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ORIGINAL ARTICLE

Long-term soil transplant simulating climate change with latitude significantly alters microbial temporal turnover

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To understand soil microbial community stability and temporal turnover in response to climate change, a long-term soil transplant experiment was conducted in three agricultural experiment stations over large transects from a warm temperate zone (Fengqiu station in central China) to a subtropical zone (Yingtan station in southern China) and a cold temperate zone (Hailun station in northern China). Annual soil samples were collected from these three stations from 2005 to 2011, and microbial communities were analyzed by sequencing microbial 16S ribosomal RNA gene amplicons using Illumina MiSeq technology. Our results revealed a distinctly differential pattern of microbial communities in both northward and southward transplantations, along with an increase in microbial richness with climate cooling and a corresponding decrease with climate warming. The microbial succession rate was estimated by the slope (*w* value) of linear regression of a log-transformed microbial community similarity with time (time–decay relationship). Compared with the low turnover rate of microbial communities *in situ* ($w = 0.046$, $P < 0.001$), the succession rate at the community level was significantly higher in the northward transplant ($w = 0.058$, $P < 0.001$) and highest in the southward transplant ($w = 0.094$, $P < 0.001$). Climate warming lead to a faster succession rate of microbial communities as well as lower species richness and compositional changes compared *with in situ* and climate cooling, which may be related to the high metabolic rates and intense competition under higher temperature. This study provides new insights into the impacts of climate change on the fundamental temporal scaling of soil microbial communities and microbial phylogenetic biodiversity.
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Introduction

One of the great scientific challenges in 21st century ecology is to understand the response, succession and stability of biological communities to potential threats from anthropogenic disturbances, such as climate change (Thomas *et al.*, 2004; Bellard *et al.*, 2012; Fussmann *et al.*, 2014). Given the fundamental role of microbial communities in biogeochemical cycling, their responses to climate change may lead to ecosystem structure repercussions and feedback to the climate system (Wardle *et al.*, 2004; Bardgett *et al.*, 2008; Castro *et al.*, 2010; Singh *et al.*, 2010; Gutknecht *et al.*, 2012). Previous studies indicated that temperature is an important determinant of soil microbial composition (Castro *et al.*, 2010; Vanhala *et al.*, 2011; Zhou *et al.*, 2012), diversity (Pold and DeAngelis, 2013) and ecological functions, such as soil respiration (Schindlbacher *et al.*, 2011; Zhao *et al.*, 2014), organic matter decomposition (Conant *et al.*, 2011) and nitrification (Long *et al.*, 2012; Zhao *et al.*, 2014). However, information is still lacking on the relationship between microbial community succession and multiple environmental changes resulting from climate change.

The transplantation of soils between different geoclimatic regions provides a powerful approach to test the responses of microbial communities to climate change scenarios that simultaneously alter

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multiple factors (Bottomley *et al.* 2006; Waldrop and Firestone, 2006; St John *et al.*, 2011; Vanhala *et al.*, 2011; Zumsteg *et al.*, 2013; Sun *et al.*, 2014; Zhao *et al.*, 2014). In general, an increase in temperature and precipitation is expected in southward transplantation (climate warming), whereas a decrease in these parameters is expected in northward transplantation (climate cooling) at northern latitudes along the coastal areas. The soils transplanted to the north/south acquire colder/warmer climate features. Thus, we were able to analyze the climatic effects on the sensitivity of microbial communities. The climatic effect on microbial communities simulated by soil transplantation has been reported, but is still under debate. For example, soils transplanted from north to south resulted in a loss of microbial biomass and changes in the microbial community structure and functions in response to the warmer climate, which indicates that exposure to a temperature increase of 4.5 °C for 2 years was sufficient to change the soil biology (Vanhala *et al.*, 2011). Waldrop and Firestone (2006) found that microbial biomass, composition, enzyme activities and respiration decreased when soils under the oak canopies were transplanted to an open grassland environment with higher maximum temperature and lower soil water content. Bottomley *et al.* (2006) also reported that the fungal and bacterial community structures of forest soil changed significantly after transfer from forests to meadows after 2 years of incubation. Similarly, our previous studies indicated that transplanting either black soil to warmer regions (Zhao *et al.*, 2014) or red soil to colder regions (Liu *et al.*, 2014) caused significant changes in the microbial functional gene diversity and patterns. By contrast, Lazzaro *et al.* (2011) reciprocally transplanted soil samples from two different unvegetated glacier forefields (calcareous and siliceous) and found that bacterial communities were more significantly affected by seasons than by the transplantation after 15 months of incubation. Another study indicated that the bacterial community composition in grassland soil (as assessed by the phospholipid-derived fatty acid guilds) appeared to be resistant when soils were transplanted to a conifer ecosystem (Balser and Firestone, 2005). The contrasting results require further studies to examine the effects of transplantation on the microbial community structure and the mechanisms involved.

Species temporal turnover is defined as the number of species eliminated and replaced per unit time (MacArthur and Wilson, 1967; Magurran, 2004; Hatosy *et al.*, 2013). Changes in species number can be described using the time–decay relationship, which is a common model to describe the changes in community similarity over time (Nekola and White, 1999). Rates of temporal turnover vary in relation to ecosystem types (Korhonen *et al.*, 2010), local environmental factors (Werner *et al.*, 2007), disturbances (Svensson *et al.*, 2009) and temporal scales (Hatosy *et al.*, 2013). Temporal turnover has been well documented in plant and animal communities, but information on microbial temporal turnover is insufficient. Only a few studies, which were primarily based on engineered systems for relatively short periods (from minutes to months), used the time–decay relationship to test whether theoretical predictions of community assembly and dynamics are applicable to microbial communities (Oliver *et al.*, 2012; Shade *et al.*, 2013). Recently, Hatosy *et al.* (2013) studied bacterial temporal beta-diversity across different temporal scales in three marine microbial communities and found that turnover at different temporal scales appeared to be driven by different factors. The variation of soil microbial temporal turnover with climate change and the underlying mechanisms remain unknown.

To understand soil microbial community stability and temporal turnover in response to climate warming and cooling, a soil transplantation experiment was conducted in three long-standing agricultural stations located over large transects from the Fengqiu station in central China (warm temperate zone) to the Yingtan station in southern China (middle subtropical zone) and the Hailun station in northern China (cold temperate zone). Soil samples were collected from the three stations annually from 2005 to 2011 to test the following hypotheses: (i) soil transplantations will significantly alter soil microbial temporal turnover and climate warming will lead to higher microbial succession rates; (ii) different microbial groups will show differential sensitivities to temperature change perturbations; (iii) temperature is the most important factor that influences the fundamental temporal scaling of microbial biodiversity. The microbial communities were analyzed by sequencing microbial 16S ribosomal RNA (rRNA) gene amplicons with the Illumina MiSeq technology (San Diego, CA, USA). Our results revealed a distinctly different pattern of microbial communities in the northward and southward transplantations. Climate warming caused higher microbial temporal turnover and less stability, which may be attributed to high metabolic rates and intensive competition under higher temperatures.

Materials and methods

Study sites and sample collections

The long-term soil transplant experiments were conducted in agricultural experimental stations of the Chinese Academy of Sciences at three sites: the Hailun station (site N, 126° 38′ E and 47° 26′ N) in the Heilongjiang Province of northern China, the Fengqiu station (site M, 114° 24′ E and 35° 00′ N) in the Henan Province of central China and the Yingtan station (site S, 116° 55′ E and 28° 15′ N) in the Jiangxi Province of southern China. In October 2005, blocks with a size of 1.4 m in length × 1.2 m in width × 1.0 m in depth were established in each station. These blocks were surrounded by 20-cm brickwalls and

underlain with sand to isolate each from the surrounding environment. Soils from the central Fengqiu site, classified as Cambisol soil, were transported northward to the Hailun site and southward to the Yingtan site. Soil was excavated in five 0.2-m deep layers, with each layer sufficiently mixed and then repacked sequentially to maintain the soil stratification. At each site, triplicate soil blocks were established with maize cropping. Maize has been planted since 2006 at all three sites with regular fertilization of 150 kg hm^{-2} nitrogen, 75 kg hm^{-2} phosphorus and 60 kg hm^{-2} potassium in the forms of urea, $(NH_4)_2HPO_4$ and KCl, respectively. Basal fertilizer was applied before planting (half of nitrogen, all phosphorus and all potassium). The second half of nitrogen fertilizer was applied as the top dressing at large trumpet stage of maize growth. No irrigation was applied. Maize was sowed and harvested once a year. The soil samples with maize cropping from these three sites were designated as *in situ* (original Fengqiu site), northward to the Hailun site and southward to the Yingtan Site. This experiment belongs to an integrated project (The Soil Reciprocal Transplant Experiment, SRTE), which serves as a platform for a number of studies that evaluate climate and cropping effects on soil microbial diversity and its agro-ecosystem function (Sun *et al.*, 2013; Liu *et al.*, 2014; Zhao *et al.*, 2014). Triplicate soil samples from each station, one sample from each block, were collected annually in August to September from 2006 to 2011. In addition, samples of the original soil transported to each site were collected in 2005. Ten soil cores were composited from surface soil (0–20 cm) within each block and sealed in a polythene wrapper, then stored on ice and transported to the laboratory. Any visible living plant material (for example, roots) was manually removed from the composited soil in the lab. The soil was then divided into two subsamples and stored at either 4 °C for soil geochemical variable measurements or − 80 °C for microbial community analysis. Soil geochemical variables were measured as follows: pH was determined with a glass electrode in water-to-soil ratio of 2.5:1 (v/w). Total nitrogen, nitrate (NO_3^- – N) and ammonium nitrogen (NH_4^+ – N) were measured by the Kjeldahl method (Bremner, 1965). Total phosphorus and available phosphorus were extracted by sodium carbonate and sodium bicarbonate, respectively; both were determined by the molybdenum blue method (Olsen *et al.*, 1954). Total potassium and available potassium were determined by flame photometry after extraction with sodium hydroxide and ammonium acetate, respectively (Kanehiro and Sherman, 1965). Soil organic matter (SOM) was measured by the potassium dichromate oxidation method (Allison, 1965). Soil electrical conductivity was determined with a soil conductivity meter. Cation exchange capacity (CEC) was measured in an ammonium acetate solution at pH 7 (Chapman, 1965). Climate attributes, including the annual average temperature, rainfall and relative humidity were obtained from the meteorological observation database of the experimental stations. The above ground biomass and grain weight of maize were immediately measured after harvest.

Illumina sequencing analysis of 16S rRNA gene amplicons

Microbial genomic DNA was extracted from 5 g of well-mixed soil for each sample by combining freeze-grinding and sodium dodecyl sulfate for cell lysis, and purified by agarose gel electrophoresis, followed by phenol–chloroform–butanol extraction as previously described (Zhou *et al.*, 1996). The primers 515 F (5′-GTGCCAGCMGCCGCGG-3′) and 806 R (5′-GGACTACHVGGGTWTCTAAT-3′) targeting the V4 hypervariable regions of microbial 16S rRNA genes were selected (Caporaso *et al.*, 2012). The forward and reverse primers were tagged with adapter, pad and linker sequences. Each barcode sequence (12 mer) was added to the reverse primer for pooling of multiple samples in one run of MiSep sequencing. All primers were synthesized by Eurofins/MWG (Huntsville, AL, USA).

PCR amplification was performed in triplicate using a Gene Amp PCR-System 9700 (Applied Biosystems, Foster City, CA, USA) in a total volume of 25 μl, which contained 2.5 μl of 10 × PCR buffer II, and 0.5 unit of AccuPrime *Taq* DNA Polymerase High Fidelity (Invitrogen, Carlsbad, CA, USA), 0.4 μM of each primer and 10 ng of template DNA. Thermal cycling conditions were as follows: an initial denaturation at 94 °C for 1 min, followed by 25 cycles at 94 °C for 20 s, 53 °C for 25 s and 68 °C for 45 s, with a final extension at 68 °C for 10 min.

Following amplification, 2 μl of the PCR product was used for agarose gel (1%) detection. The triplicate PCR reactions for each sample preparation were combined and quantified with PicoGreen. From each sample, 200 ng of the PCR product was collected and pooled with other samples for one sequencing run. The pooled mixture was purified with a QIAquick Gel Extraction Kit (QIAGEN Sciences, Germantown, MD, USA) and re-quantified with PicoGreen.

According to the MiSeq Reagent Kit Preparation Guide (Illumina, San Diego, CA, USA), the purified mixture was diluted and denatured to obtain the 8 pM sample DNA library and mixed with an equal volume of 8 pM PhiX (Illumina). Finally, 600 μl of the mixture library was loaded with read 1, read 2 and the index sequencing primers (Caporaso *et al.*, 2012) on a 300-cycle (2 × 150 paired ends) kit and run on a MiSeq apparatus at the Institute for Environmental Genomics of the University of Oklahoma.

After assigning each sequence to its sample according to its barcode, allowing up to two mismatches, a total of 9 48 765 reads from both ends were obtained as a partitioned run for the total 63 samples. To increase reproducibility (Zhou *et al.*, 2011b),

deep sequencing was performed with these samples. These sequences were then trimmed using Btrim with threshold of quality scores higher than 20 over a 5 bp window size and a minimum length of 100 bp (Kong, 2011). Forward and reverse reads with at least a 50 bp overlap and $<5\%$ mismatches were joined using FLASH (Magoc and Salzberg, 2011). After removing the sequences with ambiguous bases (that is, N), the sequences with lengths between 245 and 258 bp were subjected to chimera removal by U-Chime (Edgar *et al.*, 2011) using GreenGenes core 16S reference sequences. Operational taxonomic units (OTUs) were clustered using the Uclust program at the 97% similarity level (Edgar, 2010). Final OTUs were generated based on the clustering results, and taxonomic annotations were assigned to each OTU's representative sequence by the RDP 16S Classifier (Wang *et al.*, 2007). Singletons were removed for downstream analyses. Samples were rarefied at 10, 947 sequences per sample. The above mentioned steps were performed through the Galaxy pipeline at the Institute for Environmental Genomics, University of Oklahoma (http://zhoulab5.rccc.ou.edu/).

Time–decay relationship and other statistical analyses
We used linear regression to examine the relationship between the temporal distance among samples and similarity in microbial composition. The Bray–Curtis distance was used as a taxon-based metric of differences in community composition. Arrhenius (log–log) plot was used for modeling the species–time relationship in the form: $\ln(S_s) = \text{constant} - w \ln(T)$, where S_s is the pairwise similarity in community composition, T is the time interval and w is a measure of the rate of species turnover across time. A one-sample *t*-test between the original slope and a mean of bootstrapped slopes by random pairing of the original set (permuted 999 times) was performed for testing the significance of w values (Horner-Devine *et al.*, 2004; Zhou *et al.*, 2008). The significance comparison of w values among different estimations was also achieved by bootstrapping (999 times), followed by a pairwise *t*-test.

The microbial distribution patterns of northward and southward transplants were determined by nonmetric multidimensional scaling (NMDS) (Kruskal, 1964). A dissimilarity test of the microbial community composition was performed using non-parametric multivariate statistical tests and analysis of similarities (Clarke, 1993). The Mantel and partial Mantel tests were used to calculate the correlations between environmental factors and the soil microbial community (Legendre and Legendre, 2012). BIO-ENV is an algorithm identifying the best subset of environmental variables such that the Euclidean distances of scaled environmental variables have the maximum (rank) correlation with community dissimilarities (Clarke and Ainsworth, 1993). Canonical correspondence analysis (CCA) and partial CCA (Legendre and Legendre, 2012) were also used to identify the effect of soil geochemical variables, plants and climate on the microbial community composition. All the above analyses were performed in R (version 3.0.2; http://www.r-project.org/) using the vegan (Oksanen *et al.*, 2013) and ecodist (Goslee and Urban, 2007) packages. A circular maximum likelihood phylogenetic tree was constructed based on the sequences representative for each OTU as determined by Uclust. The tree was generated with MEGA 5 (Tamura *et al.*, 2011) using a neighbor-joining method with a bootstrap value of 1000 displayed using iTOL (Letunic and Bork, 2011).

Results

Effect of transplants on plant and soil geochemical variables
The average annual temperature in the Fengqiu station (*in situ*) is 14.0 °C, which decreases to 2.2 °C in the Hailun station (northward transplantation) and increases to 18.3 °C in the Yingtan station (southward transplantation) (Supplementary Figure S1a). The average annual precipitation was similar between Fengqiu and Hailun, but twice as high in Yingtan (Supplementary Figure S1b). The above-ground maize biomass fluctuated in each year after soil transplantation (Supplementary Figure S2a), which might be attributed to variation of meteorological characteristics such as temperature, precipitation and so on. However, yield production (seed weight) significantly decreased in both northward and southward transplants as compared *with in situ* (Supplementary Figure S2b), thereby indicating the significant impact of climate cooling or warming on crop yields, especially for warming-induced lower productivity. A few soil geochemical attributes also fluctuated after transplantation, such as pH, CEC and available potassium in northward transplantation and pH, CEC, SOM, available potassium, NO_3^- in southward transplantation (Supplementary Table S1).

Overall pattern of microbial succession
Soil microbial communities in the three locations were analyzed annually from 2005 to 2011 by sequencing microbial 16S rRNA gene amplicons with Illumina MiSeq technology. Interestingly, the northward transplant showed increased microbial richness in terms of the number of different OTUs (30, 870 OTUs in total with an average of 5035 ± 313 OTUs) compared with that *in situ* (30, 109 OTUs in total with an average of 4804 ± 264 OTUs), with the highest increase during the fourth year (15.6%, $P<0.001$) (Supplementary Figure S3). By contrast, southward transplant showed a decrease in microbial richness (29, 343 OTUs in total with an average of 4671 ± 228 OTUs) (Supplementary Figure S3).

Further comparison of the microbial taxonomic composition at the phylum level showed that Proteobacteria was the dominant phylum present

in all three sites, followed by Acidobacteria (Supplementary Figure S4). However, the southward transplant showed a distinct change in microbial taxonomic composition, such that the relative abundances of Proteobacteria and Bacteroidetes had significantly decreased ($P<0.05$) since 2006, whereas those of Acidobacteria and Actinobacteria had significantly increased ($P<0.05$) since 2007 (Supplementary Figure S4).

The overall pattern of microbial succession in the long-term soil transplant experiment is visualized on the first two coordinates of the nonmetric multidimensional scaling ordination based on the Bray–Curtis dissimilarity (Figure 1a). As expected, the close clustering of samples in 2005 indicated similar origins for the soils that contained similar microbial composition. A clearly different pattern was observed among samples in the three sites starting from 2006. The samples became distinctly separate from each other with time. This observation was confirmed by analysis of similarities, which showed that the microbial community structures were significantly different in each location from 2006 to 2011 (Supplementary Table S2). We calculated the pairwise distances between microbial communities in each year based on the Bray–Curtis dissimilarity, and the results are shown in Figure 1b. Obviously, the variations continuously increased between *in situ* soil and the northward transplant ($r^2=0.58$, $P<0.05$). The correlations were even more significant between *in situ* soil and the southward transplant ($r^2=0.81$, $P<0.01$), and between the northward and southward transplants ($r^2=0.91$, $P<0.01$).

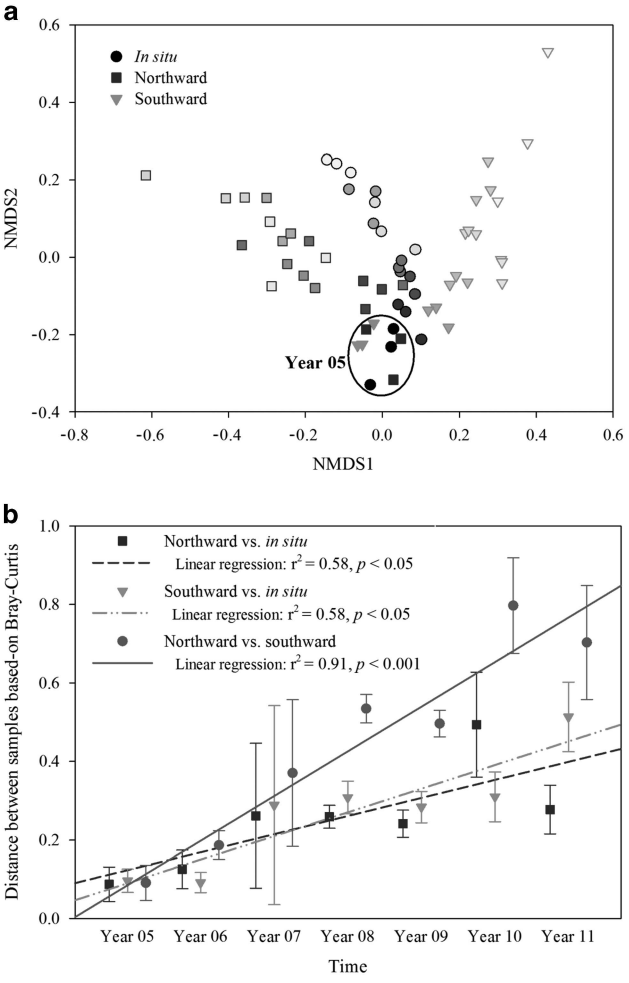

Figure 1 (**a**) Non-metric multidimensional scaling ordination based on Bray–Curtis distances showing the changes in microbial community composition with northward (square) and southward transplant (triangle) compared with microbial community in original Fengqiu station (circle). Color from deep to shallow represents the community succession from year 2005 to 2011. (**b**) Small differences among samples (based on Bray–Curtis dissimilarity) were linearly enlarged along as time elapsed. The lines denote the linear regression. Square symbols represent differences between northward and *in situ* samples; triangle symbols represent differences between southward and *in situ* samples; circle symbols represent differences northward and southward samples.

Changes in microbial temporal turnover with soil transplant

The slopes of microbial time–decay relationship were estimated by linear regression with log-transformed microbial community similarity (Figure 2). A significant time–decay relationship was observed for microbial communities *in situ*, with a low temporary turnover for the *in situ* samples ($w=0.046$, $P<0.001$) across 6 years of transplantation. Compared with the *in situ* soil, the slope was significantly steeper in the northward transplant ($w=0.058$, $P<0.001$), and even steeper in the southward transplant ($w=0.094$, $P<0.001$). Figure 3a shows the relationship between microbial temporal turnover and temperature. The northward transplant was accompanied by a larger change in temperature, that is, a decrease of 11.9 °C on the average, as compared with an increase of 4.3 °C for the southward transplant. However, climate warming significantly increased the microbial community temporal turnover in the southward transplant with higher fluctuation ($w=0.088\pm0.017$), as compared with the northward transplant ($w=0.051\pm0.013$) and *in situ* ($w=0.039\pm0.008$). To obtain general insights into the temporal change of microbial communities across different time periods, the temporal turnover of the microbial community was estimated yearly starting from 2005 (Figure 3b). The southward transplant showed a greater effect on microbial community temporal turnover than northward transplant most of the time.

The microbial time–decay relationships in taxonomic divisions were also estimated (Table 1). Considerable variations of w values were observed among different phyla. Both northward and southward transplants showed a significant increase in microbial temporal turnover at all phylum levels. The mean w values were 0.037 ± 0.023, 0.061 ± 0.027 and 0.112 ± 0.055 among different phyla of the *in situ* soil, northward transplant and southward transplant, respectively. The phyla Actinobacteria and Firmicutes

were found to be the most sensitive to either climate cooling or warming. Proteobacteria showed the least response to both northward and southward transplants. Interestingly, significant correlations were found between temporal turnover of all phyla and the taxonomic abundances ($P<0.05$) (Figure 3c). The turnovers of Proteobacteria, Bacteroidetes and Verrucomicrobia were negatively correlated with phylum abundance (r^2 of 0.18–0.40, $P<0.05$). By contrast, the turnovers of Acidobacteria, Actinobacteria, Firmicutes and Planctomycetes were positively correlated with phylum abundance (r^2 of 0.12–0.28, $P<0.05$).

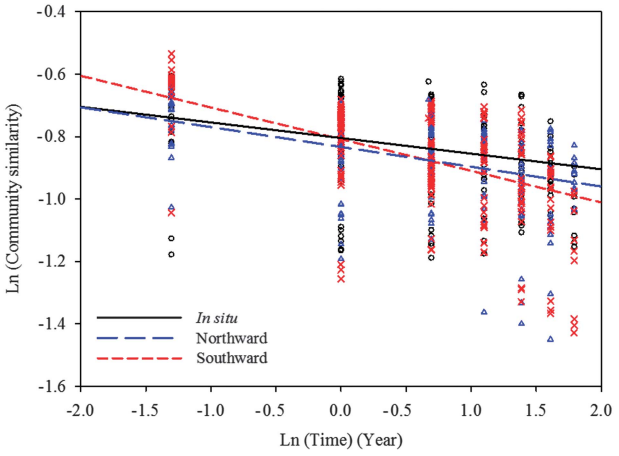

Figure 2 Time–decay curves for soil microbial communities. The slopes of all lines are significantly less than zero and significantly different for pairwise comparison.

Relative abundance of bacteria detected in situ and with soil transplant

A quite low number of microbial OTUs (78 OTUs belonging to nine phyla) were detected in all *in situ* samples and in soil transplants during the 6-year experiment. A phylogenetic tree of these bacteria was constructed using MEGA 5 (Figure 4). The relative abundances of bacteria *in situ* and with transplanting are indicated by bars. The results indicated that OTUs belonging to Acidobacteria Gp4 and Gp6, Arthrobacter, Fervidicoccus, Nitrospira, Sphingomonas, Sphingosinicella, Steroidobacter and Terrimonas were predominant. Of these OTUs,

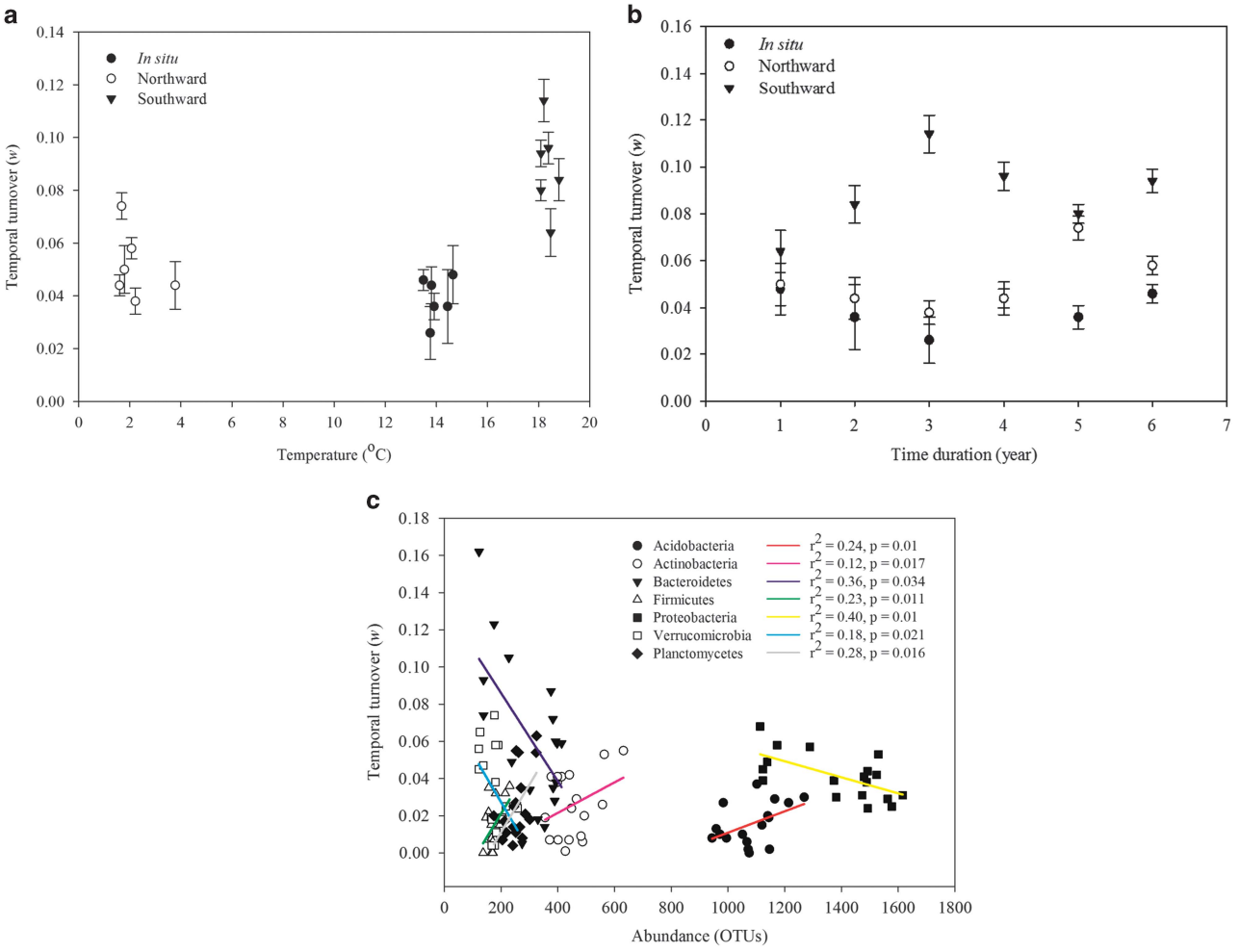

Figure 3 Relationships of temporal turnover *w* values (exponent of time–decay relationship) with (**a**) temperature, (**b**) time duration and (**c**) abundance at phylum level.

Table 1 Temporal turnover (*w* values) of bacterial communities among different phylogenetic groups

	In situ				*Northward transplant*				*Southward transplant*			
	Turnover		*Permutation test*		*Turnover*		*Permutation test*		*Turnover*		*Permutation test*	
	w	P-*value*	t	P-*value*	*w*	P-*value*	t	P-*value*	w	P-*value*	t	P-*value*
All OTUs	0.046	<0.001	−115	<0.001	0.058	<0.001	−141	<0.001	0.094	<0.001	−184	<0.001
Acidobacteria	0.020	<0.001	−86	<0.001	0.038	<0.001	−101	<0.001	0.054	<0.001	−157	<0.001
Actinobacteria	0.018	0.043	−46	<0.001	0.058	<0.001	−122	<0.001	0.084	<0.001	−189	<0.001
Armatimonadetes	0.038	0.076	−36	<0.001	0.064	0.011	−59	<0.001	0.200	<0.001	-159	<0.001
Bacteroidetes	0.076	<0.001	−98	<0.001	0.120	<0.001	−166	<0.001	0.210	<0.001	−154	<0.001
Chloroflexi	0.036	<0.001	−73	<0.001	0.048	<0.001	−83	<0.001	0.144	<0.001	−167	<0.001
Firmicutes	0.014	0.011	−54	<0.001	0.038	<0.001	−90	<0.001	0.064	<0.001	−121	<0.001
Gemmatimonadetes	0.034	0.006	−59	<0.001	0.070	<0.001	−129	<0.001	0.088	<0.001	−133	<0.001
Nitrospira	0.014	0.066	−41	<0.001	0.020	0.006	−60	<0.001	0.046	<0.001	−103	<0.001
Planctomycetes	0.042	<0.001	−116	<0.001	0.050	<0.001	−144	<0.001	0.110	<0.001	−178	<0.001
Verrucomicrobia	0.038	<0.001	−99	<0.001	0.076	<0.001	−164	<0.001	0.130	<0.001	−181	<0.001
Proteobacteria	0.082	<0.001	−170	<0.001	0.084	<0.001	−164	<0.001	0.098	<0.001	−220	<0.001

t and *P*-values are from one-sample *t*-tests on bootstrapping (999 times) for testing significance of *w* values.

northward transplant caused an increase in abundance of 27 OTUs and a decrease of 51 OTUs. Southward transplant caused an increase in abundance of 42 OTUs and a decrease of 35 OTUs.

Linkage between microbial succession and environmental factors

CCA was performed to discern the linkage between microbial succession and the environmental factors (Supplementary Figure S5). The analysis predicts the principal coordinates using a linear combination of several environmental gradients. The variation in microbial phylogenetic community structure was explained by the variation in the identified environmental gradients (40.1% with the first two constrained axes). The CCA results indicated that temperature and precipitation were important environmental attributes that control the microbial community structure in the southward transplant. Soil geochemical variables, such as pH, CEC, soil electrical conductivity, total phosphorus, total potassium and plant biomass, were also weighted favorably (long vector arrow in Supplementary Figure S5) in the control of microbial variations.

To determine how environmental factors such as temperature, plant biomass and soil geochemical variables (pH, CEC, soil electrical conductivity, total potassium and total phosphorus), affected microbial composition during the 6-year experiment, Mantel and partial Mantel tests were performed (Table 2). Temperature was found to be the most important factor that caused microbial β-diversity of all soil samples, especially in the first year of soil transplanting ($r_m = 0.708$, $P < 0.01$). Interestingly, we found that microbial community diversity in the northward transplant was mainly affected by soil geochemical variables (r_m of 0.217–0.637, $P < 0.05$), whereas that in the southward transplant was mostly influenced by temperature (r_m of 0.477–0.880, $P < 0.05$).

Discussion

Given the central and global importance of microorganisms in environments, one of the fundamental objectives is to understand how biodiversity is accumulated and maintained across time and space (Hanson *et al*., 2012; Shade *et al*., 2013). Microbial community structures and their ecological functions are sensitive in response to global climate changes (Singh *et al*., 2010; Gutknecht *et al*., 2012; Luo *et al*., 2014). However, to date, insufficient information is available on the succession dynamics, stability and responses of microbial communities under the integrated effects of climate change, such as temperature, precipitation and vegetation. In this study, we hypothesized that when soils are exposed to colder/warmer climate, the structure of the soil microbial community significantly changes as the bacteria adapts to new climatic conditions across a time span of several years. Our results supported this hypothesis. The microbial community structure was originally the same, but was altered significantly in 6 years by soil transplantation (Figure 1). The difference between any two locations continuously increased with time, which implied that the group of microbes exposed to dramatic climate change is neither resistant nor resilient during the years of the study. Recovery may fail to occur after persistent disturbances caused by climate change, which was demonstrated in a previous study wherein the transplanted soil microbial community was closer to the microbial community in the local soil than that in the original location twenty years after soil transplantation (Sun *et al*., 2014). In addition, previous studies indicated that the presence of plants may enhance the resilience of soil microbial communities (de Vries *et al*., 2012) or even inhibit the effects of soil transplantation (Liu *et al*., 2014), which might be related to the high resource availability offered by the plant (de Vries and Shade,

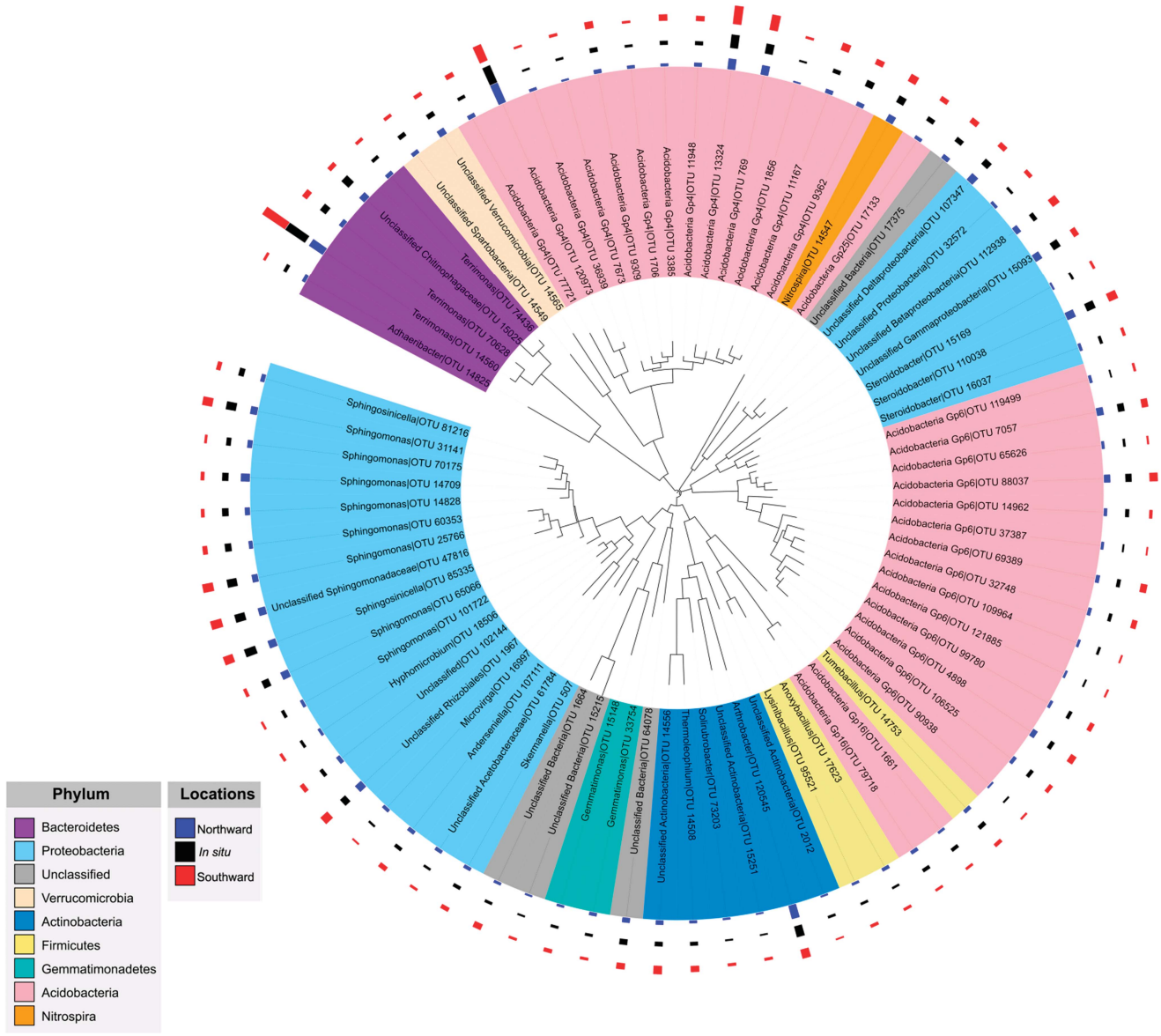

Figure 4 Circular maximum likelihood phylogenetic tree based on OTU representative sequences of bacteria detected in all samples *in situ* and with northward and southward transplant. The bars in the outer band represent the OTU numbers.

2013). However, a clear differential pattern was still observed even with maize cropping in this study. The conflicting results indicated that plants may only dampen disturbance of soil transplantation to a certain extent for a short period. Such hypothesis highlights the need to understand climate-induced changes of interactions between plants and soil communities and the corresponding feedback.

The temporal turnover of the time–decay relationship is an important indicator of the succession dynamics of biological communities. The *w* value was low across the 6-year experiment, but we still observed a significantly linear decrease in the microbial similarity with time (log transformed) for the *in situ* samples and the northward and southward transplants. The results strongly support the claim that the community similarity decays over time (time–decay), which underlies key ecological principles; this decay appears to be universal in biology (Chytry *et al.*, 2001; Korhonen *et al.*, 2010; Gonzalez *et al.*, 2012; Shade *et al.*, 2013). We compared the microbial temporal turnover in different habitats and across different temporal scales (Supplementary Figure S6). Generally, the turnover values obtained in this study (0.026–0.114) had the same magnitude as those of other studies (0–0.3) (Oliver *et al.*, 2012; Hatosy *et al.*, 2013; Shade *et al.*, 2013). The turnover values of microbes in these different studies were obtained with a variety of approaches at various temporal scales, from minutes to years. Consequently, exact comparisons at fine resolutions would be impractical. Generally, the temporal turnover of soil microbial communities is low as compared with that of larger organisms

Table 2 Mantel test and partial Mantel test results to discern correlation between the bacterial community similarity and either soil geochemical variables (pH, CEC, SOM, available potassium and NO_3^-), plant aboveground biomass and temperature

Correlation between bacterial community similarity and:	*Controlling for:*	*1 year*	*2 years*	*3 years*	*4 years*	*5 years*	*6 years*
All samples							
All variables		0.472*	0.217*				
Soil geochemical variables	Plant and climate	0.576*					0.199*
Plant biomass	Soil and climate						
Temperature	Soil and plant	0.708**		0.279**	0.367***	0.421**	0.427***
In situ							
All variables		0.560*					
Soil geochemical variables	Plant and climate						
Plant	Soil and climate						
Temperature	Soil and plant				0.184*		
Northward transplant							
All variables		0.742*		0.382*	0.424**		
Soil geochemical variables	Plant and climate	0.637**		0.254*	0.224*	0.364**	0.217*
Plant	Soil and climate				0.197*	0.21*	
Temperature	Soil and plant						
Southward transplant							
All variables			0.789***	0.50**	0.564**	0.586***	0.316*
Soil geochemical variables	Plant and climate		0.339*				0.448**
Plant	Soil and climate						
Temperature	Soil and plant		0.880***	0.5**	0.60***	0.477**	0.486***

*<0.05, **<0.01, ***<0.001. Only significant correlations were shown in the table.

(Shade *et al.*, 2013). This phenomenon might be attributed to the unique biology of microorganisms such as massive population sizes, high dispersal rates, rapid asexual reproduction and resistance to extinction. Empirical studies across a wide range of taxa showed that more diverse communities have greater temporal stability of their species composition (Shurin, 2007). Thus, the decline in turnover for microbes occurs when high diversity either facilitates colonization of new species or reduces extinction rates of extant species. Second, the much steeper slope observed in soil transplants than *in situ* soil indicated that dramatic climate change increased the microbial succession rate. This result confirmed our hypothesis that microbial temporal turnover is significantly altered by soil transplantation. The rapid elimination and replacement of species might indicate the decreased stability and reassembling process of microbial populations with dramatic climate change. This phenomenon could be explained by the species-sorting concept of the metacommunity framework, which assumes that microbial communities have the potential to adapt to new environmental conditions by adjusting their composition (Leibold *et al.*, 2004; Székely *et al.*, 2013). In addition, changes of microbial temporal turnover could also be due to differences in resident bacterial diversity present at the north and south sites. One would predict that higher colonization potential (for example, higher likelihood that more species could successfully establish in the transplanted soils) could therefore be a driving force behind the patterns observed.

Different subsets of the microbial community showed varying slopes of the time–decay relationships in response to climate change, thereby indicating the differences in sensitivity of the microbial taxonomic groups to disturbance. Some taxa, such as the phyla Actinobacteria and Firmicutes are more sensitive to climate change disturbances than others. The differential responses may affect the overarching resistance and resilience of the community by changing ecological interactions among species (de Vries and Shade, 2013). A critical challenge is to construct a molecular ecological network of microbial communities in response to changing environmental conditions (precipitation, temperature and nutrient input) (Zhou *et al.*, 2010; 2011a). Furthermore, given that changes in microbial community composition are often associated with changes in functional capabilities (Fierer *et al.*, 2007; Strickland *et al.*, 2009), further studies linking the temporal patterns of microbial community with their ecological functional processes under climate change are necessary.

We also hypothesized that the impact of southward transplant (climate warming) on microbial community is more significant than that of northward transplant (climate cooling). First, soil transplantation in the opposite directions resulted in different alterations in microbial richness (OTU number), which mostly decreased in the southward transplant and increased in the northward transplant. A previous study also indicated that soils transplanted to warmer regions lost microbial biomass (Vanhala *et al.*, 2011). This might be partially explained by the predator–prey relationships with temperature

(Fussmann *et al*., 2014). Low temperature may decrease the number of predators such as nematodes in soil aggregates, thereby increasing the population of some soil bacterial species and vice versa.

Second, the southward transplant caused more significant changes in the microbial taxonomic composition as compared with the northward transplant, thereby indicating less ecological stability in the composition of microbial communities after persistent climate warming disturbance. The relative abundances of Proteobacteria and Bacteroidetes decreased, whereas those of Acidobacteria and Actinobacteria increased in the southward transplant. These observations are in accordance with previous findings that the most abundant microbial phyla, namely, Actinobacteria, Proteobacteria, Acidobacteria, Planctomycetes and Bacteroidetes, are significantly different between the warming treatment and the controls (Luo *et al*., 2014). Deslippe *et al.* (2012) also observed that climate warming led to a significant reduction in the evenness of microbial communities; it was associated with the significant increase in the dominance of Actinobacteria and the significant reduction of Gemmatimonadaceae and Proteobacteria. In addition, acid precipitation often occurs in the southern parts of China (Wang and Wang, 1995), thereby resulting in fluctuations of the soil pH (Krug and Frink, 1983), cation exchange equilibrium (Mcfee *et al*., 1977) and the chemical composition of soil water (Likens *et al*., 1996). All these changes may serve as environmental filters that require specific adaption strategies for microbial survival after southward transplantation (Fierer *et al*., 2007).

Third, we observed that southward transplantation had a more significant effect on microbial temporal turnover than northward transplantation. This observation is in accordance with previous findings, which stated that microbial community structures in soil transferred from a cold to a warm site induced high change rates because of higher microbial activity and faster species turnover than the reverse transfer (Zumsteg *et al*., 2013). Southward transplantation of soil causes a significant increase in temperature, which was found to be the most important factor in driving microbial temporal patterns. On the basis of the metabolic theories in ecology (Brown *et al*., 2004), higher temperature accelerates the consumption of substrate (Kirschbaum, 2004; Rousk *et al*., 2012) and, thus, may increase microbial internal competition because of lower substrate availability. The increased competition may cause higher temporal turnover and lower population numbers and population density with climate warming. However, further well-replicated, time-series experiments are required to elucidate the relative importance of temperature in controlling microbial community succession along a temperature gradient. Furthermore, aside from an increase in temperature, the southward transplantation of soil caused a significant loss in plant productivity, as well as changes of some soil physical and chemical factors (such as cation exchange capacity, soil organic matter and nitrate content).

In conclusion, despite the important roles of soil microbial communities in carbon and nitrogen cycling, as well as their intricate linkage with a variety of ecosystem functions, the stability and temporal succession in microbial communities under continuous disturbances caused by climate change are not fully understood. Microbial community structure was significantly altered by soil transplantation, which simulates climate change. Steeper temporal turnover was observed in northward and southward transplants, and warming posed a more significant impact on microbial succession dynamics. Soil transplant-induced changes in microbial community structure and temporal turnover may be important in predicting long-term ecosystem responses to global change.

Conflict of Interest

The authors declare no conflict of interest.

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Author contributions

All authors contributed intellectual input and assistance to this study and manuscript preparation. BS, JZ and YL developed the original framework. YL, YJ, FW, YY, KX, CW, YD, YQ and LW contributed reagents and data analysis. YL, KX and CW did GeoChip analysis. YL, BS and JZ wrote the paper.

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