RESEARCH PAPER

A latitudinal gradient of microbial β-diversity in continental paddy soils

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Abstract

Aim: The β-diversity of plants and animals generally decreases with increasing latitudes. Here, we tested whether this relationship also holds for soil microbes at both functional and taxonomic levels.

Location: China.

Time period: Between June and October 2013.

Major taxa studied: Soil archaea, bacteria, and functional genes.

Methods: We used a spatially explicit 'L-shaped' sampling strategy in 39 paddy fields in China to study the pattern of soil microbial β-diversity (i.e., species turnover, β_z) across a latitudinal gradient (19.75° N to 47.58° N), with 11 soil samples taken within a 100 m × 100 m plot from each field. Archaeal and bacterial communities were analysed by sequencing 16S ribosomal RNA gene amplicons using Illumina MiSeq; microbial functional genes involved in C/N/P/S cycling were detected by GeoChip.

Results: We showed that the microbial β-diversity varied considerably across taxonomic and functional groups. For both soil microbial communities and functional genes, β-diversity decreased significantly along elevated latitudes at the continental scale. Woesearchaeota of archaeal communities, Bacteroidetes of bacterial communities, and the functional genes involved in methane production displayed the greatest decreases. Both mean temperature during the growing season of rice plants and paddy soil heterogeneity contributed to the latitudinal patterns. Further analyses indicated that temperature was more important than soil heterogeneity in driving the β-diversity of microbial communities and functional genes.

Main conclusions: These results highlight the importance of temperature-driven soil microbial β-diversity and suggest the potential to predict the changes of microbial diversity with climate change.

KEYWORDS
β-diversity, latitudinal pattern, microorganisms, paddy soils, temperature

1 | INTRODUCTION

A central goal of ecology is to understand how biodiversity is generated and maintained (Green & Bohannan, 2006). Spatial patterns of both species and functional diversity provide critical information about the mechanisms controlling species coexistence and are important for predicting diversity loss in response to global environmental change and habitat degradation (Ney-Nifle & Mangel, 2000; Thomas et al., 2004). β-diversity is an important concept used to describe variations in species identities from site to site and has been measured in different ways and for various purposes (Tuomisto, 2010). The spatial patterns of β-diversity have been widely studied in plants and animals and generally decline with increasing latitude and elevation (Kraft et al., 2011; Qian & Ricklefs, 2007; Ranjard et al., 2013). Both environmental selection and stochastic processes of dispersal, speciation and extinction have been shown to influence the spatial patterns of microbial β-diversity (Dahl et al., 2009; Qian & Ricklefs, 2012; Soininen, Lennon, et al., 2007). In recent decades, patterns of microbial β-diversity have also been investigated based on the measurement of microbial taxa defined by either morphological or a few molecular markers in various habitats (Green & Bohannan, 2006; Martiny et al., 2006; Zinger et al., 2014). Habitat heterogeneity and dispersal limitation are two main ecological processes that have been shown to shape microbial β-diversity (Hanson et al., 2012; Ranjard et al., 2013), although inference is complicated by methodological hurdles related to spatial scale, sampling schemes and analytical approaches (Drakare et al., 2006; Zhou et al., 2008). However, there is still limited information on how microbial β-diversity changes with latitude and the controlling factors.

Temperature has profound and diverse effects across all levels of biological organization (Woodward et al., 2010), such as metabolic rates (Gillooly et al., 2001), foraging rates (Byström et al., 2006) and ecological networks (Ings et al., 2009). The metabolic theory of ecology (MTE) predicts that the metabolism of organisms, population growth rates, mutation, and speciation increase exponentially with environmental temperature (Brown et al., 2004). Therefore, it is expected that increases in temperature could lead to faster ecological drift, that is, stochastic processes associated with birth, death, colonization, extinction and speciation. Accordingly, β-diversity should increase under higher temperature. In a previous study on tree diversity throughout China, Qiao et al. (2012) reported significant latitudinal patterns in the β-diversity of trees, shrubs and herbs in forests; these patterns were primarily controlled by monthly mean temperature and precipitation. A recent microecological study found that β-diversity of forest soil microbes across a large latitudinal temperature gradient, from subalpine Colorado to tropical Panama, was strongly correlated with temperature (Deng et al., 2018).

The habitat heterogeneity hypothesis, on the contrary, assumes that as new habitats are added, the number of unique species increases (Kallimanis et al., 2008). Studies of soil microbes showed that locations that differ more in their soil parameters also tend to differ more in microbial community composition (Griffiths et al., 2011; Ranjard et al., 2013), as the microbes utilize a diverse set of soil

factors such as organic matter and nitrogen. These results suggested that soil heterogeneity should also increase microbial β-diversity. It has been well recognized that both the MTE-based kinetic process and the soil heterogeneity contribute to the microbial β-diversity (Brown, 2014; Shen et al., 2009); however, there is still insufficient understanding about the relative importance of these two potential β-diversity drivers. Recent research on microbial β-diversity patterns and their potential drivers was conducted in natural forest ecosystems, and the results are confounded by the influences of plant diversity (Wang et al., 2009). Thus, monoculture ecosystems should have advantages for determining the relative importance of temperature and soil heterogeneity on microbial β-diversity and the underlying mechanism, as we can partially reduce the habitat heterogeneity derived from plant diversity.

Paddy soil ecosystems are considered a typical type of 'artificial wetland' that is flooded during the period of rice cultivation. The alternating anaerobic and aerobic soil environment between the flooding period and other seasons represents a unique habitat for soil microorganisms (Schmidt & Eickhorst, 2013). It is expected that such habitats are appropriate for detecting the relationships between microbial β-diversity and temperature and soil heterogeneity by partially reducing, if not eliminating, the influences of plant diversity. Additionally, paddy soils cover 150 million ha globally (Global Rice Science Partnership, 2013), representing one of the world's most important agricultural ecosystems. This wide distribution area can provide an ideal habitat for studying microbial β-diversity at wide spatial scales.

Thus, in this study, we collected a total of 429 soil samples from paddy fields throughout rice cropping regions in China to investigate the spatial pattern of microbial β-diversity and evaluate the relative importance of temperature and soil heterogeneity on β-diversity. Our primary hypotheses are that (a) the microbial β-diversity at both functional and taxonomic levels decreases with latitude across continental scale in paddy soils, (b) both environmental temperature and soil heterogeneity are the influencing factors of the latitudinal pattern, with more profound effects of temperature due to the relatively homogenous habitat in this human-managed monoculture ecosystem.

2 | METHODS

2.1 | Site description and sampling

A total of 429 soil samples were collected between June and October 2013 after harvesting rice from 39 paddy fields located in 13 regions throughout the main rice cropping areas in China (19.75° N to 47.58° N, 110.41° E to 126.92° E). The sampling area covered five temperature zones from North to South China: cold temperate zone, middle temperate zone, warm temperate zone, subtropical zone and tropical zone. The paddy fields were distributed in 13 regions, Hailun (HL), Changchun (CC), Shenyang (SY), Yuanyang (YY), Fengqiu (FQ), Lin'an (LA), Quzhou (QZ), Zixi (ZX), Jian'ou (JO), Changting (CT),

Hengyang (HY), Qingxin (QX) and Haikou (HK), with wide variation in the mean temperature during the growing season (Temp) of rice plants, ranging from 16.0 to 27.8°C. Three sites in the same region were located relatively close, within 20 km, to ensure that the climate, soil type and farming practices, such as cropping system, fertilization, and irrigation scheme, were relatively similar. Eleven soil samples were taken from within a 100 m × 100 m plot in each field using a spatially explicit 'L-shaped' sampling design: one sample in the centre and five samples along each vertical direction (1, 6, 16, 36

and 76 m from the centre; Figure 1a). At each sampling point, five soil cores (2.5 cm in diameter) in the upper 15 cm of soil were taken and mixed thoroughly, and any visible living plant material (e.g., roots) was manually removed from the composite soil sample. The soil was transported to the laboratory on dry ice. Subsamples (50 g) were immediately collected in sterile conical tubes, capped and then placed at −80°C for genetic analysis. Other subsamples were stored at 4°C for measuring the soil geochemical variables. Detailed field information is shown in Supporting Information Table S1.
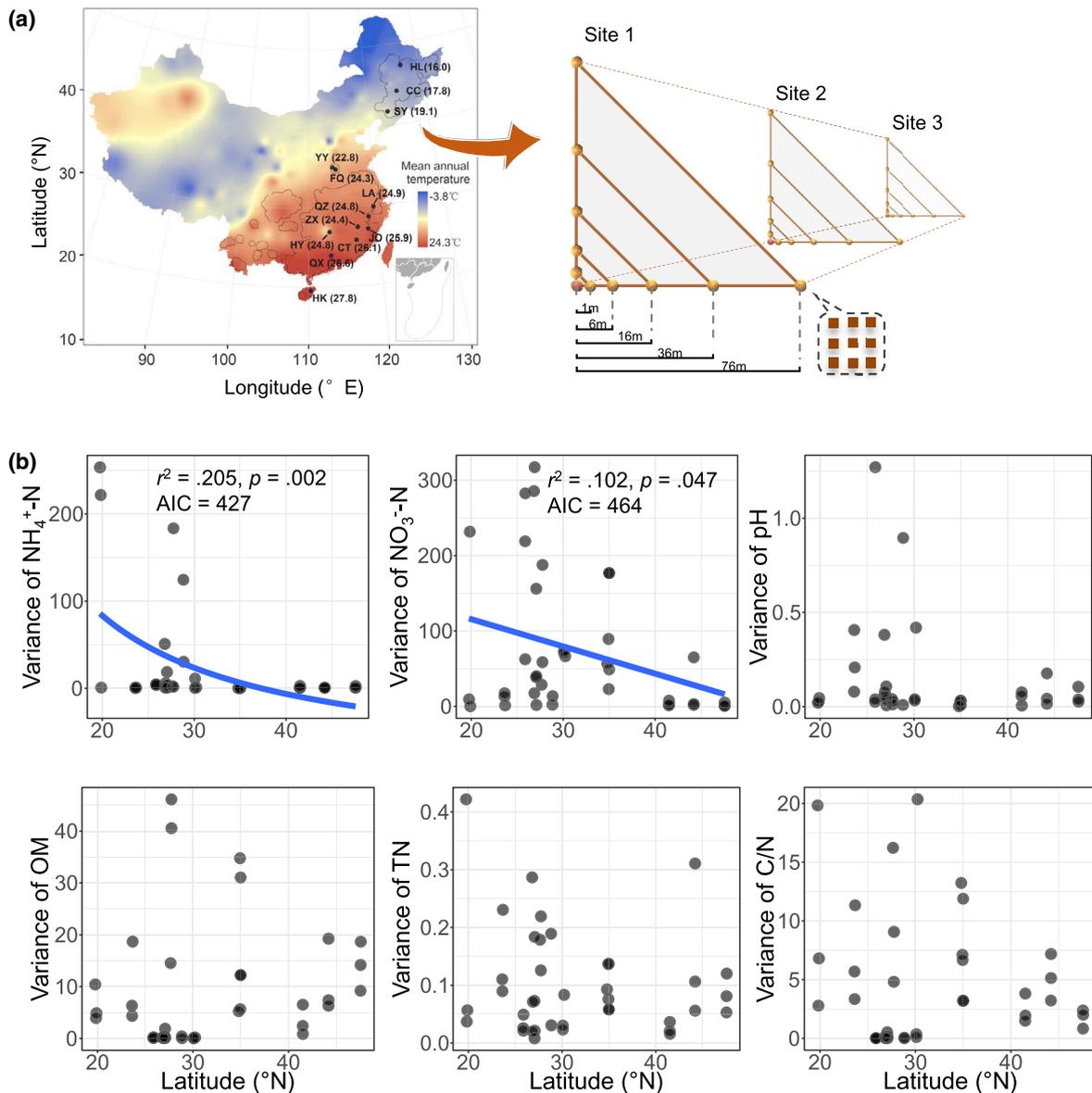
FIGURE 1 Geographic pattern of soil heterogeneity in paddy soils spanning a wide latitudinal gradient in China. (a) Sampling strategy with a nested design. Samples were taken from 39 paddy soil sites located in 13 regions of China. Number in parentheses represents mean temperature during the growing season of rice plants (°C) in sampling region. At each site, 11 nested samples were collected at distances of 1, 6, 16, 36 and 76 m. (b) The latitudinal patterns of soil heterogeneity, calculated using the variance of each individual soil variable grouped by site. Linear, exponential and inverse models were used to estimate the relationships between latitude and soil heterogeneity indices, and the best-fit models with low Akaike's information criterion (AIC) scores and high r^2 values are presented. CC = Changchun; CT = Changting; FQ = Fengqiu; HK = Haikou; HL = Hailun; HY = Hengyang; JO = Jian'ou; LA = Lin'an; OM = organic matter; QX = Qingxin; QZ = Quzhou; SY = Shenyang; TN = total nitrogen; YY = Yuanyang; ZX = Zixi [Colour figure can be viewed at wileyonlinelibrary.com]

The soil geochemical variables were measured as follows. Soil pH was determined with a glass electrode in a water : soil ratio of 2.5:1 (v/w). Total nitrogen (TN), nitrate nitrogen (NO_3^--N) and ammonium nitrogen (NH_4^+-N) were measured by the Kjeldahl method (Bremner, 1960). Organic matter (OM) was measured by the dichromate oxidation method (Allison, 1965). The soil texture was determined by laser diffraction particle size analysis (Beckman Coulter Inc., Brea, CA). In general, soil geochemical attributes varied greatly among the sites (Supporting Information Table S1). For example, soil pH varied from 3.56 to 8.65 and OM ranged from 2.21 to 71.26 g/kg throughout the paddy fields. We calculated soil heterogeneity using the variance of each individual soil variable within a site. The variances of soil NH_4^+-N and NO_3^--N decreased significantly with elevated latitudes, while soil pH, OM, TN and C/N were relatively homogenous among sampling sites (Figure 1b).

2.2 | Gene amplicon sequencing

Microbial genomic DNA was extracted from 2 g of well-mixed soil from each sample by combining freeze-grinding and sodium dodecyl sulphate for cell lysis and purification by agarose gel electrophoresis, followed by phenol–chloroform–butanol extraction as previously described (Zhou et al., 1996). The purified DNA was qualified and quantified with agarose gel electrophoresis, an ND-1000 spectrophotometer (NanoDrop Inc., Wilmington, DE) and Quant-iT™ PicoGreen ® dsDNA Reagent and Kits (Invitrogen, Carlsbad, CA). The primers 515F (5′-GTGCCAGCMGCCGCGG-3′) and 806R (5′-GGACTACHVGGGTWTCTA-AT-3′) for the bacterial 16S V4 region (Caporaso et al., 2012) and the primers 1106F (5′-TTW AGT CAG GCA ACG AGC-3′) and 1378R (5′-TGT GCA GGG AGC AGG GAC-3′), designed for archaea (Dubey et al., 2014), were selected. Both the forward and reverse primers were tagged with adapter, pad and linker sequences. In addition, barcode sequences (12-mer) were added to the reverse primers to allow the pooling of multiple samples in one run of MiSeq sequencing. All primers were synthesized by Invitrogen (Carlsbad, CA). Polymerase chain reaction (PCR) amplification was performed in triplicate using a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA) in a total volume of 25 µl containing 2.5 µl of 10 × PCR buffer II and 0.5 units of AccuPrime Taq DNA Polymerase High Fidelity (Invitrogen, Carlsbad, CA), 0.4 µM of each primer and 10 ng template DNA. To target bacterial and archaeal 16S ribosomal RNA (rRNA) genes, the first step of PCR was carried out using primers without the barcode and cycling conditions as follows: initial denaturation at 94°C for 1 min; 10 cycles at 94°C for 20 s, 53°C for 25 s and 68°C for 45 s; and a final extension at 68°C for 10 min. The PCR products from three replicates were combined and purified using an Agencourt AMPure XP kit (Beckman Coulter, Brea, CA) following the manufacturer's instructions and eluted in 50 µl of water. We used the purified PCR product (15 µl) as a template for the second step of PCR amplification with barcoded primers in three technical replicates under the same cycling conditions as the first step. The PCR products from the second step were examined by electrophoresis on a 1% agarose gel. The amplification products of three technical replicates were then combined and quantified by PicoGreen using a FLUOstar Optima (BMG Labtech, Jena, Germany). Equal amounts of the PCR products were pooled from different samples, purified with a Qiagen Gel Extraction Kit (Qiagen Sciences, Germantown, MD) following the manufacturer's instructions and re-quantified by PicoGreen. According to the MiSeqTM Reagent Kit Preparation Guide (Illumina, San Diego, CA), the purified mixture was diluted and denatured to obtain an 8 pM sample DNA library and mixed with an equal volume of 8 pM PhiX (Illumina, San Diego, CA, USA). Finally, 600 µl of the mixed library was loaded with read 1, read 2 and index sequencing primers (Caporaso et al., 2012) from a 300-cycle (2 × 150 paired-end) kit and run on a MiSeq at the Institute for Environmental Genomics of the University of Oklahoma.

After each sequence was assigned to its sample according to its barcode, the sequences were trimmed based on quality scores using BTRIM (Kong, 2011), and the paired-end reads were merged into longer reads by FLASH (Magoč & Salzberg, 2011). To test the trimming strategies, different sizes of trimming windows and cut-offs were used. Unqualified sequences were removed if they were too short or contained ambiguous residues. Chimeric sequences were discarded based on prediction by UPARSE (Edgar, 2013). Operational taxonomic units (OTUs) were clustered at the 97% similarity level. Final OTUs were generated based on the clustering results, and taxonomic annotations were assigned to each OTU's representative sequence by Ribosomal database project's (RDP's) 16S Classifier (Wang et al., 2007). Finally, 5,326 and 70,145 different OTUs were obtained for archaea and bacteria, respectively.

2.3 | GeoChip analysis of microbial functional genes

GeoChip 5.0 (Tu et al., 2014) was used to target the soil microbial functional genes. An aliquot of DNA (800 ng) from each sample was directly labelled with the fluorescent dye Cyanine 3 (GE Healthcare, CA), purified, resuspended in 27.5 µl of DNase/RNase-free distilled water and then mixed completely with 42 µl of a hybridization solution containing 1 × comparative genomic hybridization (CGH) blocking agent, 1 × Hi-RPM hybridization buffer, 10 pM universal standard DNA (Liang et al., 2010), 0.05 µg/µl Cot-1 DNA and 10% formamide (final concentrations). Then, the solution was denatured at 95°C for 3 min, incubated at 37°C for 30 min, and then hybridized with GeoChip 5.0 (manufactured by Agilent Technologies Inc., Santa Clara, CA). GeoChip hybridization was conducted at 67°C in an Agilent hybridization oven for 24 hr. After hybridization, the slides were washed using Agilent washing buffers at room temperature. Then, the arrays were scanned at 633 nm with a laser power of 100% and a photomultiplier tube gain of 75% with a NimbleGen MS 200 microarray scanner (Roche NimbleGen, Inc., Madison, WI). The image data were extracted using the Agilent FEATURE EXTRACTION program. The microarray data were preprocessed with the Microarray Data Manager system at the Institute

for Environmental Genomics (IEG) website (http://ieg.ou.edu/micro array), which was previously described (Liang et al., 2015). Spots with signal-to-noise ratios lower than 2.0 were removed before statistical analysis. Finally, 123,804 functional genes involved in C/N/P/S cycling were detected by GeoChip.

2.4 | Microbial β-diversity and other statistical analyses

The taxa–area relationship (TAR), the general increase of species richness with area, is the most commonly used way to assess spatial scaling of biodiversity (Arrhenius, 1921). Here, the species spatial turnover based on TARs was used as an index of microbial β-diversity and calculated separately within each paddy field. Both the power-law and semi-log TARs were estimated in our study. As the power-law TARs performed better than the semi-log models with lower Akaike's information criterion (AIC) and higher r^2 for the majority of the sites (Supporting Information Table S2), we calculated the species spatial turnover as the exponent of the power-law form of TARs ($S = cA^z$). Since a spatially explicit 'L-shaped' sampling scheme was used to collect the soil samples, five nested triangle areas were obtained for the microbial spatial pattern analysis in each paddy field. The exponent z, a measure of species spatial turnover, was estimated by linear regression through converting TARs by logarithmic transformation:

$$\ln S = \ln c + z \ln A \tag{1}$$

where S is the observed gene or taxa richness, A is the area in the nested design (0.5, 18, 128, 648 and 2,888 m^2), $\ln c$ is the intercept in log-log space, and the taxa–area exponent, z, is a measure of species spatial turnover (hereafter β_z).

For comparison, to assess the robustness of latitudinal patterns of soil microbial β-diversity, we also calculated the β-diversity of soil microbial communities and functional genes based on the Sørensen dissimilarity index (β_{sor}). The β_{sor} can be partitioned into species turnover (β_{sim}), which indicates species replacement, and nestedness (β_{nes}), which shows the species loss or gain (Baselga, 2010). These two β-diversity components often demonstrate complementarity, thus reflecting different elements of β-diversity (Hill et al., 2017). The detailed calculation methods of β_{sor} and the two components are provided in Supporting Information (Methods). The calculation of β-diversity indices was applied to all functional genes and the bacterial and archaeal communities, as well as to the phylogenetic groups at the phylum or class level.

The significance of differences in β-diversity among the soil microbial communities and functional genes or their subgroups was tested using Duncan's multiple range tests at $p < .05$ after one-way analysis of variance (ANOVA). Pearson correlations between β-diversity and environmental conditions and all the linear and nonlinear regressions, with β-diversity components as dependent variables and geoclimate or soil heterogeneity as independent variables, were

analysed in R 3.5.1 (R Core Team, 2018). Here, the geoclimatic factors included mean temperature and precipitation during the growing season of rice plants (Temp and PGS). For the linear and nonlinear regressions, the goodness of fit was assessed using AIC and r^2 values. Variance partitioning analysis was used to determine the contribution of temperature and soil heterogeneity and their interactive effects to microbial β-diversity. We conducted the variance partitioning analysis using standard methods based on the results of multiple regressions (Legendre & Legendre, 1998).

3 | RESULTS

3.1 | Latitudinal patterns of soil microbial β-diversity

Significant TARs were observed for both soil microbial communities and functional genes at 39 sites ($p < .05$; Supporting Information Figure S1, Table S3). The exponent of the power-law form of TARs (that is, β_z) varied between different groups (Figure 2a), with an average of .017 ± .010 for the microbial functional genes ($r^2 = .679$–.989), .056 ± .021 for the archaeal community ($r^2 = .862$–.999) and .070 ± .008 for the bacterial community ($r^2 = .964$–.999). Microbial functional genes showed the lowest β_z values ($p < .05$), followed by the archaeal community, and the soil bacterial community showed the highest β_z values ($p < .05$). The β_z values also showed considerable variation within each group, with the highest being Woesearchaeota of the archaeal community, Bacteroidetes and Firmicutes of the bacterial community, and the functional genes involved in nitrification.

To discern potential latitudinal patterns of microbial β-diversity, we used linear, exponential and inverse models to estimate the relationships between latitude and β_z (Table 1). The best-fit models, with low AIC scores and high r^2 values, are presented in Figure 2b. For both soil microbial communities and functional genes, the β_z decreased significantly with latitude; the r^2 values were .384 ($p < .001$, AIC = −264), .160 ($p = .029$, AIC = −189) and .152 ($p = .017$, AIC = −263) for functional genes (inverse model), archaea (linear model) and bacteria (linear model), respectively. β-diversity of taxonomic and functional groups decreased with increasing latitude, with the steepest slopes exhibited by Woesearchaeota among the archaeal community, Bacteroidetes among the bacterial community, and the functional genes involved in methane production (Supporting Information Figure S2).

For comparison, to assess the robustness of latitudinal patterns of soil microbial β-diversity, we also calculated the β-diversity of soil microbial communities and functional genes based on the Sørensen dissimilarity index (β_{sor}). Consistent with the results of β_z, the β_{sor} of microbial functional genes also showed the lowest values ($p < .05$), followed by the archaeal community, and the soil bacterial community showed the highest β_{sor} values ($p < .05$) (Supporting Information Figure S3). For both soil microbial communities and functional genes, the β_{sor} decreased significantly with latitudes (Supporting Information Figure S4). Further details are provided in Supporting Information (Results).

(a)

(b)
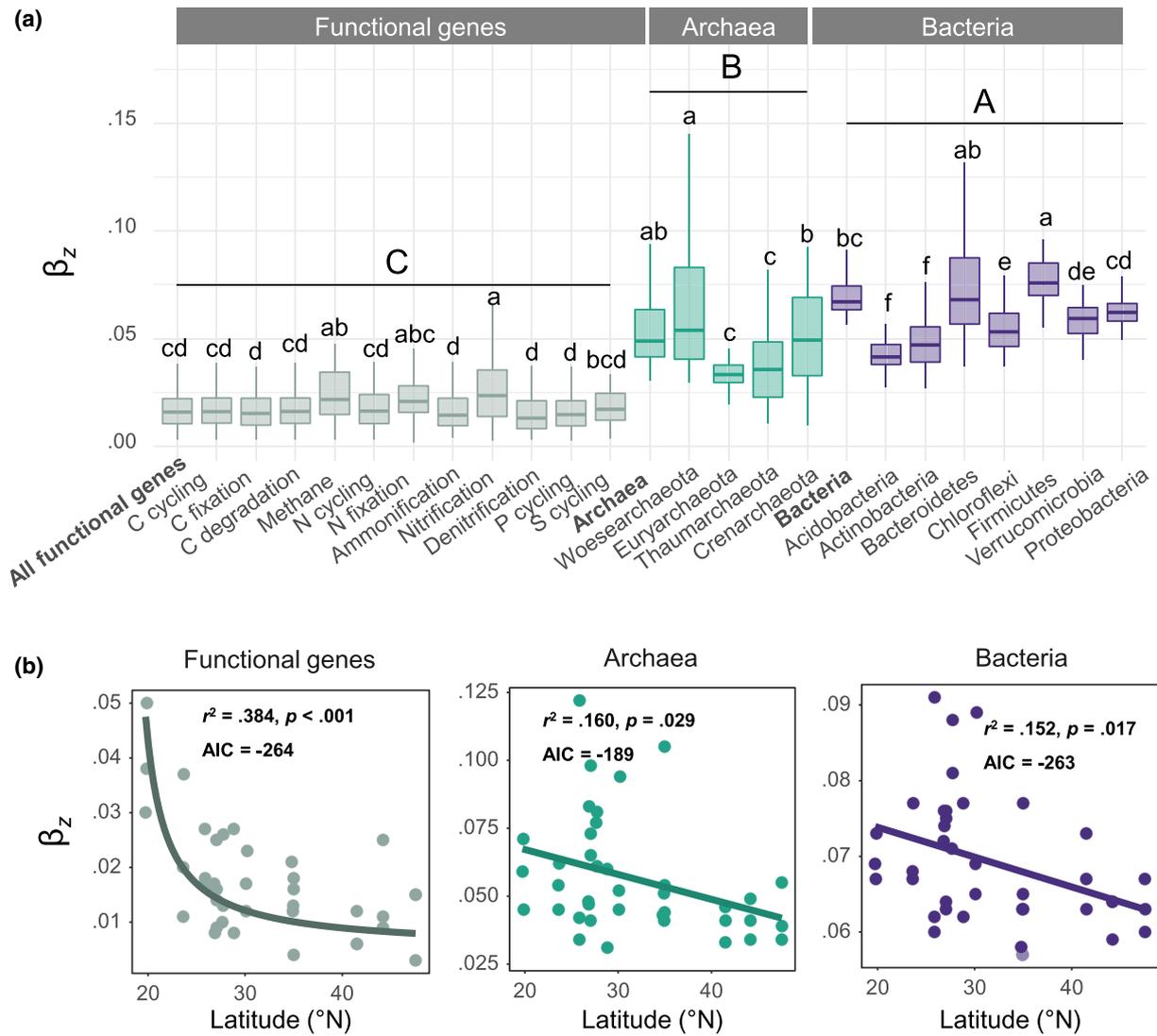
FIGURE 2 Geographic pattern of β-diversity of functional genes, archaea, and bacteria in China's paddy soils. (a) The microbial β-diversity based on the exponent of the power-law form of taxa–area relationships (TARs; β_z) for different taxonomic groups and subgroups of functional genes. Bold text on the x axis indicate all functional genes and the bacterial and archaeal communities, others indicate different taxonomic groups and subgroups of functional genes. Upper-case letters indicate significant differences (Duncan's multiple-range test at $p < .05$) between the functional genes, archaea, and bacteria; lower-case letters indicate significant differences between subgroups. (b) The latitudinal patterns of microbial β-diversity. Linear, exponential and inverse models were used to estimate the relationships between latitude and β-diversity, and the best-fit models with low Akaike's information criterion (AIC) scores and high r^2 values are presented [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Drivers of the β-diversity of soil microbes

We further examined the relationships between the β-diversity and environmental factors, including geoclimate and soil geochemical heterogeneity. Pearson correlation analysis indicated that temperature during the growing season of rice plants was significantly and positively correlated with the β_z of functional genes ($R = .498$, $p = .001$, AIC = −255) and of the archaeal community ($R = .339$, $p = .034$, AIC = −189) (Table 1). Soil heterogeneity variables, specifically the variances in soil pH, NH_4^+-N and NO_3^--N, were also significantly and positively correlated with the β_z of functional genes, archaea, and bacteria. Site-level variation in soil pH, widely considered to be one of the most important factors influencing soil microbial diversity, failed to predict

the β_z of functional genes and archaea. The potential important role of temperature in affecting the β_z of soil functional genes, archaea, and bacteria was also supported by the results inferred from variation partitioning analysis (Table 2), as temperature (12.10%–16.32%) contributed more than soil heterogeneity (4.08%–9.90%) to the variations in microbial β-diversity. Note that a substantial amount of the variation in microbial β-diversity (74.20%–76.56%) could not be explained by the environmental factors measured.

    Linear, exponential and inverse models were used to fit the best models between temperature during the growing season of rice plants and the β_z values (Supporting Information Table S4). The models with low AIC scores and high r^2 values are presented in Figure 3. For both soil microbial communities and functional genes, β_z increased

TABLE 1 Pearson correlation between β-diversity (β_z) of the soil functional genes and microbial communities and environmental conditions

| Environmental conditions	Functional genes			Archaea			Bacteria		
	R	p	AIC	R	p	AIC	R	p	AIC
Temperature	**.498**	**.001**	**−255**	**.339**	**.034**	**−189**	.308	.056	−261
Precipitation	**.597**	**<.001**	**−262**	.186	.257	−185	**.362**	**.024**	**−262**
Soil heterogeneity									
pH	−.026	.832	−244	.074	.052	−188	**.119**	**.018**	**−263**
OM	−.027	.916	−244	−.025	.792	−184	−.005	.370	−258
NH_4^+-N	**.179**	**.004**	**−253**	−.004	.358	−185	−.011	.452	−257
NO_3^--N	−.027	.994	−244	**.190**	**.003**	**−193**	.037	.126	−259
TN	.011	.238	−246	−.017	.544	−184	−.016	.524	−257
C/N	.050	.091	−248	−.009	.418	−185	−.011	.447	−257

Note.: Temperature and precipitation refer to the mean temperature and accumulated precipitation during the growing season of rice plants, respectively. The heterogeneity of soil was indicated by the variance of each soil variable (pH, OM, NH_4^+-N, NO_3^--N, TN and C/N) within a site. $p < .05$ indicates significant correlations and is listed in bold font.

Abbreviations: OM, organic matter; TN, total nitrogen; AIC, Akaike's information criterion.

TABLE 2 Variation partitioning analysis of microbial β-diversity (β_z) explained by mean temperature during the growing season of rice plants and soil heterogeneity

	Temperature (%)	Soil heterogeneity (%)	Shared (%)	Unexplained (%)
Functional genes	12.38	4.08	6.98	76.56
Archaea	16.32	4.65	4.83	74.20
Bacteria	12.10	9.90	2.36	75.64

Note: Temperature refers to the mean temperature during the growing season of rice plants.
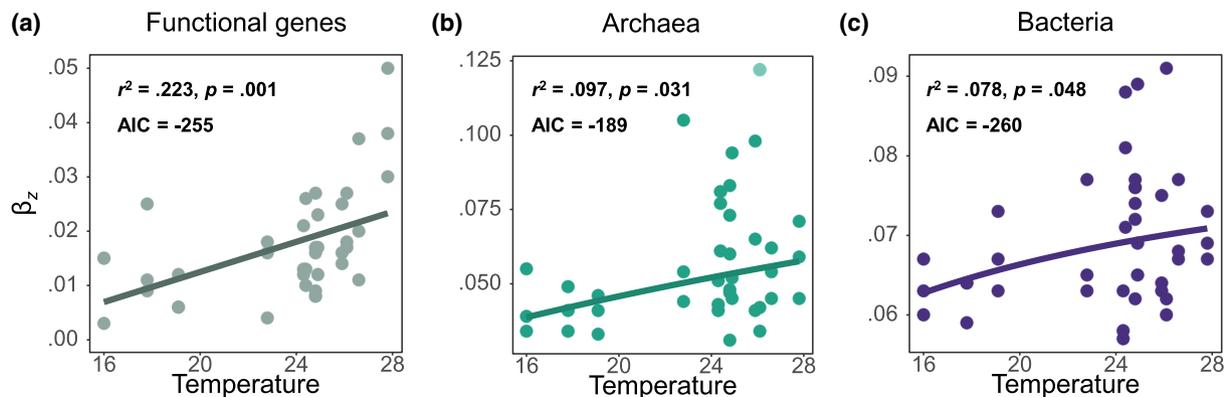
FIGURE 3 The associations between temperature and β-diversity of functional genes, archaea, and bacteria in paddy soils. Temperature refers to the mean temperature during the growing season of rice plants. Linear, exponential and inverse models were used to estimate the relationships between environmental temperature and β-diversity, and the best-fit models with low Akaike's information criterion (AIC) scores and high r^2 values are presented [Colour figure can be viewed at wileyonlinelibrary.com]

significantly with temperature; the r^2 values were .223 ($p = .001$, AIC = −255), .097 ($p = .031$, AIC = −189) and .078 ($p = .048$, AIC = −260) for functional genes (linear model), archaea (inverse model) and bacteria (inverse model), respectively. The significant relationships between microbial β-diversity and temperature were further supported by another β-diversity index, β_{sor} (Supporting Information Tables S4–S6, Figure S5). Collectively, our results indicate that temperature is more important than soil heterogeneity in predicting the β-diversity of soil microbes in paddy fields across China.

4 | DISCUSSION

Microbial β-diversity varied significantly among soil microbial communities and functional genes at a continental scale, with higher spatial scaling rates of bacteria (.070 ± .008) and archaea (.056 ± .021) than functional genes (.017 ± .010). This indicates faster taxonomic turnover of soil bacteria and archaea than functional genes in response to disturbances and global cultivated land degradation (Thomas et al., 2004). Significantly lower microbial β-diversity of functional genes may be due

to the following reasons: (a) many functional genes are more vulnerable to horizontal gene transfer (conjugation, transduction, and natural transformation) compared to phylogenetic markers such as 16S rRNA genes (Rensing et al., 2002; Thomas & Nielsen, 2005). Thus, more homogeneous functional gene patterns could be expected at local scales with lower β_z values compared to species/taxa derived from phylogenetic marker gene sequencing; (b) functional genes are always more conserved and hence less variable compared to microbial taxa due to functional redundancy within the ecosystem (Colin et al., 2017); (c) the methodology might also have influences. Microarray-based hybridization using GeoChip might underestimate the β_z values if the probes on the arrays miss some genes in the given microbial community (Zhou et al., 2008). If these genes exhibit high spatial variability, the estimated β_z values of functional genes could be underestimated.

Latitudinal patterns of β-diversity have been documented in macro-organisms such as North American mammals (Rodríguez & Arita, 2004), vascular plants (Qian & Ricklefs, 2007), and many other groups summarized in meta-analyses (Drakare et al., 2006; Soininen et al., 2018; Soininen, McDonald, et al., 2007). In this study, microbial β-diversity for both soil microbial taxonomic and functional groups decreased with increasing latitude over a wide spatial scale, from 19.75° N to 47.58° N, suggesting a more heterogeneous spatial pattern of soil microbes at low latitudes in paddy soils. Tu et al. (2016) found a similar trend for forest soil diazotrophic communities across North America. There are most likely two possible explanations for this latitudinal pattern of β-diversity. First, the latitudinal β-diversity gradient may be partially due to the direct effects of temperature, as temperature had more explanatory power than any of the geochemical properties for the changes in microbial β-diversity in this study. On the one hand, higher temperatures will enhance the stochasticity in community assemblies (Ren et al., 2017), which may increase the variation in microbial communities under similar or even identical conditions, causing higher β-diversity. On the other hand, regions that experience colder extremes may impose harsher environmental filtering on species (Silva et al., 2015), which leads to more homogeneous selection for cold-tolerant taxa at higher latitudes, reducing β-diversity. Second, the latitudinal β-diversity gradient may be related to soil heterogeneity (Ranjard et al., 2013). As environmental conditions across landscapes differ, species sorting should result in local communities that differ in species composition (Hammill et al., 2018). The relatively small contributions of soil heterogeneity attributes to microbial β-diversity compared to those of temperature in our study were possibly due to the less heterogeneous habitat that paddy soil ecosystems provided for microbial taxonomic groups and functional genes because of the long-term alternation of wet and dry farming practices. In general, higher temperatures in low-latitude regions caused higher metabolic rates and more stochastic assembly, resulting in greater community dissimilarity (Liang et al., 2015; Zhou et al., 2016).

In this study, we observed positive associations between temperature and β-diversity of both taxonomic and functional groups in paddy soils. These findings, together with previous studies (Tu et al., 2016; Zhou et al., 2016) that demonstrated that the biodiversity of forest soil microbial groups was strongly and positively affected by environmental temperature, suggest that both local species richness (α-diversity) and community dissimilarity (β-diversity) increase with environmental temperature. Compared to the relatively large amount of variation in microbial α-diversity explained by temperature ($r^2 = .40–.82$; Wang et al., 2009; Zhou et al., 2016), temperature explained less variation in microbial β-diversity in our study ($r^2 = .08–.30$). This result indicated that the mechanisms underlying large-scale patterns of β-diversity are likely to be more complicated than those for α-diversity. A previous study of woody plants sampled along latitudinal and elevational gradients indicated that the spatial pattern of β-diversity is intrinsically linked to α- and γ-diversity (Kraft et al., 2011). Thus, any process that changes α-diversity will alter β-diversity when γ-diversity remains unchanged. Myers et al. (2015) further suggested that the alterations in β-diversity are partly due to changes in community size or species abundance distribution (α-diversity) through random sampling effects.

By examining the spatial patterns of soil microbial β-diversity over a broad spatial range in paddy fields, we found that the β-diversity of microbial taxonomic and functional groups significantly declined with increasing latitude. Temperature possibly played a more important role in mediating microbial β-diversity than soil heterogeneity, despite the considerable unexplained variation of microbial β-diversity. Our findings have important implications for predicting ecological consequences of biodiversity under future climate change scenarios. As microbial β-diversity was positively related to environmental temperature, climate warming may increase the variability in communities and intensify the vulnerability of biodiversity when the habitat area is reduced.

AUTHOR CONTRIBUTIONS

All authors contributed intellectual input and assistance to this study and manuscript. B.S. and Y.L. developed the original framework. Y.L., X.X., N.Z., H.N. and Y.Y. contributed reagents and data analysis. X.X., Y.L. and J.Z. wrote the paper.

DATA AVAILABILITY STATEMENT

Raw sequence data for 16S rRNA gene amplicons were deposited in the National Center for Biotechnology Information (NCBI) BioProject Accession No. PRJNA562601. Raw sequence data for Archaea were deposited in the Genome Sequence Archive (publicly accessible at http://bigd.big.ac.cn/gsa) under accession number CRA001673. The GeoChip data are available in the repository Figshare, https://doi.org/10.6084/m9.figshare.9746303. All the tables in the main text and Supporting Information are available as flat files (.csv) in Figshare under the project 'A latitudinal gradient of microbial β-diversity in continental

paddy soils', https://figshare.com/projects/A_latitudinal_gradient_of_microbial_-diversity_in_continental_paddy_soils/84998

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.