred as the selective force determining how widely OTUs are distributed across the sites analyzed here.

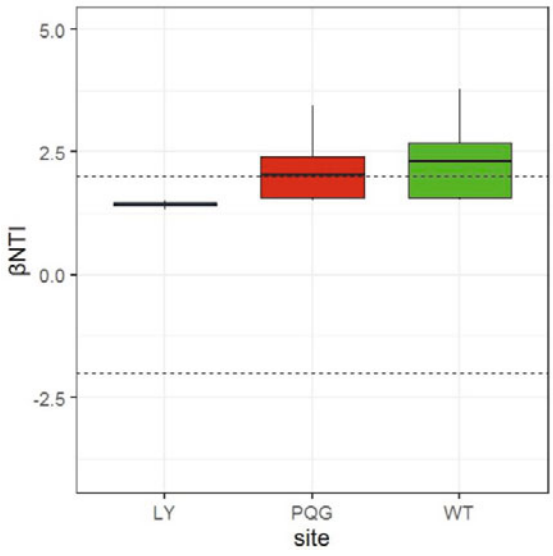

Fig. 11. Boxplot showing the βNTI distribution among sites. Horizontal dashed lines indicate upper and lower significance thresholds at βNTI = +2 and −2, respectively. The relative influences of variable selection or homogeneous selection were evaluated as the fraction of its comparisons with βNTI > +2 or βNTI < −2, respectively. The relative influence of dispersal limitation or homogenizing dispersal were evaluated as the fraction of its comparisons with |βNTI | < 2.

The influence of ecological processes on assembly mechanisms

Null deviation values varied among sites (ranging 0.32–0.54; Fig. 9). The bacterial community structure at WT deviated more considerably from the null-expected value (relative null deviation = 0.46), followed by those at PQG (0.39) and those at LY (0.36). Thus, bacterial community assembly at WT was more relatively driven by deterministic processes compared to those at LY that were more relatively driven by stochastic process.

Soil microbial communities along the SOC gradient exhibited a strong phylogenetic signal (K = 0.32, $P < 0.01$), indicating that more closely related bacterial taxa shared more similar niche partitioning. βNTI increased with increasing SOC ($R = 0.55$, $P < 0.01$) (Fig. 10). Finally, the microbial communities at WT (βNTI = 2.34) and PQG (2.11) were both shaped to a greater extent by variable selection (βNTI > 2), while those at LY were more shaped by homogenizing dispersal (|βNTI| < 2 and $RC_{bray} < -0.95$) (Fig. 11 and Supplementary data Table S5).

Discussion

Deterministic and stochastic processes can represent two complementary components along a continuum of ecological processes that shape community structures (Chase and Myers, 2011; Zhou and Ning, 2017). This continuum varies based on environmental conditions or the characteristics of organisms inhabiting the environments (Zhou and Ning, 2017; Tripathi *et al*., 2018). A previous study indicated that fungal communities were initially strongly governed by deterministic processes, but later less so when extending along a well-established glacier forefront chronosequence, as based on same analysis method of this study (i.e., β-diversity-based null model) (Tian *et al*., 2017). The level of deviation reported herein is lower than that which was reported for the soil fungal communities. One explanation for this difference is that bacteria may possess greater metabolic functional plasticity (Massana and Logares, 2013), thereby rendering them less influenced by environmental filtering compared to fungal communities.

The microbial communities at WT (βNTI = 2.34) and PQG (βNTI = 2.11) were both shaped by variable selection. This may be due to the high elevational gradients present at WT and the larger sampling scales at PQG that could lead to higher environmental heterogeneity. Previous studies have confirmed that shifts in selective pressure resulting from shifts in environmental conditions could be the primary cause of high compositional turnover, and this is referred to as variable selection (Dini-Andreote *et al*., 2015). In contrast, the microbial communities at LY were more driven by homogenizing dispersal (|βNTI| < 2 and $RC_{bray} < -0.95$). This observation may be related to the smaller elevational gradient and sampling scales at the LY site. Shorter geographical distances and flat landscapes may contribute to the dispersal of bacterial cells. High dispersal rates potentially homogenize community compositions, thereby leading to lower compositional turnover and thus less deviation from the null model (Leibold *et al*., 2010). In principle, high dispersal rates can overwhelm selection-based influences at the population level (Dias, 1996).

The taxa that are not generalists or specialists, but fall in the continuum between the two (defined as 'other taxa' here), play an important role in ecosystems. Importantly, ecological groups can have potentially different ecological responses to varying environmental conditions (Liao *et al*., 2016). Our results demonstrate that ecological groups exhibit different niche optima and degrees of specialization (i.e., niche breadths) along gradient of SOC. Given this observation, we infer that the ecological groups we defined represent a tolerance gradient to environmental heterogeneity, which is consistent with previous analyses (Kolasa and Li, 2003).

The results reported here indicate that SOC can act as a stringent environmental filtering and lead to changes in phylogenetic diversity patterns. Relationships between SOC and bacterial community assembly has also been observed across a broad range of microbial ecosystems (Bastida *et al*., 2013). For example, SOC decomposition rate was significantly and positively correlated to total microbial biomass, bacterial biomass, Actinomycete PLFAs, and soil enzyme activities along the northern slope of Changbai Mountain (Xu *et al*., 2015).

The community assembly processes identified here varied along the SOC gradient with a transition from homogenizing dispersal to variable selection. Previous studies have suggested that the relative influences of stochastic and deterministic community assembly processes can vary with successional age of soils that can primarily be attributable to soil pH co-varying with age (Tripathi *et al*., 2018). This suggests that the degree to which stochastic and deterministic processes shape soil bacterial community assembly is a consequence of soil pH rather than successional age, per se (Tripathi *et al*., 2018). Following this observation, we hypothesize that the community assembly processes varied among sites due to SOC variation among sites. In addition, the assembly mechanisms of habitat generalists may differ from specialists (Futuyma and Moreno, 1988; Van Tienderen, 1991), and this could be related to their different ecological responses, like the differential preferences and degrees of specialization along the SOC gradient investigated here.

Microbial communities can display complex patterns of variation in composition across environmental contexts, and this variation can affect potential metabolic functions and ecosystem functions (Louca *et al*., 2017). Our results indicate that different ecological groups have the potential to perform different community functions as a consequence of different community compositions and structures.

Conclusion

Our results demonstrate that microbial community assembly processes varied along a gradient in SOC, wherein a transition from homogenizing dispersal to variable selection was observed. The ecological groups defined here exhibit differential tolerances for environmental heterogeneity. The assembly mechanisms inferred differed among ecological groups, and this could be related to differences in niche optima and degrees of specialization for groups (i.e., niche breadths) along the environmental gradient. Moreover, the ecological groups exhibited differential community functional potentials that varied

with community composition and structure.

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Conflict of Interest

The authors declare that they have no competing interests.

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