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Climatic factors have unexpectedly strong impacts on soil bacterial β-diversity in 12 forest ecosystems

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ABSTRACT

It is critical to identify the community assembly patterns (*i.e.*, deterministic or stochastic processes) of soil microbes and the potential driving factors to better predict the belowground biodiversity and functioning in forest ecosystems. Here, a combined approach of neutral model and multivariate analysis was employed to examine the soil bacterial communities in 12 undisturbed forests in China, spanning a wide latitudinal range from 21.6°N to 50.8°N. A clear divergent pattern was found for community composition, indicating that deterministic processes dominated the community assembly of soil bacteria. The α-diversity (richness) nonlinearly changed from tropical to cold temperate zones, with the lowest and highest values detected in subtropical and temperate zones, respectively. Although no latitudinal pattern was observed for β-diversity (community variation), there were clear climate zone patterns. Unlike the minor effects of mean annual precipitation (MAP) and temperature (MAT) on bacterial α-diversity, MAP and MAT were important factors affecting soil bacterial β-diversity. Soil pH was a strong driver of α- and β-diversity, but plant factors had only minor effects. Altogether, this study highlights the unexpected importance of climatic factors in shaping bacterial β-diversity in forest soils. Our findings have implications for future investigations of bacterial community dynamics in forest ecosystems, particularly the responses of community composition to global climate change scenarios across large geographical scales.

1. Introduction

Unravelling the pattern of community assembly and its underlying mechanisms is important for a better understanding of biodiversity maintenance, community stability and ecosystem functioning (Hooper et al., 2002; Nemergut et al., 2013). Deterministic (niche-based) and stochastic (neutral) processes are regarded as two main forces in shaping community assembly and have been widely applied to interpret the community assembly processes of macro-organisms (Kraft et al., 2008; Ellwood et al., 2009). The niche-based theory states that deterministic factors, including environmental variables, biotic interactions and species traits, modulate the local microbial community. In this scenario, a community should be convergent towards a single pattern under similar environmental conditions and divergent under different environmental conditions (Zhou et al., 2013). The neutral theory, by contrast, assumes that many natural community patterns can be generated by ecological drift, which leads to dispersal-assembled communities mainly or solely due to dispersal (immigration) rather than adaptation to habitats (Hubbell, 2001; Alonso et al., 2006).

Soil bacteria rank among the most abundant and diverse groups of organisms on Earth and play key roles in biogeochemical cycling and ecosystem functioning. Despite the fact that bacterial cells have small sizes and short generation times, researchers are beginning to evaluate the relative importance of determinism and neutrality in structuring bacterial community assembly (*i.e.*, Powell et al., 2015) with the help of molecular techniques to unravel their vast diversity. Previous studies have shown that the relative role of deterministic and stochastic processes in the assembly of soil bacterial communities is highly dependent on spatial scale (Caruso et al., 2011). For example, determinism plays a dominant role at a relatively larger geographic scale, whereas

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stochasticity dominates at a smaller scale. The study of Powell et al. (2015), which is based on the scale of Scotland, reported that soil bacterial communities were predominantly impacted by deterministic processes under reduced land-use intensity, such as semi-natural grasslands, woodlands, moors and bogs. However, the relative importance of determinism and stochasticity in shaping soil bacterial diversity along a much larger latitudinal gradient in natural forest ecosystems remains less understood.

Characterizing bacterial α-diversity (*e.g.*, richness and/or phylogenetic diversity) and β-diversity (*i.e.*, community composition/variation) is fundamental to understanding ecological functioning and the underlying mechanisms that generate, drive and maintain bacterial biodiversity in ecosystems (Legendre and De Cáceres, 2013; Reese et al., 2018). At a large scale, although the pattern of decreasing "macrobial" diversity from the tropics to the poles (*i.e.*, latitudinal diversity gradient, LDG) has been documented for > 200 years (Amend et al., 2010; Kinlock et al., 2018), it remains less understood whether microbes exhibit a similar LDG (Fierer and Jackson, 2006; Zhou et al., 2016). Previous studies reported that microbial diversity patterns showed unimodal (Shi et al., 2014), monotonically decreasing (Fuhrman et al., 2008; Tedersoo et al., 2014), or nonlinear third-order polynomial (Tedersoo et al., 2014; Wang et al., 2016b) patterns with increasing latitude. No broad consensus is achieved for a microbial LDG pattern, and there is an urgent need to characterize the key drivers of microbial community across a large scale.

Previous studies have elucidated the distribution patterns of soil bacteria at large geographic scales but generated inconsistent results. For instance, across a broad range, some studies found that the soil bacterial β-diversity was significantly impacted by spatial variables (Martiny et al., 2011), soil pH and organic matter (Fierer and Jackson, 2006; Tian et al., 2018), whereas other studies reported that salinity and plant community composition were crucial environmental determinants of the bacterial community composition (Lozupone and Knight, 2007; Wang et al., 2016b; Reese et al., 2018). More importantly, the mean annual precipitation and temperature, rather than soil pH, have been recognized as the strongest predictors of microbial diversity and composition at the global (Tedersoo et al., 2014) and continental (Zhou et al., 2016) scales. Overall, bacterial diversity and/or community composition are influenced by different environmental factors, depending on ecosystem differences and spatial scales. Therefore, to elucidate the determinants that dominate bacterial community β-diversity, we need more empirical evidence from ecosystems that are less impacted by anthropogenic disturbances, such as natural and undisturbed forests. This knowledge can help us to better identify and compare the relative roles of neutral and niche processes in structuring soil bacterial community under the consistent ecosystem-type.

In this study, we examined the soil bacterial community in 12 undisturbed forests across a broad-scale latitudinal range in China (>4000 km, covering a latitude of 21.6°–50.8° N), using Illumina high-throughput sequencing. Unlike the available findings about microbial latitudinal diversity (*e.g.*, Wang et al., 2016b; Tian et al., 2018), we first employed a neutral model approach to generate neutral predictions. The predicted community was subsequently analysed and compared to the observed β-diversity to achieve three possible outcomes: the observed β-diversity equals the neutral prediction or is greater (divergence) or smaller (convergence) than the neutral prediction. We aimed to reveal the soil bacterial LDG pattern and to decipher the relationships between the bacterial community diversity and the habitat turnover based on soil, plant and climatic properties. The key factors influencing the bacterial community assembly patterns were identified through multivariate statistical analysis. We hypothesized that: (H_1) a clear deterministic pattern would be observed for the bacterial community assembly processes; (H_2) the bacterial LDG pattern would be different from that of macro-organisms; (H_3) in addition to soil pH, annual temperature and/or annual precipitation which represent the typical climatic characteristics across large spatial scales, will strongly shape the bacterial diversity.

2. Materials and methods

2.1. Study sites and soil collection

This study was conducted in 12 permanent forest sites established by the Chinese Forest Biodiversity Monitoring Network (CForBio), ranging from the latitude of 21.6°N to 50.8°N in China (Supplementary Fig. S1). As shown in Fig. S1, the forest types included two tropical (seasonal) rain forests (XSBN and NG), four subtropical evergreen broad-leaf forests (DHS, HSD, GTS, and BDGS), one mixed evergreen broad-leaved and deciduous broad-leaved forest (TTS), two warm-temperate deciduous broad-leaved forests (BTM and DLS), two temperate broad-leaved Korean pine forests (CBS and LS), and one cold temperate monsoon coniferous forest (GH). Basic information about these forest sites was described previously (Ji et al., 2019). Briefly, 20 quadrats (20 m × 20 m), at least 45 m apart from each other (mean = 247 m), were established in each site. In each quadrat, 10 soil cores (3.5 cm diameter, 10 cm depth) were randomly collected and combined into a composite sample, which resulted in a total of 240 composite samples. The soil samples were transported on ice to the laboratory and sieved through a 2-mm sieve to remove roots and debris. One portion of the samples was stored at −80 °C until DNA extraction; another portion was air-dried for analyses of the basic soil properties.

2.2. Climatic factors and soil parameters

Latitude, longitude and plant data (richness and basal area; the latter was measured by determining the area of individual trees and adding the measurements together) at the sites were provided by the CForBio. Estimates of the mean annual temperature (MAT) and the mean annual precipitation (MAP) were obtained from the WorldClim database (www.worldclim.org) with a resolution of 2.5 min. Soil pH was determined with a soil-to-water ratio of 2:5 (*w/v*) using a glass electrode (FE20, Mettler Toledo). Soil total carbon (TC) and total nitrogen (TN) were determined with an Elementar Vario EL III (Elementar Analysensysteme GmbH, Germany). Total phosphorus (TP) was measured by an inductively coupled plasma-atomic emission spectrometer (ICP-AES, iCAP 6300, Thermo Jarrell Ash Co. USA). We calculated the ratios of TC to TN (C:N) and TN to TP (N:P). The basic soil properties and climate factors are shown in Table 1.

2.3. DNA extraction, PCR and high-throughput sequencing

Genomic DNA was extracted from 0.25 g frozen soil using the PowerSoil DNA isolation kit (MoBio Laboratories, Inc. USA) according to the manufacturer's instruction. The possible inhibitory effects of humic substances were tested by PCR, and 10-fold diluted DNA was used in all subsequent PCR amplifications using the primers 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′). The thermocycling conditions were as follows: 94 °C for 5 min, followed by 35 cycles of 50 s at 94 °C, 1 min at 52 °C, and 1 min at 68 °C. A barcode was added to the 5′ side of the primer 806R to distinguish the sample origin. The PCR products were purified using a PCR product gel purification kit (Axygen, Union City, CA, USA). The yields of purified PCR products were measured using a TBS 380 fluorescence spectrophotometer (Promega, USA), and 50 ng DNA from each of the 240 purified PCR products were pooled and adjusted to 10 ng μL^{-1}. The pooled DNA was subjected to sequencing on an Illumina MiSeq PE250 instrument.

2.4. Sequence processing and diversity analysis

Using 'Quantitative Insights into Microbial Ecology' (QIIME v.1.7.0), raw sequences were quality filtered to remove low-quality reads that

Table 1
The climate zone types, basic soil properties and climate factors of 12 forest sites.

Site	Climate zone	pH	TC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	C:N	N:P	MAT (°C)	MAP (mm)
BDGS	Subtropic	4.21 ± 0.04f[a]	11.39 ± 0.422a	0.796 ± 0.019a	0.778 ± 0.046cd	14.28 ± 0.329def	1.080 ± 0.058c	11.5	2105
BTM	Temperate	4.88 ± 0.07cd	6.233 ± 0.508cd	0.444 ± 0.041d	0.536 ± 0.050de	14.44 ± 0.384de	0.900 ± 0.117cd	15.1	886
CBS	Temperate	5.48 ± 0.05b	7.950 ± 0.529bc	0.652 ± 0.044abc	1.162 ± 0.053 ab	12.26 ± 0.188 fg	0.553 ± 0.022d	3.6	700
DHS	Subtropic	3.78 ± 0.01g	4.078 ± 0.248def	0.290 ± 0.015e	0.156 ± 0.007f	13.98 ± 0.272defg	1.894 ± 0.102b	20.9	1929
DLS	Temperate	6.71 ± 0.05a	7.104 ± 0.581c	0.536 ± 0.042bcd	0.838 ± 0.052c	13.26 ± 0.213defg	0.633 ± 0.023cd	4.8	550
GH	Temperate	4.93 ± 0.07c	11.93 ± 1.364a	0.507 ± 0.051cd	0.921 ± 0.047bc	23.50 ± 0.830a	0.572 ± 0.070d	−5.3	450
GTS	Subtropic	4.68 ± 0.04de	4.034 ± 0.254def	0.208 ± 0.016e	0.136 ± 0.018f	19.79 ± 0.450b	1.948 ± 0.224b	15.3	1964
HSD	Subtropic	4.12 ± 0.03f	3.056 ± 0.188ef	0.231 ± 0.010e	0.078 ± 0.003f	13.08 ± 0.353efg	3.014 ± 0.114a	19.6	1744
LS	Temperate	5.64 ± 0.08b	11.80 ± 0.561a	0.703 ± 0.038a	1.026 ± 0.060abc	17.24 ± 0.799c	0.702 ± 0.031cd	−0.3	676
NG	Tropic	6.54 ± 0.05a	5.327 ± 0.174cde	0.549 ± 0.014bcd	1.210 ± 0.166a	9.696 ± 0.136h	0.575 ± 0.059d	22	1500
TTS	Subtropic	3.78 ± 0.05g	10.37 ± 0.964 ab	0.667 ± 0.047 ab	0.446 ± 0.022e	15.25 ± 0.367cd	1.545 ± 0.121b	16.2	1375
XSBN	Tropic	4.51 ± 0.04e	2.285 ± 0.099f	0.187 ± 0.005e	0.252 ± 0.013ef	12.19 ± 0.278g	0.782 ± 0.049cd	21.8	1493

[a] Values (mean ± SE) in the same column without shared letters denote significant difference at $P < 0.05$, as indicated by Tukey's HSD test. TC, total carbon content; TN, total nitrogen content; TP, total phosphorus content; C:N, ratio of TC to TN; N:P, ratio of TN to TP; MAT, mean annual temperature; MAP, mean annual precipitation.

lacked a valid primer sequence or barcode sequence, contained ambiguous bases, or had an average quality score < 20. Chimeric sequences were detected using the "chimera.uchime" command in Mothur 1.32.2 (Schloss et al., 2009) and were removed from further analysis. The non-chimeric sequences were grouped into different operational taxonomic units (OTUs) at a 97% similarity level based on the UPARSE pipeline using USEARCH v8.0 after the dereplication and exclusion of singletons. The sequence number per sample was normalized to the smallest sample size of 6066 reads using the 'sub.sample' command in Mothur (Schloss et al., 2009). Representative sequences from OTUs were selected through the 'get.oturep' command and were identified by a basic local alignment search tool (BLAST) search against the Greengenes database (DeSantis et al., 2006), using an E value < e^{-50}. The resultant bacterial community matrices were further used for analyses of the bacterial diversity.

Bacterial α-diversity was defined using the observed OTU richness (*i.e.*, OTU number at a sequencing depth of 6066 reads per sample) and the calculated phylogenetic diversity (PD). We calculated the bacterial PD based on the Faith's approach (Faith, 1992), which is the sum of the total phylogenetic branch length of detected OTUs in each sample. First, a phylogenetic tree was constructed using the 'FastTree2' program (Price et al., 2010) based on the selected representative sequences. Second, based on the obtained tree, Faith's PD was calculated using the 'Picante' package (Kembel et al., 2010; Zhou et al., 2016) in R3.0.2 (R Core Team, 2015). Bacterial community composition was ordinated using nonmetric multidimensional scaling (NMDS) with dissimilarity matrices using the 'metaMDS' function in the 'vegan' package (Oksanen et al., 2013). A multivariate regression tree (MRT) was further computed to delineate the relative importance of climatic and soil characteristics in structuring the bacterial community compositions using the 'MVPART' function in the 'mvpart' package (De'Ath, 2002). The raw sequences have been submitted to the Environmental Genomic Cloud (http://egcloud.cib.cn) with the sample nos. REA0001594 to REA0001833 under the project number PRJ000007.

2.5. Neutral model analysis

We adopted a neutral model approach using the neutral model of metacommunity and local community dynamics (Hubbell, 2001) to estimate the immigration and dispersal parameters and used these estimates to simulate the outcomes of neutral community assembly. Briefly, the data matrix of the sample-OTUs was used to estimate the parameters theta (Θ, diversity index) and immigration rate (I) of the neutral theory. The formula was used for multiple samples to estimate the neutral parameters using the PARI/GP codes (Etienne, 2007). Based on the estimated parameters, the PARI/GP function 'urn2.gp' was performed to create 100 communities of equal size under the assumption of neutral assembly (Etienne, 2007). The detailed processes conducted for simulation of neutral community were described previously (Maaß et al., 2014).

Output files were imported into the R program to calculate the pairwise dissimilarities (β-diversity) among all communities within each simulation (Powell et al., 2015). The potential importance of ecological stochasticity was evaluated by a comparison (standardized effect size, SES) between the observed community data and the corresponding expectations that were generated by the neutral models. Briefly, the SES was calculated by using the following formula: ($Dissimilarity_{obs.}$ – $Dissimilarity_{exp.}$)/standard deviation of the $Dissimilarity_{exp.}$, in which $Dissimilarity_{obs.}$ and $Dissimilarity_{exp.}$ denote the dissimilarities of the observed and the simulated communities, respectively. If the SES value was not significantly different from the neutral expectation, the community assembly was regarded as stochastic; otherwise, community assembly was regarded as deterministic. In the case of a significant difference being detected between the SES and zero, a positive effect size indicated divergence in community assembly compared to the neutral model, whereas a negative effect size indicated convergence compared to the neutral model. The standard errors were calculated as bootstrapped 95% confidence intervals.

2.6. Estimation of community and habitat turnover

We used the approach described in Powell et al. (2015) to estimate the strength of the community and habitat turnover across the sites and to investigate the relationship between the bacterial community and the habitat turnover. Briefly, pairwise bacterial β-diversity (based on the Sørensen index) was calculated using the 'labdsv' package (Roberts, 2016) in the program R 3.0.2 (R Core Team, 2015). Habitat turnover (environmental dissimilarity, *Ed*) was calculated from the Euclidean distance between sites based on the environmental factors of soil, plant and climatic parameters, using the following formula: $Ed = 1\text{-}Euc_d/Euc_{max}$, where Euc_d is the Euclidean distance, and Euc_{max} is the maximum distance between sites in the matrix.

2.7. Statistical analysis

Multiple comparisons of group means among the 12 forest sites were carried out with Tukey's HSD test after one-way ANOVA or pairwise comparisons after the nonparametric Kruskal–Wallis test where data did not satisfy homogeneity of variance, at $P < 0.05$, which indicated a significant effect of site on the basic soil properties and OTU richness. The relationships between bacterial α-diversity (richness and PD) and environmental factors (latitude, soil, climate and plant parameters) were analysed using the type II linear regression (ordinary least squares) in the 'lmodel2' package (Legendre, 2011). Similarly, the relationships between the observed β-diversity and geographic distance (Log_{10} transformed, at the sample level) or habitat turnover (*Ed*, at the site

level) were also analysed using the type II linear regression approach. To evaluate the effects of location and environmental factors on bacterial α- and β-diversity, permutational multivariate analysis of variance (PerMANOVA) was conducted based on Bray-Curtis dissimilarity matrices using the 'adonis' function in the 'vegan' package (Oksanen et al., 2013) with 999 permutations. In order to estimate the importance of location (climatic zone and research site) and environmental (MAT, MAP, soil and plant related variables) factors to bacterial community composition/variation (β-diversity), we conducted RandomForest modelling analysis using the 'randomForest' package (Liaw and Wiener, 2002). The significance of each predictor was further assessed with the 'rfpermute' package (Archer, 2016).

Structural equation modelling (SEM) was used to disentangle the causal relationships between environmental factors (basic soil variables, climatic factors and plant parameters) and bacterial OTU richness (α-diversity) and community composition (β-diversity), respectively. Prior to the SEM construction, we investigated the interrelationships among the environmental variables by the Mantel test with the Bray-Curtis dissimilarity measurement using the 'mantel' function in the 'Ecodist' package (Goslee and Urban, 2007). We obtained both *P* and *r* values (correlation coefficients) from the Mantel test between any two parameters of univariate (*e.g.*, single soil or climate variable, richness, etc.) and multivariate (*i.e.*, bacterial community composition as sample-OTUs matrix) data. Variables significantly ($P < 0.05$) related to at least one other variable were kept for the subsequent SEM analyses. The *r* values obtained from the Mantel test were used as input data to construct the SEM. Based on *a priori* and theoretical knowledge, we assumed a conceptual model that basic soil properties and climatic factors would alter the soil N:P ratio and/or plant, which consequently affected soil bacteria. Maximum likelihood estimation method was used to compare the SEM with the observation. Adequate model fits were indicated by a non-significant χ^2 test ($P \geq 0.05$), high goodness-of-fit index (GFI > 0.90), low Akaike information criterion (AIC) value, and low root mean square error of approximation (RMSEA < 0.05). The SEM analyses were performed using AMOS 22.0.0 (Amos Development Corporation, Meadville, PA). A Mantel correlogram was calculated to test the correlation between the partial residuals in the bacterial community and the geographic distance at different spatial scales. All statistical and multivariate analyses were conducted in R 3.0.2.

3. Results

3.1. High-throughput sequencing analysis

After quality control, we obtained a total of 11,975,634 quality filtered 16S rRNA gene sequences, which were clustered into 10,108 bacterial OTUs. After normalization, we obtained 9262 bacterial OTUs (1,455,840 reads), which were distributed in 43 phyla, 128 classes, and 182 orders. The dominant bacterial phyla were Proteobacteria (34.2%), Acidobacteria (27.8%), Verrucomicrobia (9.6%), Actinobacteria (9.3%), Bacteroidetes (5.1%), Planctomycetes (4.4%), Crenarchaeota (2.6%), and Chloroflexi (2.0%). Rarefaction curves tended to reach an asymptote at 20 samples, indicating that our sampling effort was sufficient to recover the majority of distinct bacterial OTUs for each forest site (Fig. S2A).

3.2. The latitudinal patterns of richness and phylogenetic diversity

The bacterial OTU number (*i.e.*, richness) was significantly different among the 12 forest sites, as indicated by the nonparametric Kruskal–Wallis test ($P < 0.05$). The mean values of bacterial richness ranged from 990 (TTS) to 1678 (DLS). No significant difference was detected between XSBN and NG in the tropical zone (Fig. S2B). However, in the subtropical region, significantly higher richness was observed in GTS than in other forest sites, and the lowest OTU richness was detected in the TTS site. In general, the OTU numbers were higher (mean = 1465) in the temperate zone than in the subtropical zone (mean = 1158). The highest OTU number, 1,678, was detected in the DLS site, whereas the lowest number, 1,296, was observed in the high-latitudinal GH site (Fig. S2B). To address the relationships between bacterial OTU richness and phylogenetic diversity (PD) with latitude, we tested linear and nonlinear (up to fifth-order polynomial functions) models and selected the best-fit models according to the corrected Akaike information criterion (AICc) values. We found that the cubic regression models could best explain the variation of bacterial OTU richness ($R^2 = 0.321$) and PD diversity ($R^2 = 0.334$). In general, the observed bacterial OTU richness and PD diversity consistently decreased from the tropical to subtropical areas, then increased with the increasing latitude and peaked at mid-latitude (*c.* 44°N) temperate regions, but declined toward the pole (Fig. 1). The bacterial α-diversity (represented by OTU richness here) was significantly influenced by forest types or location factors of the climatic zone and the sampling site (Table 2). In particular, the results of PerMANOVA indicated that bacterial α-diversity was strongly ($P < 0.001$) impacted by soil pH, N:P, TP, MAP, MAT, and plant richness, which could be important drivers in determining bacterial diversity (Table 2). Pearson's correlation analyses showed similar results (Fig. S3).

3.3. Simulations of community assembly processes using the neutral model

The observed community β-diversity of the bacteria was higher than those of the corresponding 100 simulated communities generated by the neutral model approach (Fig. 2A). The standardized effect size (SES) value of the bacterial community was significantly higher than that of neutral assembly (effect size = 0) (Fig. 2B). The neutral model analysis results provided strong evidence for significant divergence in soil bacterial communities. This non-neutral assembly process was supported by the relatively higher immigration parameter estimates of *Theta* (135, the value estimated for the entire metacommunity) and *I* (441, the value estimated for each local community) values from the neutral model, which indicated high immigration rates of soil bacteria.

3.4. Bacterial β-diversity and its latitudinal pattern

A Mantel correlogram demonstrated a significant spatial correlation between the bacterial community and the geographic distance at a spatial scale of 0–20 km (Fig. S4). This indicated that spatial autocorrelation was not significant, because the nearest geographic distance between two forest sites was 78 km in our study. The results showed that bacterial β-diversity (*i.e.*, community variation or dissimilarity) significantly increased with increasing geographic distance (Fig. S5A). Notably, the NMDS analysis showed that bacterial community composition was significantly different among climate zones (Fig. 3A). Within each of the tropical, subtropical and temperate regions, bacterial community compositions were clustered on the basis of specific sampling sites (Fig. 3B). Although a marginally significant ($P = 0.059$) relationship was observed between bacterial β-diversity and environmental turnover (*Ed*, Fig. S5B), bacterial community composition was more strongly related to environmental factors, including soil pH ($R^2 = 0.83$, $P < 0.001$), MAT ($R^2 = 0.81$, $P < 0.001$), MAP ($R^2 = 0.74$, $P < 0.001$), plant richness ($R^2 = 0.46$, $P < 0.001$), N:P ($R^2 = 0.43$, $P < 0.001$), and TP ($R^2 = 0.42$, $P < 0.001$) based on the 'envfit' analyses (Fig. 3B). The results of PerMANOVA and regression analysis using RandomForest also showed that the bacterial β-diversity was significantly related to all environmental factors ($P < 0.05$), but was more strongly (as indicated by higher R^2 values) impacted by soil pH, MAP, MAT, N:P, plant richness, and TP as compared to other factors (Table 2). The soil bacterial community composition of the 12 forest sites was first divided into two habitat types according to MAP, followed by soil pH and MAT or latitude, according to the multiple regression tree (MRT) analysis (Fig. 4). This result indicated that, in addition to soil pH, MAP played a critical

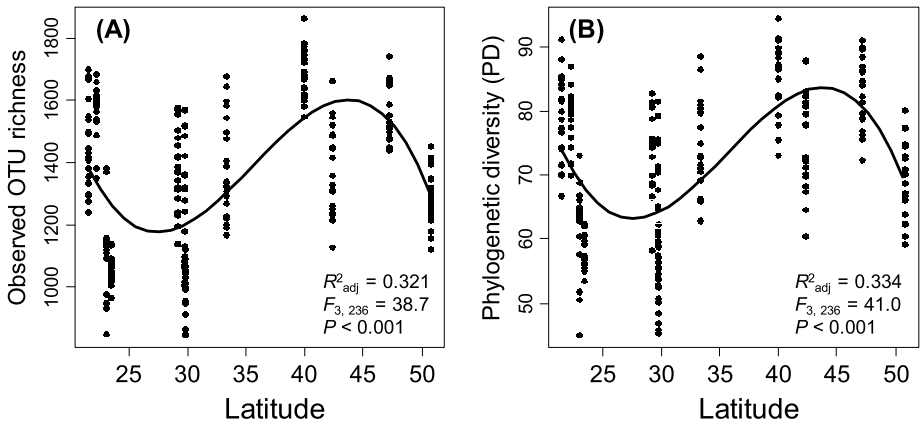

Fig. 1. (A) Relationships between the observed bacterial OTU richness and latitude and **(B)** between the bacterial phylogenetic diversity (PD) and latitude. Lines indicate best-fitting polynomial (cubic regression) functions.

Table 2
The results of PerMANOVA and regression using RandomForest (RF) to reveal the effect of the climate zone, research site, and environmental factors on the bacterial α-diversity (OTU richness as a proxy) and β-diversity (variation of community composition).

Parameters	α-diversity				β-diversity				
	PerMANOVA				PerMANOVA				RF
	Df	*F*	R^2	*P*	Df	*F*	R^2	*P*	*P*
Location factors									
Climate zone	2	99.35	0.456	**< 0.001**[a]	2	57.30	0.326	**< 0.001**	**< 0.001**
Site	11	67.41	0.765	**< 0.001**	11	23.81	0.535	**< 0.001**	**< 0.001**
Environmental factors									
MAT[b]	1	21.20	0.082	**< 0.001**	1	54.85	0.187	**< 0.001**	**< 0.001**
MAP	1	49.38	0.172	**< 0.001**	1	68.05	0.222	**< 0.001**	**< 0.001**
pH	1	319.7	0.573	**< 0.001**	1	69.87	0.227	**< 0.001**	**< 0.001**
TC	1	0.095	0.0004	0.772	1	12.35	0.049	**< 0.001**	**0.024**
TN	1	3.171	0.013	0.078	1	11.58	0.046	**< 0.001**	**0.008**
TP	1	62.77	0.209	**< 0.001**	1	37.85	0.137	**< 0.001**	**< 0.001**
C:N	1	3.545	0.015	0.053	1	11.31	0.045	**< 0.001**	**< 0.001**
N:P	1	116.5	0.329	**< 0.001**	1	41.58	0.149	**< 0.001**	**< 0.001**
Plant basal area	1	0.459	0.002	0.496	1	3.765	0.016	**0.004**	**0.022**
Plant richness	1	17.24	0.068	**< 0.001**	1	38.23	0.138	**< 0.001**	**< 0.001**
Plant community composition	1	8.839	0.036	**0.003**	1	2.802	0.012	**0.010**	**0.004**

[a] The *P* values < 0.05 were indicated in bold.
[b] MAT, mean annual temperature; MAP, mean annual precipitation; TC, total carbon content; TN, total nitrogen content; TP, total phosphorus content; C:N, ratio of TC to TN; N:P, ratio of TN to TP.

role in shaping the bacterial community composition at a large scale.

3.5. Relationships among bacterial α- and β-diversity and environmental factors

We performed SEM analyses with Mantel *r* values (correlation coefficients) as input to examine the direct and indirect influences of soil, plant, and climatic parameters on the bacterial richness (α-diversity) and community composition (β-diversity). For plant parameters, only plant species diversity (richness) was finally included in the SEM analyses because of the relatively weak effects of plant basal area and plant community composition on the bacterial community. The final SEMs explained 32% and 55% of the variations in the soil bacterial richness (Fig. 5A) and community composition (Fig. 5C), respectively. Bacterial richness was significantly and directly influenced by soil pH ($\lambda = 0.506$) and N:P ($\lambda = 0.199$), and was indirectly (non-significantly) affected by MAP ($\lambda = 0.045$) via soil N:P (Fig. 5A). Bacterial community composition (β-diversity) was significantly and directly impacted by soil pH ($\lambda = 0.635$), followed by MAP ($\lambda = 0.211$), MAT ($\lambda = 0.198$), and N:P ($\lambda = 0.188$) (Fig. 5C). Additionally, both soil bacterial richness and community composition were less impacted by plant diversity based on the results of the standardized total effects (Fig. 5B and D).

4. Discussion

4.1. Divergence dominated bacterial community assembly

Previous studies documented that the assembly of bacterial communities depends largely on deterministic process (niche-based) driven by contemporary environmental characteristics, such as soil pH, temperature, salinity, and nutrients (Fierer and Jackson, 2006; Lozupone and Knight, 2007; Wang et al., 2016a). Meanwhile, the bacterial communities could also be driven by stochastic processes, such as geographical separation and dispersal limitation (Wang et al., 2013). However, the relative importance of deterministic and stochastic processes in generating and maintaining the bacterial diversity needs to be examined in more ecosystems and at larger scales. Here, we determined whether the soil bacterial community assembly follows neutrality or not (divergent and convergent) at broad geographic scales using the neutral model method. A clear divergent pattern was observed in our study, which indicated that deterministic processes drove bacterial community assembly, thus supporting our first hypothesis (H_1). High ecological or

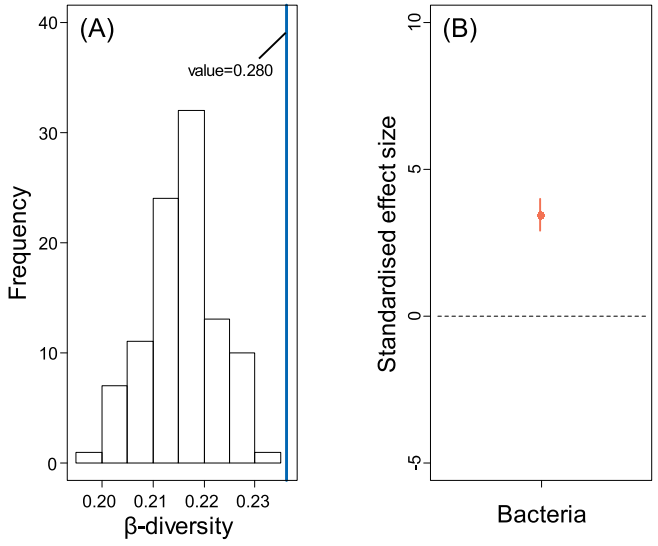

Fig. 2. (A) The observed bacterial β-diversity (community dissimilarity as Sørensen index), which is marked by blue lines, was compared to the frequency distribution of the β-diversity obtained from 100 simulations under the neutral model. **(B)** The standardized effect size (SES) relative to the neutral community assembly is indicated by the dash line. The mean (points) and the 95% confidence interval (vertical lines) of the central tendency of the observed β-diversity are presented relative to those of 100 simulated communities. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

environmental heterogeneity, such as climatic features (MAT and MAP), abiotic factors (soil properties), and biotic attributes (*e.g.*, plant parameters) probably drove these strongly divergent bacterial communities. In fact, the large spatial scale (a latitudinal gradient of 30° and a geographic distance of 4000 km) in this study, which represents greater niche breadth and climatic or environmental heterogeneity compared with a previous study by Powell et al. (2015), could result in the dominance of determinism. Although environmental filtering was characterized to primarily drive the divergence pattern of soil bacterial community in the current study, other factors such as intraspecific variation (*e.g.*, Laughlin et al., 2012) and biotic/trophic interactions (Pontarp and Petchey, 2016; Ning et al., 2019) may also influence the community assembly process, which should be investigated in the future.

4.2. Latitudinal pattern and drivers of the bacterial α-diversity

In this study, in contrast to the latitudinal diversity gradient (LDG, diversity decreases with increasing latitude) of macro-organisms, we found that bacterial α-diversity (OTU richness and phylogenetic diversity) increased from the subtropics to mid-latitude temperate zones (Fig. 1A and B), and thus our second hypothesis (H_2) 'bacterial LDG pattern would be different from that of macro-organisms' was supported. Not surprisingly, the microbial LDG was indeed considered to be different or even contrary to the "macrobial" LDG (Amend et al., 2010; Tian et al., 2018). In fact, our finding was in accordance with a recent study in which a significant increase in the bacterial α-diversity was observed in higher-latitude temperate forests compared with that of lower-latitude subtropical or tropical forests (Tian et al., 2018). First, it could be explained by the difference in resource availability between the (sub)tropical and temperate zones (Tedersoo and Nara, 2010). Compared with the lower-latitude (sub)tropical zones, the higher-latitude temperate zones generally show lower biological decomposition and nutrient leaching due to lower temperature and/or precipitation, thus leading to higher soil organic matter (SOM). Indeed,

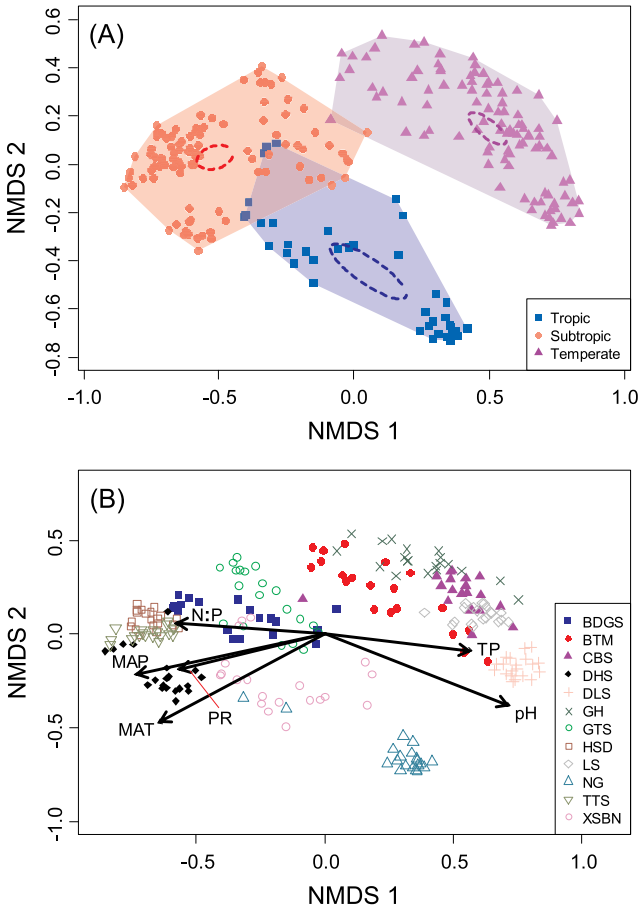

Fig. 3. Non-metric multidimensional scaling (NMDS) of the bacterial community composition based on three climate zones **(A)** and 12 forest sampling sites **(B)**. Circles with a dashed line are 95% confidence ellipses of tropical (blue), subtropical (pink), and temperate (purple) forest types **(A)**. Significant variables of soil pH ($R^2 = 0.83$, $P < 0.001$), MAT ($R^2 = 0.81$, $P < 0.001$), MAP ($R^2 = 0.74$, $P < 0.001$), PR ($R^2 = 0.46$, $P < 0.001$), N:P ($R^2 = 0.43$, $P < 0.001$), and TP ($R^2 = 0.42$, $P < 0.001$) in 'envfit' (based on 999 permutations) are presented as vectors in the ordination graph; The arrow lengths indicate the strength of the relationship between the environmental variables and bacterial community composition **(B)**. MAT, mean annual temperature; MAP, mean annual precipitation; PR, plant richness; TP, total phosphorus content; N:P, ratio of total nitrogen to TP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

two previous studies have highlighted that SOM played a critical role in driving the LDG of soil bacteria, at both the global and regional scales (Delgado-Baquerizo et al., 2016; Tian et al., 2018). Second, the less stable climate along with prominently temporal heterogeneity, which was associated with greater pronounced seasonality in temperate zones (Amend et al., 2010), may result in higher bacterial diversity than that in tropical or subtropical regions. In addition, the reduced α-diversity with increasing latitude from the mid-latitude temperate zone could be attributed to low survival and growth ability of a majority of soil bacteria in harsh environments (*e.g.*, low temperatures). However, given the temporal dynamic of microbial biodiversity, more experimental evidence from multiple seasonal sampling and more data sets are required to fully illustrate soil bacterial LDG.

Our results indicated that soil pH, N:P, TP, MAP, MAT, and plant richness were significantly associated with the soil bacterial α-diversity (Table 2 and Fig. S3). The SEM results suggested that bacterial richness was significantly and directly influenced by soil pH and N:P ratio. Unsurprisingly, soil pH has been recognized as a key driver influencing the

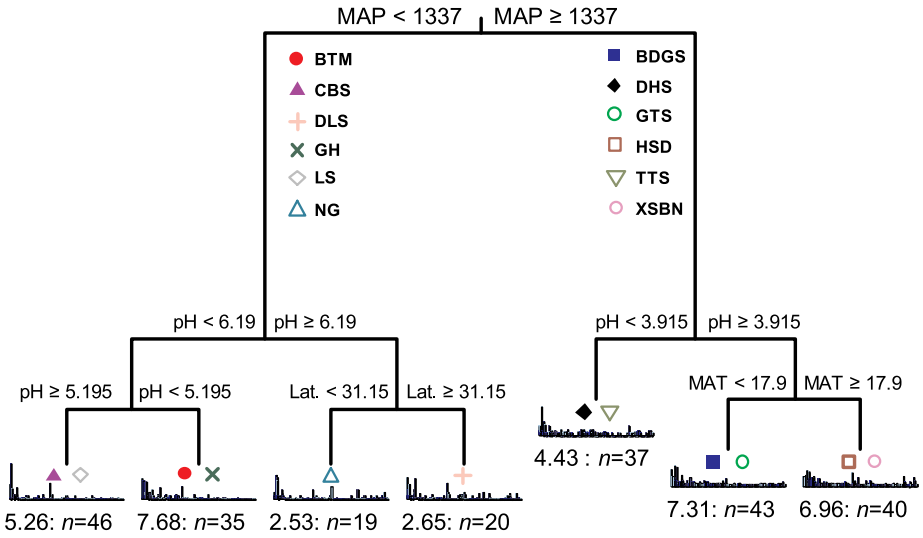

Fig. 4. Results of a multiple regression tree (MRT) analysis of the bacterial community composition (β-diversity) associated with different variables of the mean annual precipitation (MAP), soil pH, latitude (Lat.), and mean annual temperature (MAT). All 12 forest sites were first divided into two habitat types according to the lower (<1337 mm, $n = 120$) and higher (≥1337 mm, $n = 120$) MAP.

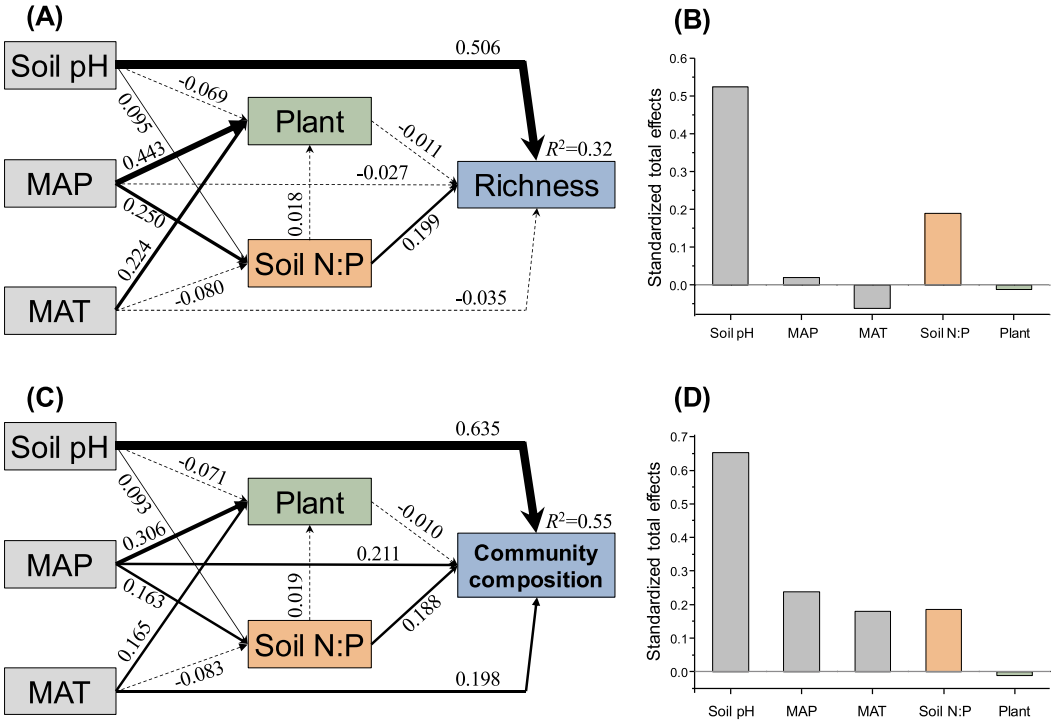

Fig. 5. Structural equation modelling (SEM) showing the causal relationships among key soil variables, climatic factors, plant diversity, and bacterial OTU richness (α-diversity, **A**) and community composition (β-diversity, **C**). The parameters of the final model for bacterial α-diversity (β-diversity) are: maximum likelihood, $\chi^2 =$ 3.42 (5.54), df = 3 (3), $P = 0.431$ (0.313), goodness-of-fit index = 0.930 (0.902), Akaike information criterion = 63.4 (45.5), and the root mean square error of approximation (RMSEA) = 0.027 (0.024). Solid lines and dashed lines indicate significant and non-significant pathways, respectively. The width of the solid lines indicates the strength of the causal effect. Numbers next to the arrows are standardized path coefficients and are indicative of effect size of the relationship. R^2 values represent the proportion of variance explained for the bacterial richness and community composition. Adequate model fits are indicated by a non-significant χ^2 test ($P \geq 0.05$), high goodness-of-fit index (GFI), low Akaike information criterion (AIC), and low root mean square error of approximation (RMSEA < 0.05). The standardized total effects (direct plus indirect effects) derived from SEM analyses for bacterial richness (**B**) and community composition (**D**) were also shown using histograms.

bacterial diversity in many previous studies (*e.g.*, Fierer and Jackson, 2006). The impact of N:P ratio might be attributed to both soil N and P contents, which are known to be important nutrient substrates for maintaining the growth and metabolism of soil microbes. Moreover, the SEM results showed weak effects of MAT and MAP on bacterial α-diversity. Although the environmental temperature and precipitation have

been reported as important factors shaping microbial diversity (Tedersoo et al., 2014; Zhou et al., 2016; He et al., 2017), bacterial diversity (richness) did not significantly change along a precipitation gradient (Angel et al., 2010). This discrepancy regarding the impacts of environmental temperature and precipitation on soil bacterial α-diversity cannot be fully explained by the available studies and more evidence is needed to reveal the relevant mechanisms.

4.3. Bacterial β-diversity and related key drivers

The dissimilarity in species composition (β-diversity) provides fundamental insights into the mechanisms of community assembly. Compared with α-diversity, the patterns and mechanisms that are related to β-diversity across biogeographic gradients are much less documented. In general, the latitudinal patterns of β-diversity could be driven by local processes (*e.g.*, habitat filtering and stochastic drift) and biogeographic and evolutionary processes (*e.g.*, dispersal, speciation and extinction); the latter determines the size of the species pool (Kraft et al., 2011; Xu et al., 2015). In this study, we found that the observed bacterial β-diversity was significantly and positively correlated to the geographic distance among samples (Fig. S5A), which was supported by a previous study at the continental scale (Martiny et al., 2011). Compared with the plant β-diversity (*e.g.*, Qian and Ricklefs, 2007; Kraft et al., 2011), no significant latitudinal pattern of bacterial β-diversity was observed, which might be attributed to the high abundance and dispersal capabilities of soil microbes.

In spite of the marginally significant ($P = 0.059$) relationship between bacterial β-diversity and habitat turnover (*Ed*) (Fig. S5B), we still considered that bacterial β-diversity would be shaped by deterministic processes (environmental filtering). In addition to being profoundly separated by climatic zones (Fig. 3A and Table 2), we also found that bacterial β-diversity was strongly driven by soil properties, such as soil pH and N:P (Figs. 3B and 5C and Table 2). Our results agree with previous findings that soil pH and phosphorus had strong influences on the bacterial community composition (*e.g.*, He et al., 2008; Rousk et al., 2010). More importantly, MAP was identified as the first contributor to the separation of the bacterial community into two main clusters in the MRT tree (Fig. 4). Changes in precipitation have been recognized as important factors influencing microbial composition, especially the fungal community structure (Cregger et al., 2012; Tedersoo et al., 2014). Notably, we demonstrated that MAP could also play a vital role in the bacterial β-diversity in this study. Given that different taxa have distinct inherent tolerances to soil water stress and nutrient use strategies, water availability can directly affect the bacterial community with shifts in the osmotic pressure and resource/substrate availabilities, which can subsequently induce bacterial physiological stress, growth and metabolic activity responses (Raich and Potter, 1995; Borken and Matzner, 2009). Plant parameters significantly, but to a lesser extent, affected the soil bacterial β-diversity in our study (Table 2). Previous studies also reported that the plant parameters, including plant diversity and community composition, had impacts on the soil bacterial β-diversity (Wang et al., 2016b; Reese et al., 2018). The SEM path analyses, however, showed no significant plant effects on the soil bacterial richness and community composition, which further suggested that, compared with soil pH and climatic conditions, plant variables played minor roles in determining the bacterial community structure in forest soils at the scale examined here. Additional research will be necessary to unravel the mechanism by which climatic factors, especially MAP, shape the bacterial β-diversity (community variation) and potential functioning to resist or adapt to precipitation alterations under global climate change scenarios (Reese et al., 2018).

5. Conclusions

A divergent pattern was found for soil bacterial community composition through a neutral model simulation approach. Our results demonstrated that deterministic processes influenced the outcome of bacterial community assembly via environmental variations along a large-scale latitudinal gradient. Previous studies in a variety of habitats have reported that soil pH, salinity and carbon content impacted the bacterial community (Fierer and Jackson, 2006; Lozupone and Knight, 2007; Delgado-Baquerizo et al., 2016); we provide evidence that MAP was an additional driver for the bacterial community based on results from relatively uniform forest soils. Moreover, we acknowledge that other variables, which potentially influence the soil bacterial diversity and community composition, may be unexplored in this study and need to be further examined in future investigations. Taken together, our findings highlight that, in addition to soil pH, climatic factors are equivalently important factors shaping soil bacterial β-diversity (*i.e.*, community composition/variation). This study has implications for improving the predictability of soil bacterial community dynamics in forest ecosystems under global climate change conditions across a broad-scale latitudinal range.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107699.

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