


Dissimilar responses of fungal and bacterial communities to soil transplantation simulating abrupt climate changes

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Abstract

Both fungi and bacteria play essential roles in regulating soil carbon cycling. To predict future carbon stability, it is imperative to understand their responses to environmental changes, which is subject to large uncertainty. As current global warming is causing range shifts toward higher latitudes, we conducted three reciprocal soil transplantation experiments over large transects in 2005 to simulate abrupt climate changes. Six years after soil transplantation, fungal biomass of transplanted soils showed a general pattern of changes from donor sites to destination, which were more obvious in bare fallow soils than in maize cropped soils. Strikingly, fungal community compositions were clustered by sites, demonstrating that fungi of transplanted soils acclimatized to the destination environment. Several fungal taxa displayed sharp changes in relative abundance, including *Podospora*, *Chaetomium*, *Mortierella* and *Phialemonium*. In contrast, bacterial communities remained largely unchanged. Consistent with the important role of fungi in affecting soil carbon cycling, 8.1%–10.0% of fungal genes encoding carbon-decomposing enzymes were significantly ($p < 0.01$) increased as compared with those from bacteria (5.7%–8.4%). To explain these observations, we found that fungal occupancy across samples was mainly determined by annual average air temperature and rainfall, whereas bacterial occupancy was more closely related to soil conditions, which remained stable 6 years after soil transplantation. Together, these results demonstrate dissimilar response patterns and resource partitioning between fungi and bacteria, which may have considerable consequences for ecosystem-scale carbon cycling.

KEYWORDS

carbon-decomposing genes, climate change, high-throughput sequencing, soil microbial community, soil transplantation

1 | INTRODUCTION

Climate changes have affected soil carbon cycling in terrestrial ecosystems, and this cycling is increasingly recognized to be differentially modulated by bacteria and fungi (Andresen et al., 2014). Fungi are powerful lignocellulose decomposers, whereas bacteria generally rely on the availability of soluble substrates and consequently contribute less to stabilize soil carbon (McGuire & Treseder, 2010). Fungi also produce chitin, which is recalcitrant to decomposition (Clemmensen et al., 2013). Moreover, fungal hyphae facilitate formation of soil aggregates, which physically protects soil organic carbon from decomposition and leaching (Six, Conant, Paul, & Paustian, 2002). As a result, fungi play a major role in mediating below-ground carbon cycling in terrestrial ecosystems (Baldrian et al., 2012; Zifcakova, Vetrovsky, Howe, & Baldrian, 2016). However, bacteria are increasingly recognized to play a more important role in litter decomposition than previously thought (Glassman et al., 2018; Lopez-Mondejar et al., 2018; Wilhelm, Singh, Eltis, & Mohn, 2019). Shifts in bacterial composition were found to have a stronger effect on grassland litter decomposition rates than fungi, while initial bacterial or fungal abundance appeared not to affect litter decomposition (Glassman et al., 2018). As different fungal and bacterial guilds interactively regulate soil carbon accumulation (Kyaschenko, Clemmensen, Karlton, & Lindahl, 2017), there is high uncertainty about how changes in microbial communities affect soil carbon stability and provide feedbacks to climate.

As one of the largest biodiversity reservoirs, soil microbial communities have been extensively investigated for their responses to climate change. When measured based on phospholipid fatty acids (PLFAs) with ^{13}C -glycine tracer or quantitative PCR (polymerase chain reaction) targeting bacterial 16S rRNA genes and fungal rRNA genes, total biomasses of fungal communities were affected by multifactorial climate changes of elevated atmospheric CO_2 concentration, warming, wetting and drying, which showed distinct patterns compared to bacterial communities (Andresen et al., 2014; Castro, Classen, Austin, Norby, & Schadt, 2010). In addition, the phylogenetic distribution of bacterial and fungal taxa and their relative abundance varied among climate change treatments. Soil rewetting triggered large changes in the relative abundance of active bacterial phyla including *Acidobacteria*, *Verrucobacteria*, *Actinobacteria* and *Firmicutes*, but had little effect on active fungal phyla (Barnard, Osborne, & Firestone, 2013). Climate warming led to an increasingly divergent succession of soil microbial communities in an Oklahoma grassland, with higher impacts on fungi than on bacteria (Guo et al., 2018). In contrast, warming rapidly changed bacterial communities in Arctic tundra soils (Yang et al., 2017), but changes in fungal communities by experimental warming in an Arctic site were not apparent until after 17 years of treatment (Deslippe, Hartmann, Mohn, & Simard, 2011). In general, fungal and bacterial responses often reflect the specificities of each studied ecosystem, and it remains impossible to fully incorporate

microorganisms into predictive models (Lladó, López-Mondéjar, & Baldrian, 2017).

Here, we examine fungal and bacterial communities in three reciprocal soil transplantation experiments over large transects (i.e., relocating ecotypes from one climatic regime to others regimes to simulate abrupt climatic shifts, which has been historically documented). For example, there is evidence for abrupt climate warming over a region of at least hemispheric extent in 11,600 years ago, which caused the Greenland temperature to rise 15°C within a few decades (Severinghaus, Sowers, Brook, Alley, & Bender, 1998). This is alarming, given that abrupt warming might recur under human forcing (Alley et al., 2003). The rationale behind soil transplantation manipulation is based on long-standing observations that global warming causes a shift in climatic regimes toward higher latitudes at a rate of 17.6 km per decade, on average, hence moving the bioclimatic envelopes of species (Walther, 2010). Therefore, reciprocal soil transplantation experiments provide a valuable strategy to address the question of how soil microbial communities respond to climate differences under comparable soil physicochemical conditions (Waldrop & Firestone, 2006; Zumsteg, Bååth, Stierli, Zeyer, & Frey, 2013). Recently, this strategy has provided important insights into elucidating the effect of climate changes on microbial communities (Balser & Firestone, 2005; Liang et al., 2015). PLFA analysis showed that a fungal biomarker was significantly changed by soil transplantation while bacterial biomarkers remained largely unchanged (Balser & Firestone, 2005). However, PLFAs had limited resolution for fingerprinting in quantifying microbial community. At our study site, simulated climate warming by southward soil transplantation led to a faster succession rate of bacterial communities as well as lower species richness and compositional changes than in situ and northward soil transplantation (Liang et al., 2015). However, it remains unclear how fungal communities respond to simulated climate changes at this site. Cutting-edge environmental genomics techniques, such as high-throughput sequencing and functional gene arrays, present an opportunity to address these issues.

Microbial communities are essential for mediating a variety of ecological processes, which are subjected to the influence of climate changes. Therefore, we initiated a study to compare fungal and bacterial responses to climate changes. Given that fungal communities are changed more substantially than bacterial communities by simulated climate changes (Balser & Firestone, 2005) or by seasonal variations (Zifcakova et al., 2016), our first hypothesis is that fungal communities are more responsive to climate changes than bacterial communities. If so, we dismiss the recent hypothesis that pH and organic matter primarily drive environmental filtering in soil fungal communities (Glassman, Wang, & Bruns, 2017). In addition, fungi are believed to be more important in carbon-decomposing processes (Baldrian et al., 2012; Zifcakova et al., 2016), although bacterial biomass is often quantitatively more abundant. Because abundance determines functional roles in complex microbial communities (Rivett & Bell, 2018) and relative abundances of carbon-decomposing genes are positively linked to soil carbon decomposition rates (Morales,

Cosart, & Holben, 2010; Zhao et al., 2016,2014), our second hypothesis is that carbon-decomposing genes derived from fungi will also be more influenced by climate changes than those derived from bacteria.

2 | MATERIALS AND METHODS

2.1 | Site description and sample collection

We conducted the reciprocal soil transplantation study at three agricultural experimental stations of the Chinese Academy of Sciences: Hailun station in Heilongjiang Province (126°38'E, 47°26'N), Fengqiu station in Henan Province (114°24'E, 35°00'N) and Yingtan station in Jiangxi Province (116°55'E, 28°15'N). The Hailun, Fengqiu and Yingtan stations were thereafter designated as the N, C and S sites according to their locations from north, centre to south, respectively (Supporting Information Figure S1). The N site has Mollisol soils with a cold temperate monsoon climate. The C site is about 1700 km south of the N site with Inceptisol soils and a warm temperate monsoon climate. The S site is 800 km south of the C site with Ultisol soils and a middle subtropical monsoon climate. As described previously (Zhao et al., 2014), we set up 1.4 × 1.2 × 1.0-m (length × width × depth) plots fenced by 20-cm concrete walls and underlaid by quartz sand at each station to prevent soil intrusion from the surrounding area. As intact soil in the plot was difficult to handle, we excavated soils in five layers with 1.4 × 1.2 × 0.2 m (length × width × depth) per layer in October 2005, and then reciprocally transplanted these to the concrete plots sequentially. Six Mollisol soil plots were transplanted to the C site and another six to the S site. Six other Mollisol plots were simultaneously excavated but remained at the N site to serve as controls. Similar manipulations were conducted for Inceptisol and Ultisol soils. For each soil type, triplicate plots were randomly selected to be cropped with maize, and other plots were kept bare fallow to disentangle the effects of simulated climate changes from those of maize cropping. Weeds were manually removed, and there was no irrigation to any plot.

In 2011, we collected soil samples from bare fallow and maize cropped plots, resulting in a total of 54 samples (2 [bare fallow and maize cropped] × 3 [N, C and S site] × 3 [2 transplanted plots + 1 control plot] × 3 [triplicates] = 54). Samples at the N and C sites were collected in September and samples at the S site were collected in July. The time to collect samples was based on the local time of crop harvest, which synchronized the effects of maize cropping but inevitably failed to consider seasonal differences between the S site and the N/C sites that affect soil microbial communities. Ten soil cores of 2 cm in diameter (0–15 cm depth) from each plot were collected and thoroughly mixed to make one soil sample. Mollisol soil at the original N site was designated as N, and transplanted Mollisol soils to the C site and the S site were designated as NC and NS, respectively. Similar designation was used for transplantation of the Inceptisol (the C site) and Ultisol soils (the S site). A suffix “m” was designated if the soil was cropped with

maize. Soil for DNA extraction was stored at –80°C, and soil for geochemical analyses was stored at 4°C.

2.2 | Experiments with microbial communities

We determined microbial biomass based on the PLFA content measurement using 2 g of dry weight soil with a modified Bligh–Dyer protocol (Okabe, Toyota, & Kimura, 2000). After incubation in 15 ml of chloroform/methanol/phosphate (1:2:0.8 by vol.) buffer, we collected the chloroform phase and divided it into glycolipids, neutral lipids and phospholipids using a silicic acid-bonded solid-phase extraction column. Phospholipids were then saponified, methylated and measured by using a Sherlock Microbial Identification System (MIDI Inc.). PLFA peaks were identified by comparison with known standards.

We extracted microbial DNA from 5 g of soil using a freeze-grinding method and purified by 0.5% of low-melting-point agarose gel electrophoresis as previously described (Sun et al., 2014). DNA quantity and purity were determined by a PicoGreen method and a Nanodrop device (Nanodrop Inc.) using A_{260}/A_{230} and A_{260}/A_{280} absorbance ratios, respectively.

We prepared DNA with a two-step PCR to limit amplification biases (Wu et al., 2017), which amplified DNA in the first step with the nonbarcoded primers and used these amplicons as template for a second round of PCR that utilized barcoded primers. We used primers gITS7F (5'-GTGARTCATCGARTCTTTG-3') and ITS4R (5'-TCCTCCGCTTATTGATATGC-3') to target the internal transcribed spacer (ITS) II region of fungal ribosome-encoding genes, and used primers 515F (5'-GTGCCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') to target the V4 hypervariable region of the bacterial 16S rRNA gene. PCR amplification was performed in a volume of 25 µl containing 1 µm of each primer, 2.5 µl of 10× PCR buffer II, 0.1 µl AccuPrime Taq DNA Polymerase High Fidelity (Invitrogen), and 5 µl of template DNA for the first round PCR and 15 µl of template DNA for the second round of PCR. Thermal cycling conditions for ITS amplification were as follows: initial denaturation at 94°C for 3 min, 12 cycles for the first round of PCR and 24 cycles for the second round of PCR at conditions of 94°C for 30 s, 55°C for 30 s and 68°C for 30 s, and final extension at 68°C for 7 min. Thermal cycling conditions for 16S rRNA V4 region amplification were as follows: initial denaturation at 94°C for 1 min, 10 cycles for the first round of PCR and 20 cycles for the second round of PCR at conditions of 94°C for 20 s, 53°C for 25 s and 68°C for 45 s, and final extension at 68°C for 10 min. Amplified PCR products were used for MiSeq sequencing (Illumina) at the Institute for Environmental Genomics at the University of Oklahoma.

We used a functional gene array, GeoChip 4.6, to examine microbial functional potential as previously described (Ding et al., 2015; Yue et al., 2015). As sequence of the same functional gene usually differs by microbial host, probe design in GeoChip allows for differentiating microbial genes and (to a certain extent) microorganisms. In brief, we labelled DNA with the fluorescent nucleic acid dye Cy5, hybridized the labelled DNA to GeoChip slides for 16 hr, and

then scanned them on a NimbleGen scanner (MS 200 Microarray Scanner). We quantified the signal intensity of GeoChip with IMAGENE version 6.0 (Biodiscovery).

2.3 | Measurements of environmental variables

We measured soil pH in a water suspension (2.5:1 of soil/water) with a pH meter (Mettler Toledo Instruments), soil organic matter by dichromate oxidation, moisture content by an oven-drying method (Lu, 1999), total nitrogen by Kjeldahl digestion, available nitrogen by the Illinois Soil Nitrogen Test diffusion method (Khan et al., 2001), total and available phosphorus by a molybdenum blue method, and total and available potassium by flame photometry (FP6400A, CANY Precision Instrument Co.), as previously described (Liu et al., 2015).

2.4 | Data analyses

We processed sequencing data on the Galaxy pipeline (<http://zhoulab5.rccc.ou.edu>) as previously described (Zhao et al., 2016). We discarded low-quality sequences, which had more than one undetermined nucleotide (N), sequence reads <100 bp, or low-quality scores <25. We trimmed sequences to 250–350 bp for the fungal ITS and 245–260 bp for the 16S rRNA V4 region amplicon after combining the forward and reverse sequences. After chimera check using the UCHIME method, we classified the fungal ITS sequences into operational taxonomic units (OTUs) with 97.5% similarity (according to the tipping point between clustering similarities and OTU numbers, Supporting Information Figure S2) and 16S rRNA V4 region amplicon sequences with 97% similarity by UCLUST (Edgar, Haas, Clemente, Quince, & Knight, 2011). Singletons that were detected only once across all samples were removed. Rarefaction curve analyses were conducted (Supporting Information Figure S3) by rarefying samples to 9,917 sequence reads per sample for the fungal ITS and to 10,947 sequence reads for the 16S rRNA V4 region amplicon sequences. We assigned taxonomic annotations of OTUs to representative sequences by a UNITE version 7.1 training set for the fungal ITS (Kõljalg et al., 2013), and a 16S rRNA training set Greengenes by RDP CLASSIFIER for the 16S rRNA V4 region amplicon (Wang, Garrity, Tiedje, & Cole, 2007). We calculated the relative abundance (RA) of sequences as follows: $RA_{ij} = (S_{ij} / \sum_{j=1}^N S_{ij}) \times 100$, where S_{ij} is the sequence number of the j th OTU in the i th sample.

We processed raw data from GeoChip 4.6 on the IEG pipeline (<http://ieg.ou.edu/microarray/>) using a standard method to remove low-quality data. In brief, we discarded signals with signal to noise ratio (SNR) <2.0, where $SNR = (\text{signal mean} - \text{background intensity}) / \text{background standard deviation}$, or signals detected only once in three replicates. We calculated gene abundance by logarithmically transforming the signal intensity and then dividing it by the mean signal intensity of each sample.

We used nonmetric multidimensional scaling (NMDS) to examine microbial distribution patterns and multiple regression tree (MRT) analysis to examine the relative effect of transplantation

and soil origin on microbial community compositions (De'Ath, 2002). We used Similarity Percentages (SIMPER) analysis to assess the contribution of individual species to overall dissimilarity of microbial communities between pairwise samples using Bray–Curtis dissimilarities (Warton, Wright, & Wang, 2012). We used partial Mantel tests to analyse the effect of environmental variables on microbial community compositions (Smouse, Long, & Sokal, 1986), and variation partition analysis (VPA) to reveal the individual and interactive effects of climate variables, soil chemical variables and soil nutrient variables on microbial community variations (Borcard, Legendre, & Drapeau, 1992). All of the above analyses were carried out using R software (version 3.3.0; R Foundation for Statistical Computing) with the VEGAN (version 2.3-5) and MUPART (version 1.6-1) packages. We determined the statistical significance of differences in environmental variables among all treatments using one-way ANOVA (analysis of variance) followed by the least significant difference (LSD) test in SAS (version 6.1) (SAS Inc.) with the 95% confidence interval.

To examine the relationship between microbial community compositions and environmental variables, we identified samples wherein a certain OTU was detected. We then subtracted the lowest value of each environmental variable in these samples from the greatest value to generate an environmental range of each variable for each OTU (Barberan et al., 2014). The total environmental range is the average of all environmental variable ranges, normalized to the range 0–1.

3 | RESULTS

3.1 | Effects of climate change on soil microbial communities

In both bare fallow and maize cropped soils, bacterial biomass was ~1–3-fold more abundant than fungal biomass, with the highest biomass at the N site (Table 1). Southward transplantation of bare fallow soils from the N site decreased ($p < 0.05$) fungal biomass from 3.3 to 0.9 nmol/g at the C site and 1.6 nmol/g at the S site, bacterial biomass from 12.0 nmol/g at the N site to 4.6 nmol/g at the C site and 3.9 nmol/g at the S site, and total microbial biomass from 42.3 nmol/g at the N site to 18.8 nmol/g at the N and S sites. Southward transplantation of maize cropped soils from the N site also decreased fungal, bacterial and total microbial biomass, albeit to a lesser extent. These results suggested that climate warming could decrease soil microbial biomass. In contrast, northward transplantation of bare fallow soils from the C site to the N site increased ($p < 0.05$) fungal biomass from 0.7 to 2.2 nmol/g, bacterial biomass from 2.1 to 7.2 nmol/g, and total microbial biomass from 9.6 to 27.5 nmol/g. The other transplantation treatments, such as from the C site to the S site and from the S site to the C site, also showed a general pattern of changes of microbial biomass from donor sites to destination.

A total of 5,896 fungal OTUs were identified (see Materials and methods for details). In both bare fallow and maize cropped soils,

TABLE 1 Microbial biomass measurements

Sample name	Microbial biomass (nmol/g dry weight)		
	Fungi	Bacteria	Total
N ^a	3.3 ± 1ab ^{b,c}	12 ± 1.0a	42.2 ± 8.6ab
NC	0.9 ± 0.3efg	4.5 ± 1.2cd	18.7 ± 6efghi
NS	1.6 ± 0.4cdefg	3.9 ± 0.3de	18.9 ± 3.6defghi
C	0.7 ± 0.1g	2.1 ± 0.5ef	9.6 ± 0.6i
CS	1.1 ± 0.4efg	1.5 ± 0.2f	11.8 ± 2.3hi
CN	2.2 ± 0.8c	7.2 ± 3.5b	27.5 ± 9.9cde
S	1.8 ± 0.5cdef	3.4 ± 0.4def	21.3 ± 4.8defgh
SC	0.7 ± 0.2g	3.1 ± 0.7def	11.8 ± 2.2hi
SN	1.2 ± 0.2defg	3.9 ± 0.2de	19.4 ± 2.4defghi
Nm	3.5 ± 1.2a	11.4 ± 1.7a	43.1 ± 12.7a
NCm	3.5 ± 0.8a	6.3 ± 0.6bc	28.7 ± 3.6cd
NSm	2.3 ± 0.7bc	4.8 ± 0.3cd	24.2 ± 3.7cdef
Cm	2.2 ± 0.9cd	4.1 ± 1.7de	18.1 ± 4.4efghi
CSm	1.4 ± 0.6cdefg	2.8 ± 1.3def	16.2 ± 7.3fghi
CNm	1.6 ± 0.5cdefg	4.8 ± 1cd	22.3 ± 8.1defg
Sm	1.5 ± 0.2cdefg	3.8 ± 0.5de	16.6 ± 0.3fghi
SCm	0.8 ± 0.3fg	2.9 ± 0.9def	13.1 ± 3.5ghi
SNm	1.8 ± 0.3cde	4.8 ± 1.8cd	32.9 ± 4.9bc

^aMollisol soil at the donor N site is designated as N, and transplanted Mollisol soils to the C site and the S site are designated as NC and NS, respectively. Similar designation is used for the Inceptisol (the C site) and Ultisol soils (the S site). A suffix "m" is designated for soil cropped with maize. ^bValues are shown as mean ± SD. ^cLetters next to each value indicate significance of differences. Treatments with the same letter are not significantly different ($p > 0.05$) as determined by one-way ANOVA followed by LSD test in SAS version 6.1.

fungal communities were clustered primarily by new site location (Figure 1a,b), suggesting that fungal community compositions in transplanted soils have shifted towards those in destination soils. To verify it, MRT analysis, a statistical technique that splits data into different levels and clusters based on experimental treatments (De'Ath, 2002), was used to rank the relative importance of site location and soil origin effects on fungal community, showing that site location overrode soil origin in affecting fungal community composition in both bare fallow and maize cropped soils (Supporting Information Figure S4a,b).

In both bare fallow and maize cropped soils, the fungal genus *Podospora* was abundant at the N site (1.82%–7.06%) but showed low abundance of 0.19%–1.81% at the C and S sites, suggesting that *Podospora* are suited for soil environment at the N site (Figure 2a). SIMPER analysis, which evaluated the contribution of individual genera to the dissimilarity between pairwise sites, showed that *Podospora* contributed to 5.20%–5.55% of the dissimilarity of fungal communities between the N site and other sites (Supporting Information Table S1). Similarly, another abundant genus at the N site (*Chaetomium*), known to survive in Antarctic soils (Robinson, 2001; Singh, Puja, & Bhat, 2006), contributed to 6.59%–7.76% of the dissimilarity of fungal communities between the N site and other

sites. At the C site, *Mortierella* was abundant in both bare fallow and maize cropped soils (1.79%–5.34%) but not in other sites, which contributed to 5.07%–5.29% of the dissimilarity of fungal communities between the C site and other sites. At the S site, *Phialemonium* was abundant in both bare fallow and maize cropped soils (0.40%–15.25%), which was much higher than other sites and contributed to 10.24%–10.28% of the dissimilarity of fungal communities between the S site and other sites. The relative abundance of *Glomus* was also higher at the S site. Coincidentally, both *Phialemonium* and *Glomus* could be simulated in abundance by soil warming (Fitter, Heinemeyer, & Staddon, 2000; Staddon, Gregersen, & Jakobsen, 2004).

An explanation for the clustering of fungal communities by site location is possible microbial intrusion from surrounding soils. To test this, we examined bacterial community compositions in bare fallow soils, based on the sequencing data, to reveal the influence of native soil microorganisms on the transplanted soils. Only 2.4%–14.2% of OTUs in the surrounding soils were also detected in the transplanted soils (Supporting Information Figure S5b). Considering microbes below the detection level at the original site but becoming more abundant at the transplanted site, which were not related to soil intrusion but would be included in the 2.4%–14.2% overlap, soil intrusion from the surrounding area, if any, was minor. In addition, soil pH, a relatively stable environmental variable, remained unchanged in this study (Table 2). For example, soil pH at the C site was ~8 after transplanting to the N and S sites and substantially different from local soil (pH 6.2 at the N site and 5.3 at the S site), further excluding the possibility of an influence from surrounding soil.

In sharp contrast to observations with fungi, bacterial communities, based on a total of 46,782 OTUs, clustered primarily by soil origin (Figure 1c,d). This result was verified by MRT analysis (Supporting Information Figure S4c,d). An unclassified genus of the class *Spartobacteria* was the most abundant genus in both bare fallow and maize cropped soils at the N site (16.65%–32.69% in relative abundance), which contributed the most to dissimilarity of the bacterial communities between the N site and the other sites (19.34%–33.68%; Figure 2b; Supporting Information Table S1). *Gp4* of the phylum *Acidobacteria* was the most abundant genus at the C site (7.62%–11.99% in bare fallow and maize cropped soils), followed by *Gp6* of the phylum *Acidobacteria* (5.56%–8.71% in bare fallow and maize cropped soils), which together contributed to 12.30%–18.24% of the bacterial community dissimilarity between the C site and other sites. *Conexibacter* was also abundant at the S site (3.30%–9.93% in bare fallow and maize cropped soils) but not at the other sites, which contributed to 7.51%–8.90% of the bacterial community dissimilarity between the S site and the other sites.

3.2 | Effects of climate change on carbon-decomposing genes

We examined the signal intensities of probes in the functional gene array GeoChip targeting fungal and bacterial genes encoding

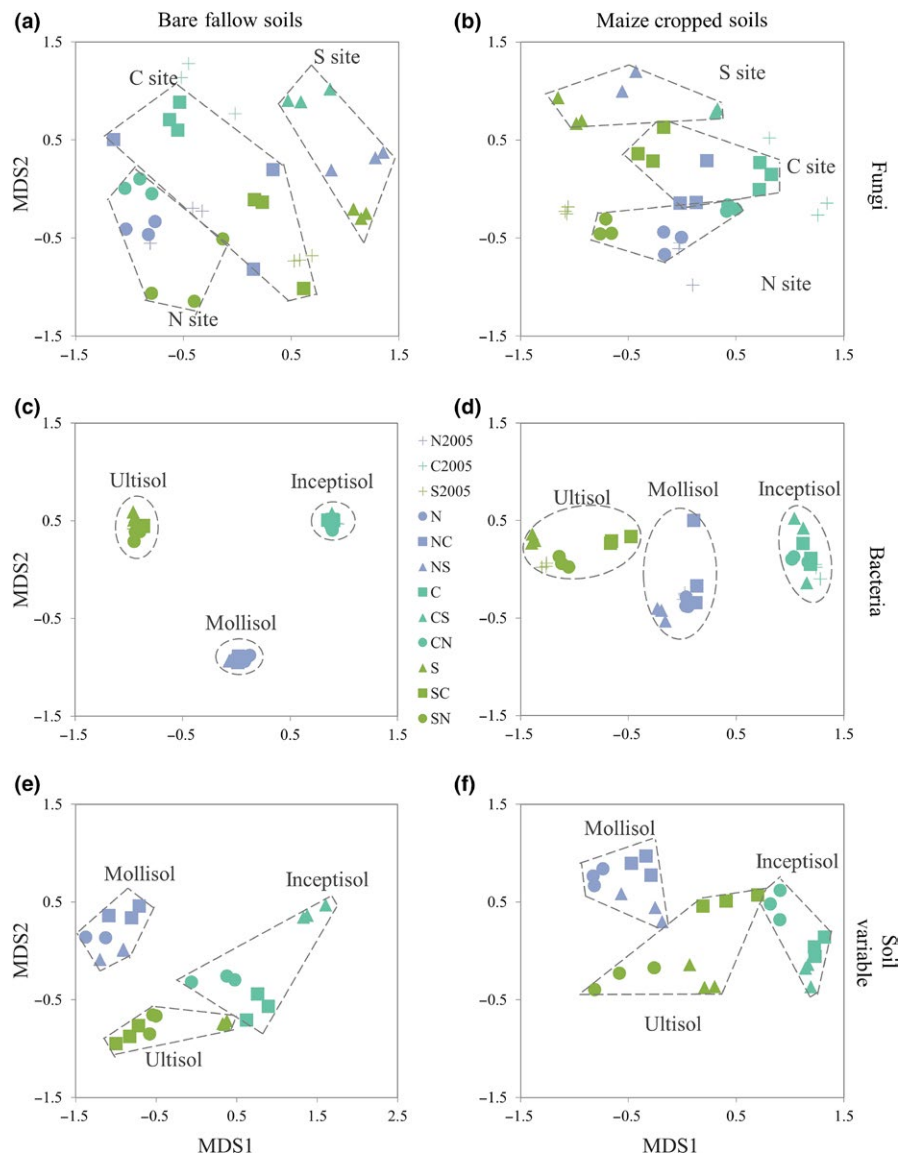


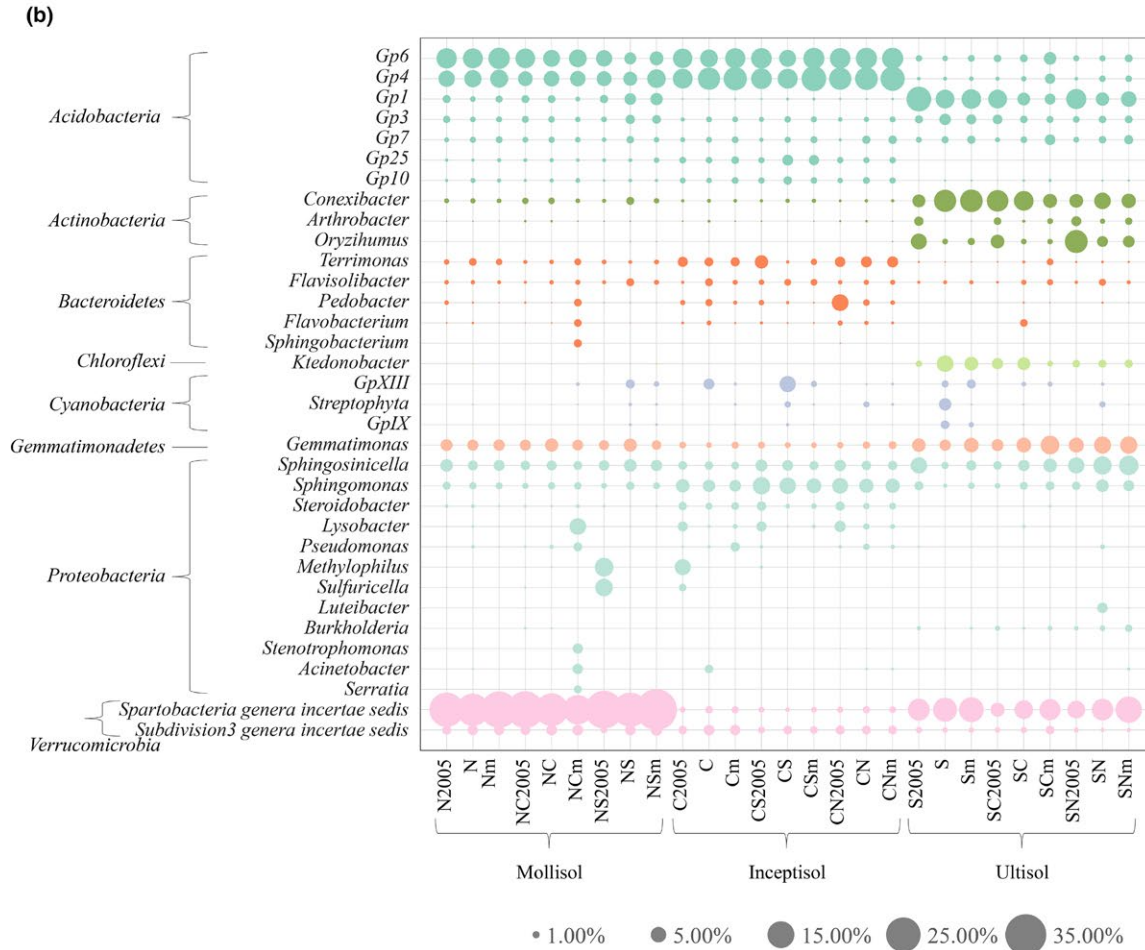
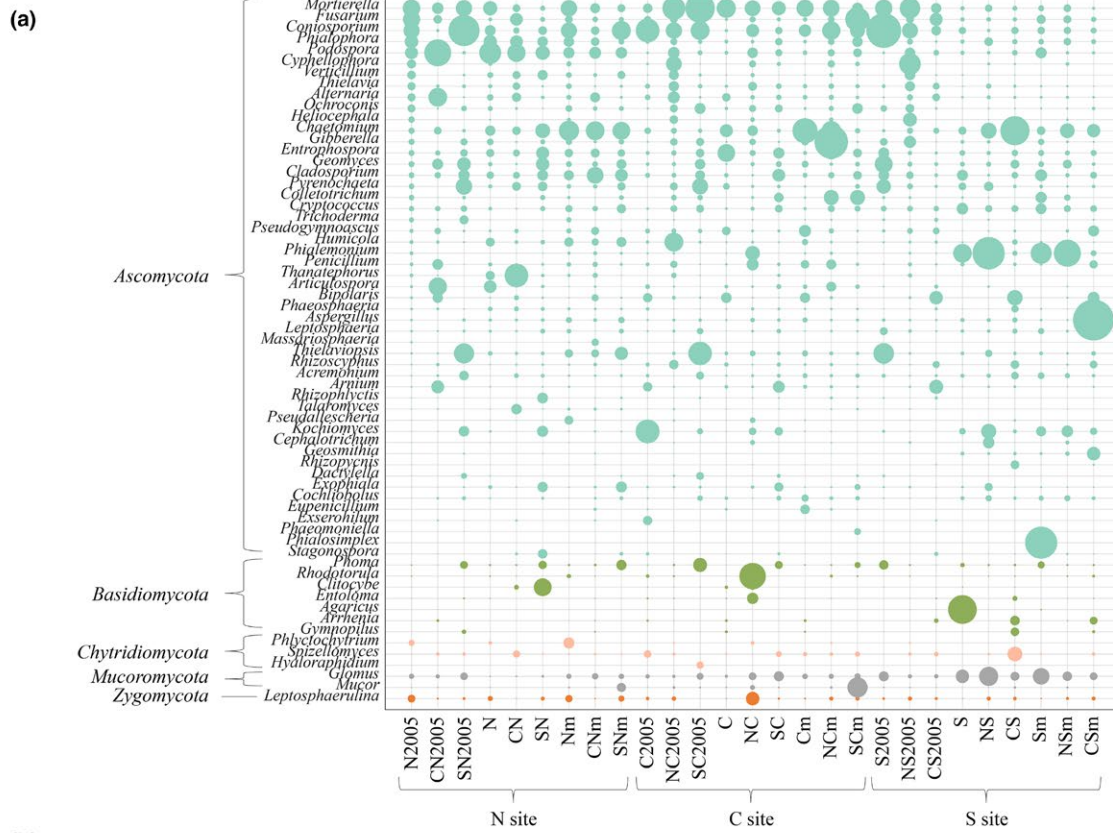
FIGURE 1 Nonmetric multidimensional scaling (NMDS) showing microbial community compositions. (a) Fungal communities in bare fallow soils; (b) fungal communities in maize cropped soils; (c) bacterial communities in bare fallow soils; (d) bacterial communities in maize cropped soils; (e) soil variables in bare fallow soils; and (f) soil variables in maize cropped soils. Panels (a–d) include soil samples collected in 2005 [Colour figure can be viewed at wileyonlinelibrary.com]

carbon-decomposing enzymes. A total of 10.1%–14.1% of fungal carbon-decomposing genes in bare fallow soils, and 4.0%–6.8% of those genes in maize cropped soils, increased significantly ($p < 0.05$) in relative abundance as a result of southward soil transplantation (Figure 3a,b). By contrast, 1.1%–3.4% of fungal carbon-decomposing genes in bare fallow or maize cropped soils decreased by southward soil transplantation. The relative abundance of fungal chitin-decomposing genes increased the most and decreased the least in bare fallow and maize cropped soils. Only 6.5%–8.6% of fungal genes in bare fallow soils and 1.4%–2.2% in maize cropped soils increased significantly ($p < 0.05$) by northward soil transplantation (Figure 3c,d). In addition, 2.4%–5.6% of fungal carbon-decomposing genes in bare fallow or maize cropped soils decreased by northward soil transplantation.

About 4.8%–10.4% of bacterial genes increased ($p < 0.05$) in transplanted bare fallow soils (Figure 3a,c), which was significantly ($p < 0.05$) fewer than those from fungi. A total of 1.2%–5.1% of the bacterial genes increased in transplanted maize cropped soils (Figure 3b), fewer ($p < 0.06$) than those from fungi. By contrast, 1.6%–5.0% of bacterial carbon-decomposing genes decreased in transplanted bare fallow or maize cropped soils, similar to those genes derived from fungi.

3.3 | Effects of climate change on soil variables

Southward transplantation of bare fallow soils at the N site significantly ($p < 0.05$) decreased available potassium (AK) from 202 to 168 mg/kg at the C site and to 164 mg/kg at the S site, whereas northward transplantation of the soils at the S site increased



($p < 0.05$) it from 109 to 208 mg/kg at the C site and to 203 mg/kg at the N site (Table 2). Other soil nutrients, including soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available phosphorus (AP), ammonium ($\text{NH}_4\text{-N}$) and nitrate ($\text{NO}_3^- \text{- N}$), remained largely unchanged by soil transplantation. As a result, soil physicochemical variables clustered by soil origin in both bare fallow and maize cropped soils (Figure 1e,f), similar to observations for bacterial communities.

3.4 | Relationships between environmental variables and microbial communities

We defined OTU occupancy as the number of samples wherein an OTU is present, and environmental range as the breadth of environmental conditions wherein an OTU is present (see Materials and methods for details). We observed a stronger correlation between occupancy and environmental range for fungi ($R^2 = 0.62$) than bacteria ($R^2 = 0.39$; Supporting Information Figure S6), suggesting that OTUs ubiquitous in the samples also tend to be persistent under a wide range of environmental conditions. Most ranges of soil variables of fungal OTUs were significantly ($p < 0.001$) broader than those of bacterial OTUs (Table 3). Examples included soil pH (fungal range of 1.86 ± 0.02 vs. bacterial range of 1.53 ± 0.01), soil density (fungal range of 0.35 ± 0.003 vs. bacterial range of 0.33 ± 0.001), TP (fungal range of 0.30 ± 0.003 vs. bacterial range of 0.25 ± 0.001) and TK (fungal range of 8.21 ± 0.10 vs. bacterial range of 6.57 ± 0.04). In sharp contrast, the annual average temperature (annual T) range of fungal OTUs was narrower than that of bacterial OTUs (fungal range of 8.89 ± 0.11 vs. bacterial range of 11.82 ± 0.04 , $p < 0.001$), and the annual rainfall (annual R) range of fungal OTUs was narrower than that of bacterial OTUs (fungal range of 529.26 ± 6.79 vs. bacterial range of 719.15 ± 2.27 , $p < 0.001$), suggesting that fungi were more sensitive to climate conditions.

Mantel tests verified that annual T ($r = 0.39$, $p = 0.001$) and annual R ($r = 0.50$, $p = 0.001$) were the most influential for fungal communities, followed by soil pH ($r = 0.31$, $p = 0.001$), TK ($r = 0.23$, $p = 0.001$), TP ($r = 0.16$, $p = 0.001$) and AK ($r = 0.16$, $p = 0.001$; Table 4). In contrast, soil pH ($r = 0.63$, $p = 0.001$), TP ($r = 0.53$, $p = 0.001$) and TK ($r = 0.54$, $p = 0.001$) were the most influential for bacterial communities. These soil variables were largely unaltered by soil transplantation (Table 2), providing an explanation for bacterial community resistance to soil transplantation.

As our results indicated that climate variables of annual T and annual R, soil pH, and soil nutrient variables of SOM, TN, TP and TK were important for shaping both fungal and bacterial communities, we used VPA to reveal both independent and interactive effects of these variables on the microbial community variations (Supporting Information Figure S7). The results further verified the significant

contributions of climate variables to fungal communities ($p = 0.001$). The other two groups of environmental variables also contributed significantly and largely independently to fungal communities ($p = 0.001$). Each of those groups of environmental variables also contributed to bacterial community variations ($p < 0.005$). The contribution per climate variable was highest for the fungal community. Notably, soil pH and soil nutrient variables interactively contributed 5.7% to bacterial communities, but only 0.1% to fungal communities, suggesting that these variables were more influential on bacterial communities.

4 | DISCUSSION

4.1 | Investigation of research hypotheses

This study provides valuable insights into the dissimilar response of fungal and bacterial communities to abrupt climate change and highlight the important role of fungi in soil carbon decomposition. Our findings provide support to Hypothesis 1 that fungal communities are more sensitive than bacterial communities to climate changes. Fungal communities at the same site were similar, regardless of soil origin, whereas bacterial communities of the same soil origin were more similar (Figure 1). This suggests strong influence of climate variables, including temperature and moisture, on fungal communities, which is contradictory to the findings of Glassman et al. (2017) showing that pH and organic matter primarily drive soil fungal communities. Many reasons may lead to the differences seen between the two studies, such as the extremely different scales and plant compositions. Glassman et al.'s study looked at fine spatial scales of < 1 km where annual temperatures were the same for all samples, while our study was at large spatial scales of $> 1,700$ km with widely varying annual temperatures across samples; Glassman et al.'s study was conducted in a pine forest, while our study was conducted in maize cropped or bare fallow soils; and our study covered a much more basic pH range (6.2–8.4) than that in Glassman et al.'s study (3.8–5.1). We also found that more fungal genes associated with carbon decomposition were influenced by soil transplantation than those derived from bacteria (Figure 3).

Soil transplantation over large transects reflect abrupt climate changes that are unlikely to occur over short durations, but are possible in the long term. For example, it was believed that the climate at 3,000 years BC in Henan province, the location of C site, was subtropical (Zhu, 1973), similar to the current climate of site S. In addition, there was also evidence of good acclimatization of fungal communities to climate changes within the relatively short time-period of 6 years (Figure 1). While bacterial communities at the N, C and S sites remained similar between 2005 and 2011 (Figure 1c,d), fungal communities in 2011 samples were clearly different from

FIGURE 2 Dot plot showing (a) fungal and (b) bacterial genera with relative abundance over 2% in at least one sample. Mollisol soil at the donor N site is designated as N, and transplanted Mollisol soils to the C site and the S site are designated as NC and NS, respectively. Similar designation is used for the Inceptisol (the C site) and Ultisol soils (the S site). A suffix “m” is designated for soil cropped with maize. Bare fallow soils collected in 2005 are designated with the suffix 2005 [Colour figure can be viewed at wileyonlinelibrary.com]

those in 2005 samples, implying that fungi were sensitive to yearly variations of climate.

Soil contains the largest terrestrial carbon pool on Earth (Tarnocai et al., 2009). Although much research has been done on organic matter decomposition by bacteria in terrestrial ecosystems (Berlemont & Martiny, 2013; Boer, Folman, Summerbell, & Boddy, 2005; Chase, Arevalo, Polz, Berlemont, & Martiny, 2016; Llado, Lopez-Mondejar, & Baldrian, 2017; Lopez-Mondejar, Zuhlke, Becher, Riedel, & Baldrian, 2016), it is well documented that fungi play pivotal roles in soil carbon decomposition (Baldrian et al., 2012; McGuire & Treseder, 2010; Zifcakova et al., 2016). Understanding how fungal and bacterial communities respond to climate change is important to the maintenance and prediction of the soil carbon pool. Our study supports Hypothesis 2 that carbon-decomposing genes derived from fungi are more influenced by climate changes than bacteria, consistent with the previous finding that warming favours fungal-mediated decomposition of plant litter (Pienkowski, Hodobod, & Ullmann, 2016). Our finding that soil transplantation increased the relative abundance of fungal chitin- and lignin-decomposing genes

(Figure 3) is alarming because the loss of soil recalcitrant carbon can reduce soil carbon stability, particularly in high-latitude soils, which account for one-third of the global soil carbon pool (Biasi et al., 2005).

Microbial biomass generally declined during transplantation (Table 1), which agreed with previous studies showing changes of soil microbial biomass by climate warming or seasonal succession (Bradford et al., 2008; Gou et al., 2015). Here, soils were sampled according to crop harvest time, and thus sampling dates might be a determinant of microbial biomass because soils at the S site were sampled in July while soils at the N and C sites were sampled in September.

4.2 | Different traits of fungi and bacteria causing dissimilar responses to climate changes

Soil pH either was not correlated or was less correlated with fungal communities compared to bacterial communities (Lauber, Hamady, Knight, & Fierer, 2009; Rousk et al., 2010), and fungi had a wider

TABLE 2 Environmental variable measurements

Environmental variables	N	NC	NS	C	CS	CN	S	SC	SN
Climatic variables									
Annual T ^a (°C)	2.1c ^{b,c}	13.5b	18.1a	13.5b	18.1a	2.1c	18.1a	13.5b	2.1c
Monthly T (°C)	12.4c	18b	29.8a	18b	29.8a	12.4c	29.8a	18b	12.4c
Annual R (mm)	496.2c	832.9b	1495a	832.9b	1495a	496.2c	1495a	832.9b	496.2c
Soil variables									
Soil pH	6.2 ± 0.2de	6.3 ± 0.1de	5.6 ± 0.1gh	7.9 ± 0.1b	8 ± 0ab	7.9 ± 0.1b	5.3 ± 0.1hi	5.8 ± 0.1fg	6.6 ± 1cd
SOM (g/kg)	46.4 ± 0.8bc	43.8 ± 2.3cd	41.3 ± 0.4d	8.7 ± 0.4e	7.9 ± 0.7e	9.5 ± 0.9e	9.8 ± 0.1e	10.3 ± 0.1e	9.6 ± 0.8e
WHC (%)	48.9 ± 0bc	45.8 ± 0cd	36.8 ± 0gh	25.3 ± 0k	20.7 ± 0l	31.2 ± 0ij	27.9 ± 0jk	32.8 ± 0hi	35.7 ± 0gh
Density (g/cm ³)	1.1 ± 0ij	1.1 ± 0ij	1.3 ± 0ef	1.5 ± 0a	1.5 ± 0a	1.4 ± 0b	1.4 ± 0bc	1.3 ± 0ef	1.4 ± 0cd
Soil porosity (%)	56.4 ± 0bcd	57.1 ± 0bc	47.9 ± 0g	45 ± 0hij	36.5 ± 0k	43.8 ± 0ij	43.1 ± 0j	52.1 ± 0f	46.7 ± 0gh
EC (μs/cm)	22.7 ± 3.1j	65.7 ± 3.8bc	25.7 ± 13.4j	33.1 ± 6.6hij	75.8 ± 1.5b	44 ± 0.8fgh	26.7 ± 1.8ij	23.1 ± 2.1j	62.1 ± 3.5cd
CEC (cmol/kg)	34.3 ± 1.3a	8.3 ± 0.2f	34.4 ± 0.2a	11.8 ± 0.5c	8.3 ± 0.3f	34.8 ± 0.2a	12.3 ± 0.4bc	12.3 ± 0.4bc	9.3 ± 0.2e
TN (g/kg)	1.8 ± 0.3bc	2 ± 0.2ab	1.7 ± 0c	0.6 ± 0e	0.5 ± 0.2e	0.6 ± 0.1de	0.6 ± 0.1e	0.7 ± 0.2de	0.6 ± 0e
TP (g/kg)	0.8 ± 0abc	0.8 ± 0a	0.8 ± 0ab	0.7 ± 0.1c	0.6 ± 0.1d	0.6 ± 0d	0.4 ± 0e	0.5 ± 0e	0.3 ± 0f
TK (g/kg)	18.7 ± 0.1a	19.4 ± 0.7a	19 ± 0.3a	20.6 ± 3.8a	18.3 ± 1.1a	17 ± 0.4a	9.7 ± 0.5b	10.4 ± 0.3b	9.8 ± 0.3b
AP (mg/kg)	39.6 ± 3.8ab	45.9 ± 12.2a	33.9 ± 0.7bc	7.3 ± 0.3ij	8.7 ± 0.8ij	8.7 ± 3.5ij	17.3 ± 0.7gh	21.8 ± 2.2defg	12.9 ± 1.4hi
AK (mg/kg)	201.7 ± 40.2a	168.3 ± 13.8b	164.2 ± 1.4b	99.2 ± 7.6gh	71.7 ± 8i	129.2 ± 16.1def	109.2 ± 1.4efg	208.3 ± 22.7a	202.5 ± 9a
NH ₄ -N (mg/kg)	0.6 ± 0.4f	0.6 ± 0.2def	1.5 ± 0.2abcd	0.6 ± 0.3f	1.2 ± 0.1bcdef	0.6 ± 0.4f	1.8 ± 0.5ab	1.3 ± 0.2abcdef	0.9 ± 0.1bcdef
NO ₃ -N (mg/kg)	13.3 ± 5.9a	3.5 ± 0.6efg	4.8 ± 0.3efg	4.4 ± 1.6efg	4.1 ± 0.2efg	8 ± 5.3bcde	5.3 ± 0.3defg	3.6 ± 0.9efg	0.7 ± 0.3g
Plant variables									
Seed weight (kg/ha)									
Above-ground biomass (kg/ha)									

^aAK: available potassium; Annual R: annual rainfall; Annual T: annual average temperature; AP: available phosphorus; CEC: cation exchange capacity; EC: electrical conductivity; Monthly T: average temperature in the sampling month; SD: soil bulk density; SOM: soil organic matter; TK: total potassium; TN: total nitrogen; TP: total phosphorus; WHC: water-holding capacity. ^bValues are shown as mean ± SD, calculated based on the raw data given in Supporting Information Table S2. ^cLetters after each value indicate significance of differences. Treatments with the same letter are not significantly different ($p > 0.05$) as determined by one-way ANOVA followed by LSD test in SAS version 8.1.

range in pH tolerance (5–9 units; Wheeler, Hurdman, & Pitt, 1991) than bacteria (3–4 units; Rosso, Lobry, Bajard, & Flandrois, 1995). Similarly, we found that the fungal pH range of 1.86 was significantly ($p < 0.001$) broader than bacterial pH range of 1.53 (Table 3). Partial Mantel tests further verified that fungal communities were more controlled by climate drivers, such as temperature and precipitation, than were bacterial communities. Moreover, the VPA results also showed that climate variables had the most influence on fungal communities, while soil pH, SOM, TN, TP and TK collectively played a more influential role in bacterial communities. The strong influence of climate drivers on fungi provided a reasonable explanation for our finding that fungal community compositions were more similar in samples from the same climate regime (Figure 1).

Here we found that bacterial communities were sensitive to soil conditions and could tolerate narrower ranges in soil pH, bulk density, TP and TK than fungi (Table 3). One possible explanation for the strong association between bacterial communities and these environmental variables is that physical attachment of bacteria to

particles has a strong influence on bacterial physiology and biochemistry (Ahn et al., 2006; Becquevort, Rousseau, & Lancelot, 1998; Iribar, Sánchez-Pérez, Lyautey, & Garabétian, 2007). In a study to examine bacterial communities in the Columbia River estuary, ~90% of the heterotrophic bacteria attached to particles, and this property has been used to efficiently decompose organic matter (Crump, Armbrust, & Baross, 1999; Crump, Simenstad, & Baross, 1998). In soils, bacteria either adhere to mineral particles smaller than their cells to form "bacterial microaggregates," which are mineral coatings of cell envelopes, or adhere to larger particles (Huang, Bollag, & Senesi, 2002). The adhesion between soil particles and bacteria makes it difficult to separate bacteria from soils (Richaume, Steinberg, Jocteur-Monrozier, & Faurie, 1993). Furthermore, bacteria are small enough to enter water/air-filled pores between soil particles, further associating them with soil environments. In contrast, fungal attachment to particles is limited by individual size and the hyphal network (Lehmann et al., 2011). Therefore, bacteria might be more sensitive to soil conditions than fungi.

Nm	NCm	NSm	Cm	CSm	CNm	Sm	SCm	SNm
2.1c	13.5b	18.1a	13.5b	18.1a	2.1c	18.1a	13.5b	2.1c
12.4c	18b	29.8a	18b	29.8a	12.4c	29.8a	18b	12.4c
496.2c	832.9b	1495a	832.9b	1495a	496.2c	1495a	832.9b	496.2c
6.1 ± 0ef	6.7 ± 0cd	5.8 ± 0.1fg	8.1 ± 0.1ab	7.8 ± 0.2b	8.4 ± 0a	5 ± 0.1i	6.9 ± 0c	5.3 ± 0.1hi
51.4 ± 1.2a	48.4 ± 2.4ab	45.1 ± 6.4c	8.3 ± 0.5e	7.9 ± 0.6e	10.3 ± 0.9e	9.6 ± 0.4e	10.3 ± 0.2e	8.9 ± 2.5e
71.2 ± 6.4a	48.3 ± 2bc	41.4 ± 2.1ef	26.5 ± 1.2k	28.8 ± 1.9jk	44 ± 4.6de	38.8 ± 4.5fg	37.4 ± 2.1fg	50.4 ± 2b
0.9 ± 0k	1.1 ± 0j	1.1 ± 0hi	1.4 ± 0b	1.3 ± 0de	1.2 ± 0.1gh	1.1 ± 0.1hi	1.2 ± 0.1fg	1.1 ± 0.1j
65.4 ± 0.9a	58.5 ± 0.6b	54.9 ± 0.7cde	47.6 ± 1.6g	46 ± 0.3ghi	53.5 ± 2.6def	52.6 ± 3.5ef	54.3 ± 2.2def	57.7 ± 2.8b
52 ± 5.9cde	97.1 ± 9.9a	57.1 ± 12.6def	66.6 ± 8.8bc	50.1 ± 5.5efg	75.9 ± 8b	37.6 ± 1.1hi	94.8 ± 3.6a	39.7 ± 3.1gh
34.5 ± 0.7a	8 ± 0.6f	12.8 ± 0.2b	34.4 ± 0.5a	34.8 ± 0.5a	8.3 ± 0.2f	12 ± 0.4c	8 ± 0.2f	10.9 ± 0.5d
2.2 ± 0.1a	1.9 ± 0b	1.8 ± 0.1bc	0.5 ± 0.1e	0.5 ± 0e	0.6 ± 0e	0.8 ± 0.4d	0.6 ± 0e	0.7 ± 0.1de
0.8 ± 0ab	0.8 ± 0bc	0.8 ± 0bc	0.6 ± 0d	0.6 ± 0d	0.6 ± 0d	0.4 ± 0e	0.4 ± 0e	0.4 ± 0e
18.4 ± 0.5a	18.4 ± 0.2a	12.4 ± 10.7b	17.5 ± 0.4a	17.7 ± 0.1a	17.4 ± 0.3a	9.7 ± 0.4b	9.7 ± 0.1b	9.5 ± 0.1b
26.8 ± 5.6de	28.3 ± 2.7cd	20.6 ± 3.2efg	3.5 ± 0.4j	5.9 ± 0.4j	5.3 ± 0.5j	17.3 ± 2.6gh	17.9 ± 1.4fgh	24 ± 4.7def
139.2 ± 5.8cd	131.7 ± 7.2de	128.3 ± 5.2def	73.3 ± 1.4i	75 ± 2.5i	80.8 ± 6.3hi	110 ± 5efg	106.7 ± 20.1fg	161.7 ± 17.7bc
0.6 ± 0.1ef	1.3 ± 0.7abcdef	1.5 ± 0.1abcde	0.8 ± 0.1cdef	2.2 ± 2a	0.5 ± 0.1f	1.6 ± 0.1abc	1 ± 0.4bcdef	0.9 ± 0.2bcdef
10.6 ± 6.2abc	9.9 ± 4.3abcd	12.6 ± 5.4ab	4.2 ± 0.5efg	6.3 ± 3.1cdef	4.6 ± 2.8efg	5.2 ± 0.4defg	3.5 ± 0.3efg	2.5 ± 0.9fg
	2246.2 ± 1464d	6480.8 ± 442.3a	1447.6 ± 343.2de	5340.2 ± 225.6b	1069.7 ± 128.1ef	1622.2 ± 250de	NA	3734.4 ± 118.6c
	4822.6 ± 284.5bc	5828.2 ± 125.5a	4841.3 ± 68.7bc	5232.3 ± 964.9ab	4523.8 ± 315bc	3127.8 ± 610.4d	2440.5 ± 103.1de	4354.5 ± 480c

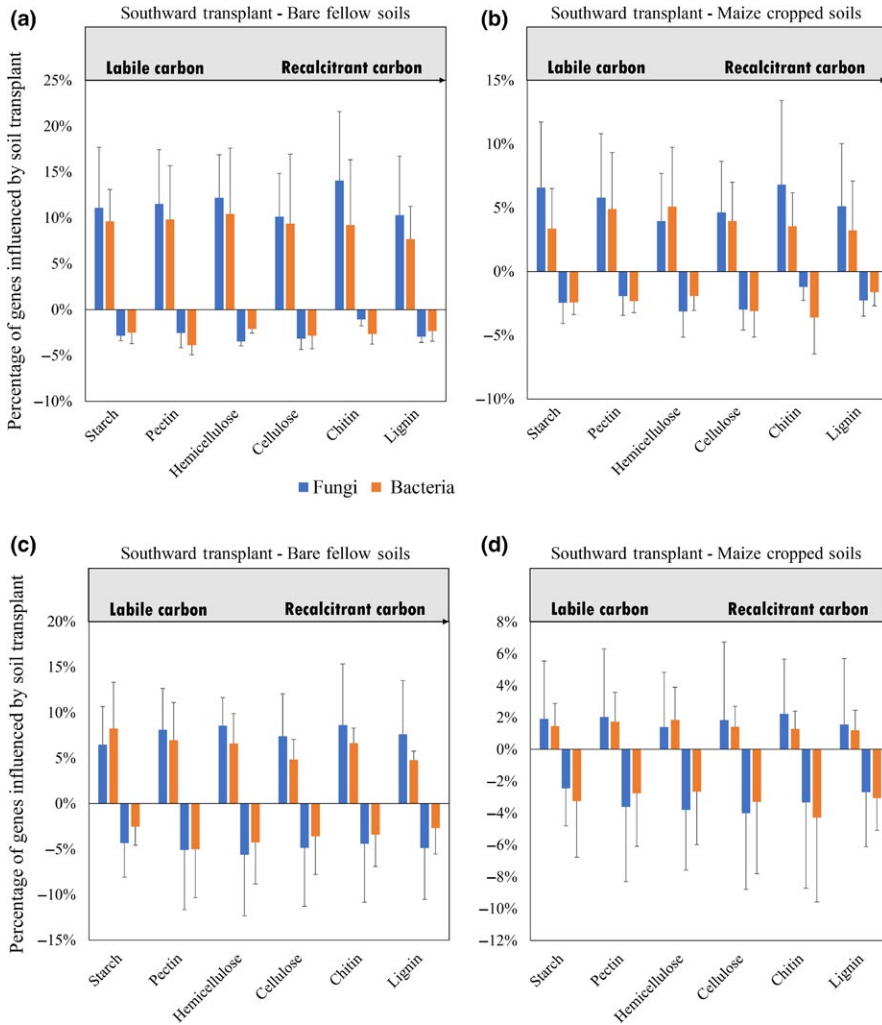


FIGURE 3 The percentage of carbon-decomposing genes changed by southward soil transplantation in (a) bare fallow soils and (b) maize cropped soils, and by northward soil transplantation in (c) bare fallow soils and (d) maize cropped soils. The x-axis is presented in the order from labile carbon to recalcitrant carbon. The y-axis is the percentage of functional gene numbers significantly ($p < 0.05$) changed by soil transplantation to total gene numbers. A total of 37 genes were analysed. Starch-decomposing genes include *amyA*, *amyX*, *apu*, *aca*, *glucoamylase*, *isopullulanase*, *npIT* and *pulA*. Pectin-decomposing genes include *endopolygalacturonase*, *exopolygalacturonase*, *pec*, *pectate lyase*, *pectin lyase*, *pectinase*, *pel_CDeg*, *Pg_Oomycetes*, *pme*, *RgaE*, *rgh* and *rgl*. Hemicellulose-decomposing genes include *ara*, *mannanase*, *xylA*, *xylanase* and *xylose reductase*. Cellulose-decomposing genes include *cellobiase*, *endoglucanase* and *exoglucanase*. Chitin-decomposing genes include *acetylglucosaminidase*, *chitin deacetylase*, *chitinase*, *endochitinase* and *exochitinase*. Lignin-decomposing genes include *glx*, *ligninase*, *mnp* and *phenol oxidase* [Colour figure can be viewed at wileyonlinelibrary.com]

Microbes can migrate to favourable environments by being motile, which is beneficial for nutrient uptake. Fungi are more motile than bacteria, although bacteria have a higher dispersal range (Schmidt, Nemergut, Darcy, & Lynch, 2014). The reason for this is that free-swimming microorganisms have a lower size limit of ~ 0.6 – $1.8 \mu\text{m}$, below which directed movement is impossible (Dusenbery, 1997). Higher motility is important for fungi because they survive using strictly heterotrophic lifestyles. In contrast, a number of bacteria are autotrophs, such as aerobic chemoautotrophic bacteria (Schmidt & Belser, 1994) and anaerobic phototrophic bacteria (Musat et al., 2008). Thus, many bacterial taxa are not constrained by the supply of available soil organic matter.

Like plants and animals, soil microorganisms are more ubiquitous in environments if they are able to thrive in a broader range of habitats, and this can often be characterized by individual larger genome sizes and high metabolic versatility (Barberán et al., 2014). These traits could be used to predict the spatial distributions of taxa and their abilities to respond to different environmental conditions. We found that the frequencies of occurrence (OTU occupancies) of both the fungal community and the bacterial community (Figure 3) were correlated with their own environmental ranges, suggesting that the habitat

breadth–distribution relationship might be another robust ecological attribute.

4.3 | Concluding remarks

In this study, we examined how climate changes affect soil microbial communities, which in turn affect soil carbon storage essential for ecosystem functioning. We showed that fungal biomass and community composition acclimatized to the destination environment, while bacterial communities remained largely unchanged. Fungal genes encoding carbon-decomposing enzymes were significantly increased to a larger extent than those from bacteria. To explain those observations, we found that fungal occupancy across samples was mainly determined by annual average air temperature and rainfall, while bacterial occupancy was related more to soil conditions, which remained stable 6 years after soil transplantation. By revealing in-depth, distinct features between fungal and bacterial responses to simulated climate changes, we propose that the higher sensitivity of fungi to climate changes emphasizes an important consideration for climate–carbon modelling, given the fundamental role of fungi in carbon decomposition studies.

TABLE 3 Environmental ranges (the breadth of environmental conditions wherein an operational taxonomic unit is present) of bacteria and fungi

Environmental variable	Fungi	Bacteria
Climatic variables		
Annual T ^a *** ^b	8.89 ± 0.11	11.82 ± 0.04
Annual R ^{***}	529.26 ± 6.79	719.15 ± 2.27
Mean climatic range ^{***}	138.07 ± 1.75	187.31 ± 0.59
Soil variables		
Soil pH ^{***}	1.86 ± 0.02	1.53 ± 0.01
SOM ^{***}	25.72 ± 0.31	20.63 ± 0.12
WHC ^{***}	24.82 ± 0.27	23.22 ± 0.09
Density ^{***}	0.35 ± 0.003	0.33 ± 0.001
Soil porosity ^{***}	14.36 ± 0.13	13.85 ± 0.04
EC ^{***}	49.97 ± 0.43	51.86 ± 0.15
CEC	19.58 ± 0.18	19.61 ± 0.07
TN ^{***}	1.05 ± 0.01	0.89 ± 0.004
TP ^{***}	0.30 ± 0.003	0.25 ± 0.001
TK ^{***}	8.21 ± 0.10	6.57 ± 0.04
AP ^{***}	23.42 ± 0.26	20.81 ± 0.10
AK ^{**}	90.43 ± 0.86	88.07 ± 0.31
NH ₄ -N ^{**}	1.34 ± 0.02	1.40 ± 0.01
NO ₃ -N ^{***}	9.00 ± 0.10	8.36 ± 0.03
Mean soil variable range ^{***}	18.04 ± 0.15	17.17 ± 0.05

^aAK: available potassium; Annual R: annual rainfall; Annual T: annual average temperature; AP: available phosphorus; CEC: cation exchange capacity; EC: electrical conductivity; SD: soil bulk density; SOM: soil organic matter; TK: total potassium; TN: total nitrogen; TP: total phosphorus; WHC: water-holding capacity. Mean environmental range is calculated as the average of all environmental variable ranges. Values are shown as mean ± SE. ^bSignificance of the difference between bacterial and fungal ranges was calculated by a *t* test in Excel and corrected by Benjamini-Hochberg multiple correction: **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

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TABLE 4 Partial Mantel tests determining correlations between microbial communities and environmental variables

Environmental variable	Fungi	Bacteria
Annual T ^a	0.39 ^{***b}	-0.04
Annual R	0.50 ^{***}	-0.02
Soil pH	0.31 ^{***}	0.63 ^{***}
SOM	-0.09	0.22 ^{***}
WHC	-0.18	-0.06
Density	-0.10	0.04
Soil porosity	-0.08	0.01
EC	-0.01	-0.01
CEC	0.010	0.04
TN	-0.11	0.18 ^{***}
TP	0.16 ^{***}	0.53 ^{***}
TK	0.23 ^{***}	0.54 ^{***}
AP	0.13 ^{**}	0.26 ^{***}
AK	0.16 ^{***}	0.24 ^{***}
NH ₄ -N	0.14 [†]	0.08 ^{***}
NO ₃ -N	-0.14	-0.07

^aAK: available potassium; Annual R: annual rainfall; Annual T: annual average temperature; AP: available phosphorus; CEC: cation exchange capacity; EC: electrical conductivity; SD: soil bulk density; SOM: soil organic matter; TK: total potassium; TN: total nitrogen; TP: total phosphorus; WHC: water-holding capacity. ^br values of Mantel tests are provided with asterisks to indicate statistical significance: [†]*p* < 0.05, ***p* < 0.01, ****p* < 0.001.

AUTHOR CONTRIBUTIONS

Y.Y., B.S. and J.Z. developed the study concept and design; F.W. collected the samples and analysed the soil physical and chemical properties; C.W. completed the DNA preparation and environmental genomics experiments; M.Z., L.W., M.W., Y.L. and L.H. performed the data analysis; and M.Z. and Y.Y. drafted the manuscript. All authors read and approved the final manuscript.

DATA ACCESSIBILITY

Both MiSeq sequencing and GeoChip data are available online (<http://www.ncbi.nlm.nih.gov/geo/>). The accession number for the MiSeq data is SRP069263 and the accession number for the GeoChip data is GSE77546.

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SUPPORTING INFORMATION

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