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Differentiation strategies of soil rare and abundant microbial taxa in response to changing climatic regimes

Yuting Liang,[1*] Xian Xiao,[1] Erin E. Nuccio,[2] Mengting Yuan,[3] Na Zhang,[1,4] Kai Xue,[4,5] Frederick M. Cohan,[6] Jizhong Zhou[5,7] and Bo Sun[1*]

[1]*State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing, 210008, China.*

[2]*Lawrence Livermore National Laboratory, Livermore, CA, 94550, USA.*

[3]*Department of Environmental Science Policy and Management, University of California, Berkeley, CA, 94720, USA.*

[4]*University of the Chinese Academy of Sciences, Beijing, 100049, China.*

[5]*Institute for Environmental Genomics, Department of Microbiology and Plant Biology, and School of Civil Engineering and Environmental Sciences, University of Oklahoma, Norman, OK, 73019, USA.*

[6]*Department of Biology, Wesleyan University, Middletown, CT, 06459-0170, USA.*

[7]*Earth and Environmental Sciences, Lawrence Berkeley National Laboratory, Berkeley, CA, 94270, USA.*

Summary

Despite the important roles of soil microbes, especially the most diverse rare taxa in maintaining community diversity and multifunctionality, how different climate regimes alter the stability and functions of the rare microbial biosphere remains unknown. We reciprocally transplanted field soils across a latitudinal gradient to simulate climate change and sampled the soils annually after harvesting the maize over the following 6 years (from 2005 to 2011). By sequencing microbial 16S ribosomal RNA gene amplicons, we found that changing climate regimes significantly altered the composition and dynamics of soil microbial communities. A continuous succession of the rare and abundant communities was observed. Rare microbial communities were more stable under changing climatic regimes, with lower variations in temporal dynamics, and higher stability and constancy of diversity. More nitrogen cycling genes were detected in the rare members than in the abundant members, including *amoA*, *napA*, *nifH*, *nirK*, *nirS*, *norB* and *nrfA*. Random forest analysis and receiver operating characteristics analysis showed that rare taxa may act as potential contributors to maize yield under changing climatics. The study indicates that the taxonomically and functionally diverse rare biosphere has the potential to increase functional redundancy and enhance the ability of soil communities to counteract environmental disturbances. With ongoing global climate change, exploring the succession process and functional changes of rare taxa may be important in elucidating the ecosystem stability and multifunctionality that are mediated by microbial communities.

Background

Since 1850, the Earth's surface temperature has increased by 0.76°C and is expected to increase by another 1.8–4.0 °C by the end of this century (IPCC, 2014), resulting in a negative impact on ecosystem functions and reduced ecosystem services (Challinor *et al*., 2014; Moore and Lobell, 2015; Liu *et al*., 2016). It is believed that rising temperature has profound and diverse effects on all levels of biological organization, from individual organisms to whole biomes (Woodward *et al*., 2010). Even for the most abundant and diverse microbes with high redundancy, studies demonstrate that warming and precipitation changes can profoundly influence soil microbial biomass, community structures (Liu *et al*., 2015) and functions (Zhao *et al*., 2014). Soil microorganisms play fundamental roles in biogeochemical cycling and are major drivers of terrestrial ecosystem productivity (Van Der Heijden *et al*., 2008; Bardgett and Van Der Putten, 2014; Delgado-Baquerizo *et al*., 2016). Plant beneficial microbes can promote plant growth by manipulating the hormonal signalling of plants, repelling or outcompeting pathogenic strains, and increasing the bioavailability of soil-borne nutrients (Jacoby *et al*., 2017). Climate can directly and indirectly affect the contributions of the microbial community to ecosystem function by

Received 22 October, 2019; revised 10 February, 2020; accepted 14 February, 2020. *For correspondence. E-mail ytliang@issas.ac.cn. Tel. 86 25 86881568; Fax 86-25-86881000. bsun@issas.ac.cn. Tel. 86-25-86881282; Fax 86 25 86881000.

altering their composition, activities and interactions (Wolters *et al*., 2000). Regional-scale variation in climate has been proposed to mediate the effects of bacterial and fungal biodiversity on ecosystem functioning in natural ecosystems (Jing *et al*., 2015).

Traditionally, the main focus of soil microbial studies has been on the abundant members of the communities because it is generally thought that they are most active and important in the biogeochemical cycle (Cottrell and Kirchman, 2003). However, abundant species represent only a small proportion of microbial diversity (Pedrós-Alió, 2012). Recent studies have increasingly emphasized the ecological importance of the rare biosphere because with similar-sized communities, rare taxa can be more metabolically active than abundant taxa (Lynch and Neufeld, 2015; Xue *et al*., 2018). Meanwhile, rare members are likely to be functionally dissimilar than the abundant members, which offer complementary functions or unique metabolic pathways to support the overall community functions (Dimitriu *et al*., 2010). Rare and abundant taxa might respond unequally to a perturbation, both in diversity and community composition, as stochastic processes are more pronounced in affecting the rare community assembly (Xue *et al*., 2018). The different responses of the two groups could then lead to potentially different roles in maintaining community functions (Jiao *et al*., 2017; Xue *et al*., 2018). However, the successional and functional changes of rare and abundant taxa in response to different climate regimes and the potential linkages to the aboveground plants are still unknown, which are essential for predicting and elucidating ecosystem stability under climate change.

Field-based translocation experiments are useful for empirically testing the responses of belowground organisms to temperature and precipitation changes simultaneously, which can allow direct attribution of ecological mechanisms to biotic responses under different climatic conditions (Fordham, 2015). Thus, a unique soil reciprocal transplant experiment (SRTE) was established in 2005 at three long-term agricultural experimental stations of the Chinese Academy of Sciences, representing three typical agricultural soil types: Phaeozem, Cambisol and Acrisol. Specifically, we reciprocally transplanted large quadrats of intact soil ($1.2 \times 1.4 \times 1.0$ m) among three geoclimatic regions: a cold temperate monsoon region, a warm temperate monsoon region and a subtropical monsoon region (Fig. 1A). Maize was planted once a year from 2006 to 2011 and was subjected to the same fertilization and management regime at the three sites (details in Methods). The SRTE serves as a platform for a number of studies examining climate and cropping effects on soil microbial diversity and its ecological functions (Sun *et al*., 2013; Zhao *et al*., 2014; Liang *et al*., 2015). Aboveground maize (including the biomass, yield, and grain and straw N, P and K nutrients) and belowground microbial communities were monitored annually from 2005 to 2011. A total of 189 soil samples were analysed based on integrated community and functional analyses using Illumina 16S rRNA gene sequencing and a functional gene microarray, GeoChip, to interrogate both soil microbial taxonomic diversity and potential functions. As previous studies have shown the distinct ecologies of the rare and abundant microbial biospheres (such as the underlying ecological processes of community assembly) (Galand *et al*., 2009; Lynch and Neufeld, 2015; Jousset *et al*., 2017), we hypothesize that changing climatic regimes will affect the diversity and composition of rare and abundant soil microbial communities to different extents. Given the high taxonomic breadth and low active loss rate (viral lysis or predation) of the rare communities (Pedrós-Alió, 2006), we propose that rare microbial diversity and community composition are more stable to changing climatic regimes relative to abundant taxa. With tremendous phylotypes in rare microbial biospheres (Galand *et al*., 2009; Lynch and Neufeld, 2015), more functional diversity can be expected in the rare communities, such as the nitrogen (N) cycling functional genes, which also respond differently to the changing climatic regimes in accordance with the changed community compositions. Here, we show contrasting responses of rare and abundant microbial diversity, composition and N cycling functions to changing climatic regimes, with the higher stability of rare taxa. Meanwhile, rare taxa may contribute disproportionately to the overall community functions relative to common taxa with higher taxonomic and functional diversities.

Results

Changes of plant and soil microbial diversity under different climatic regimes

Maize yield in Phaeozem and Cambisol is highest when the soil remained *in situ* under the original climate, compared with that transplanted to warmer and cooler climatic regimes (Additional file 1: Fig. S1a). The seed weight in Phaeozem decreased from 9840 to an average of 8568 kg ha^{-1} in the central and southern sites ($p = 0.04$), and in Cambisol it decreased from 9783 to 5502 kg ha^{-1} with warming ($p = 0.001$) and from 9783 to 6604 kg ha^{-1} with cooling ($p = 0.001$). However, seed weight significantly increased upon transplanting the Acrisol soil to cooler regions, from 3663 to 5935 kg ha^{-1} ($p = 0.002$). Temporal stability of maize yield with climate warming and cooling was evaluated by measuring the reciprocal of the coefficient of variation of seed weight, hereafter the maize yield constancy (Fig. 1B). Generally, the constancy value of maize yield for the 6-year duration (2006–2011) and 2-year durations (2006–2007,

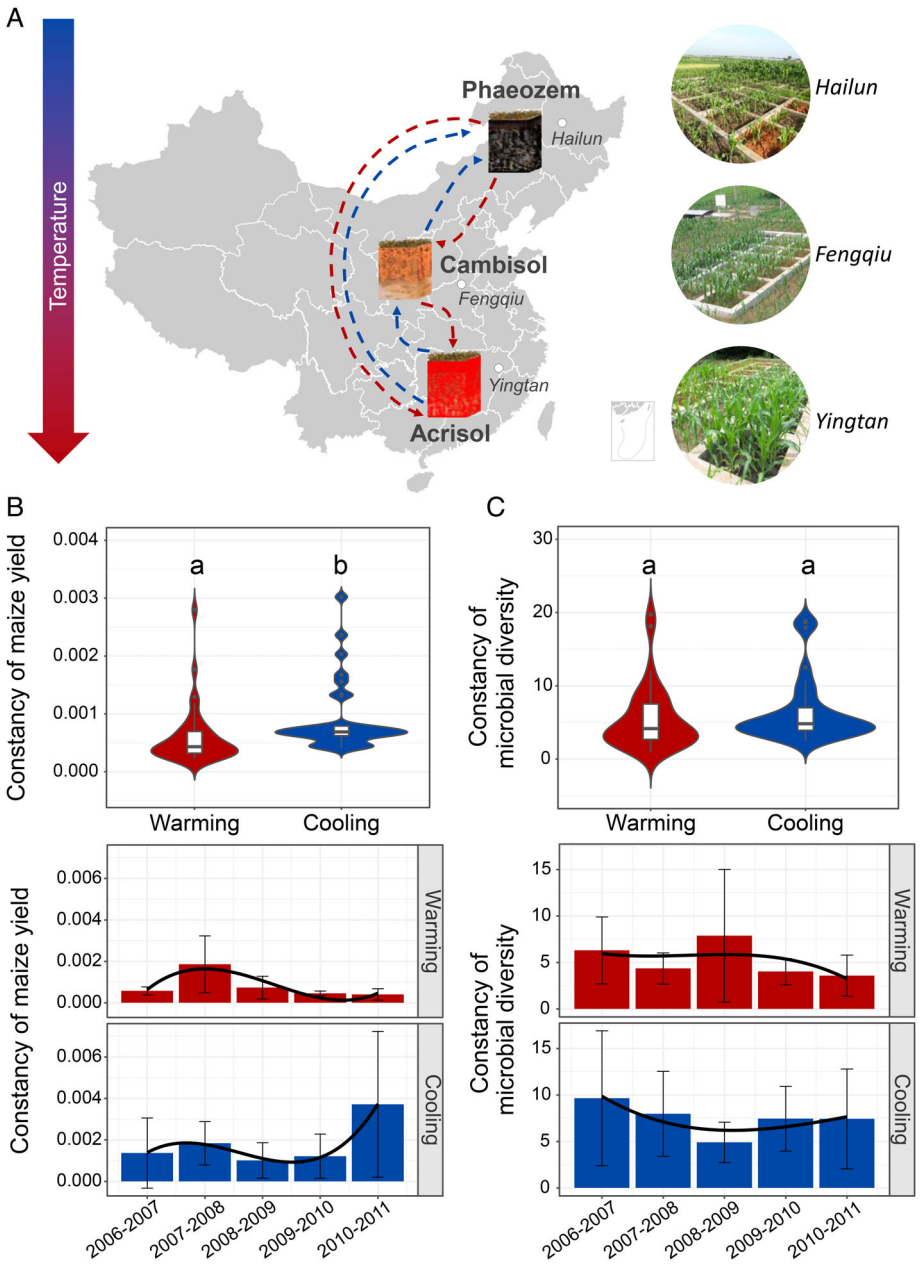

Fig. 1. Impacts of changing climatic regimes on the constancy of aboveground yield and underground microbial diversity. A. Schematic representation of the agroecosystem based on the soil reciprocal transplant experiment (SRTE) established in three geoclimatic regions in 2005, including a cold temperate monsoon climate, a warm temperate monsoon climate and a subtropical monsoon climate. The overall constancy of (B) maize yield and (C) microbial Shannon diversity with climate warming and cooling from 2006 to 2011, and the constancy for 2-year durations (2006–2007, 2007–2008, 2008–2009, 2009–2010 and 2010–2011). Different lowercase letters indicate significant differences between treatments, as revealed by one-way analysis of variance with Duncan's multiple range test at $p < 0.05$.

2007–2008, 2008–2009, 2009–2010 and 2010–2011) were higher with climate cooling than with warming. This indicated a more stable maize yield with climate cooling, especially in the late period of soil transplantation (2010–2011).

For the soils *in situ*, microbial taxonomic richness was higher in the northern Phaeozem and central Cambisol soils than in the southern Acrisol soil by 20.9% and 18.5% respectively (Additional file 1: Fig. S1b). Warming significantly decreased microbial taxonomic richness in the northern Phaeozem soil by 12.3%. There was no significant difference in the constancy of overall microbial diversity and N cycling gene richness under climate warming and cooling during the 6 years' soil transplantation (Fig. 1C, Additional file 1: Fig. S1b).

Changing climatic regimes also had strong effects on several soil geochemical attributes (Additional file 1: Fig. S2). Soil warming caused a significant decrease in soil organic matter (SOM) in the northern Phaeozem soil ($p < 0.001$) and a minor OM decrease in the central Cambisol soil ($p = 0.073$). Cooling had no significant impact on SOM. N dynamics were also altered by soil warming and cooling. Warming significantly decreased N utilization, while cooling increased N utilization ($p < 0.05$) (Additional file 1: Fig. S3).

Successions of rare and abundant taxa under changing climatic regimes

To understand the community successions of both rare and abundant taxa, we classified all operational taxonomic units (OTUs) into six categories (Dai *et al*., 2016; Xue *et al*., 2018) (Table 1). For the comparative study of abundant and rare taxa, always abundant taxa (AAT) and conditionally abundant taxa (CAT) were collectively referred to as abundant taxa, and always rare taxa (ART) and conditionally rare taxa (CRT) were collectively referred to as rare taxa. A small fraction of the total community was classified as abundant (22–42 OTUs) and accounted for almost half of the abundance of the soil microbial communities. However, OTUs that were always or conditionally rare accounted for a huge proportion of taxa (4388–4879 OTUs) and accounted for 35.2%–42.5% of the total abundance. There were certain phyla that were either abundant or rare in every ecosystem, such as Proteobacteria, Actinobacteria and Acidobacteria (Additional file 1: Fig. S4), and some phyla were always rare, such as Cyanobacteria, Armatimonadetes, Nitrospirae and Planctomycetes. Warming significantly decreased the microbial Shannon diversity of both rare and abundant taxa in the northern Phaeozem soil by 2.4% and 5.5% ($p < 0.01$) respectively, and cooling increased the microbial Shannon diversity of abundant taxa in the southern Acrisol soil by 4.1% ($p < 0.05$) (Additional file 1: Fig. S5).

A significant influence of the climate regime on both rare and abundant community structure was observed in all three soil systems. Warming and cooling induced a continuous change in belowground communities over time ($p < 0.05$) (Fig. 4A). Both rare and abundant community structures were significantly altered by warming and cooling ($p < 0.05$) based on the statistical *R*-value of analysis of similarities (ANOSIM) (Additional file 1: Table S2). The temporal turnover of rare and abundant communities under changing climatic regimes was further estimated by the slopes of the microbial time-decay relationship. By estimating the deviations of temporal turnover of microbial communities (Δ temporal turnover) under changing climatic regimes, we observed that rare taxa (Δ temporal turnover: 0.053 and 0.073) were more stable than abundant taxa (Δ temporal turnover: 0.108 and 0.103) under warming and cooling respectively (Additional file 1: Fig. S6). Based on Similarity Percentage (SIMPER) analysis, rare taxa contributed more than abundant taxa to the overall dissimilarity of microbial communities induced by climate warming and cooling (Table 2). Rare taxa accounted for 22.8%–32.3% of the variations in the overall microbial communities, while abundant taxa accounted for approximately 7.0%–17.4%.

The stability of rare and abundant taxa under changing climatic regimes was quantitatively estimated by calculating the resistance microbial α-diversity (Shannon index) under transplanted conditions in comparison with that *in situ* (Fig. 2B). Our results showed that rare taxa in soil microbial communities were more resistant to changing climatic regimes than abundant taxa under both warming and cooling ($n = 42$, $F_{1,82} = 28.17$, $p < 0.001$). The average resistance ratios (Rs) of the rare taxa in response to climate warming and cooling were 0.96 and 0.95 respectively, and those of abundant taxa were 0.80 and 0.83. The stability of rare and abundant microbial communities was further examined by evaluating the constancy of communities with changing climatic regimes across scales (Fig. 2C). Generally, the rare taxa were more stable than the abundant taxa under soil transplantation for

Table 1. A detailed description of abundant and rare OTUs at 97% similarity level.

	Phaeozem		Cambisol		Acrisol	
Category	OTU number	Relative abundance	OTU number	Relative abundance	OTU number	Relative abundance
Always abundant taxa	3 (0.06%)	30.61	0	0	0	0
Conditionally abundant taxa	19 (0.38%)	15.95	32 (0.68%)	32.46	42 (0.93%)	46.78
Always rare taxa	1161 (23.17%)	0.47	926 (19.65%)	0.35	1178 (26.11%)	0.36
Conditionally rare taxa	3718 (74.20%)	34.75	3605 (76.49%)	42.11	3210 (71.14%)	36.87
Moderate taxa	100 (2.00%)	16.55	126 (2.67%)	20.63	61 (1.35%)	11.71
Conditionally rare and abundant taxa	10 (0.20%)	1.68	24 (0.51%)	4.45	21 (0.47%)	4.21

Always abundant taxa (AAT) were defined as the OTUs with a relative abundance ≥1% in all samples.
Conditionally abundant taxa (CAT) were defined as the OTUs with a relative abundance ≥1% in some samples but never rare (<0.01%) in any samples.
Always rare taxa (ART) were defined as the OTUs with a relative abundance <0.01% in all samples.
Conditionally rare taxa (CRT) were defined as the OTUs with a relative abundance <0.01% in some samples but never abundant (≥1%) in any samples.
Moderate taxa (MT) were defined as the OTUs with a relative abundance between 0.01% and 1% in all samples.
Conditionally rare and abundant taxa (CRAT) were defined as the OTUs with a relative abundance varying from rare (<0.01%) to abundant (≥1%).

a 6-year period (n = 124, $F_{1,122}$ = 9.26, p = 0.003). The average constancy values of the rare taxa in response to climate warming and cooling were 15.48 and 10.38 respectively, and those of abundant taxa were 9.66 and 7.73.

Receiver operating characteristics (ROC) curves confirmed that including rare microbial diversity (AUC = 0.66) or abundance (AUC = 0.51) in predicting the maize yield constancy could improve the specificity and sensitivity of models compared with including the abundant microbial diversity (AUC = 0.46) or abundance (AUC = 0.40) (Fig. 2D). These results indicated the potential importance of rare taxa in the mediation of crop yield under changing climatic regimes.

Table 2. Contributions (%) of rare and abundant taxa for the difference between groups of samples in NMDS.

	In situ and warming		*In situ* and cooling	
	Phaeozem	Cambisol	Cambisol	Acrisol
Rare taxa	22.8	31.6	29.4	32.3
Abundant taxa	17.4	7.9	7.0	15.5

The direct and indirect effects of climatic and soil attributes on microbial diversity of rare and abundant taxa

A structural equation model (SEM) was fitted to investigate the direct and indirect effects of mean annual temperature (MAT), mean annual precipitation (MAP) and soil attributes (pH and OM) on the soil microbial diversity of both rare and abundant taxa (Additional file 1: Fig. S7). The final models fit both the warming (Fig. 3A) and cooling (Fig. 3B) data sets (n = 91). In the context of climate warming, MAP exerted significant direct negative effects on both rare and abundant microbial diversity (rare taxa, r = −0.66, p < 0.001; abundant taxa, r = −0.51, p < 0.001). MAT also exerted significant negative effects on abundant microbial diversity (r = −0.36, p < 0.05). Though soil pH and OM were significantly

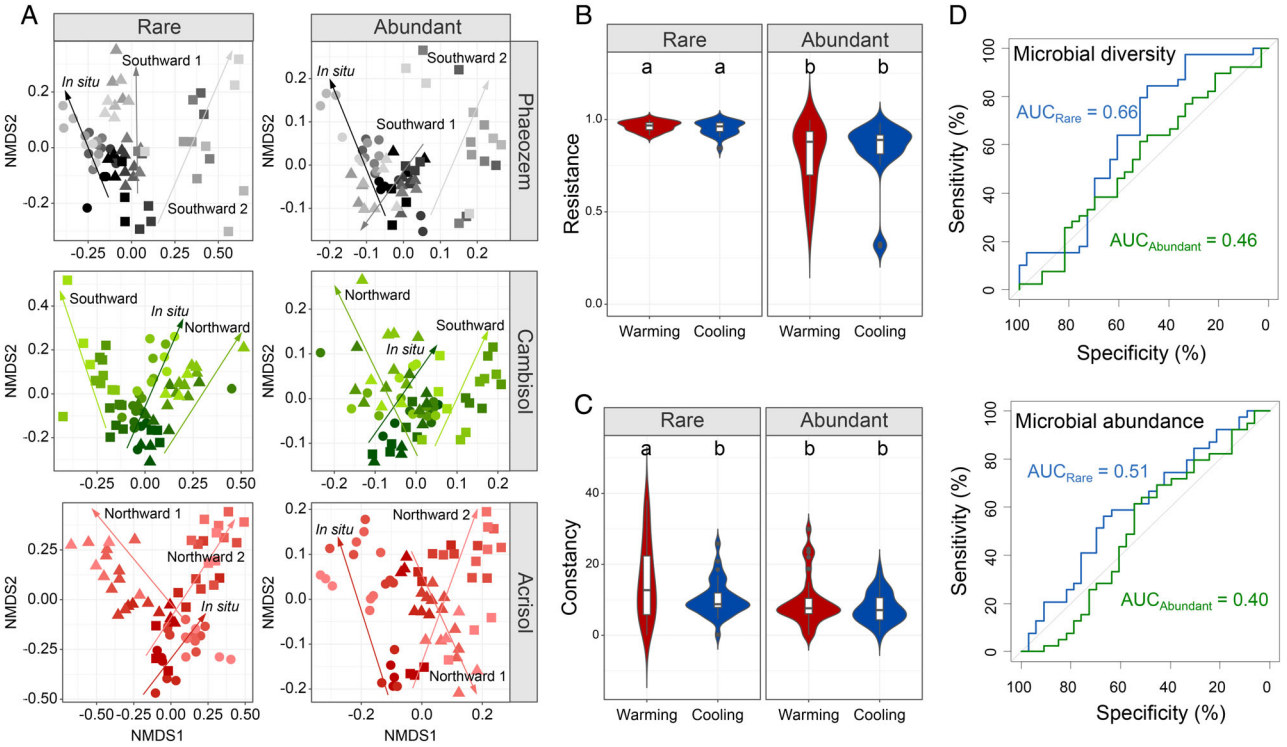

Fig. 2. Changes of the rare and abundant microbial taxonomic structure under changing climatic regimes simulated by soil transplantation (A); the stability of rare and abundant microbial communities estimated by both the indices of resistance (B) and constancy (C); and receiver operating characteristic (ROC) curves of the constancy of microbial diversity and abundance for the maize yield constancy (D). NMDS ordination was performed based on Bray–Curtis distances. Colours from dark to light indicate time dynamics from 2005 to 2011. Southward 1 and 2 indicated the Phaeozem transplanted to Fengqiu and Yingtan (climate warming) respectively; northward 1 and 2 indicated the Acrisol transplanted to Fengqiu and Hailun (climate cooling) respectively. Northward and southward indicated the Cambisol transplanted to Hailun (climate cooling) and Yingtan (climate warming) respectively. Circles always represent the soils *in situ*; triangles and squares represent cooling/warming in Phaeozem/Acrisol soils; for Cambisol, triangles represent cooling, and squares represent warming. Boxes with different lowercase letters indicate significant differences between treatments, as revealed by one-way analysis of variance with Duncan's multiple range test at p < 0.05. AUC, area under the curve.

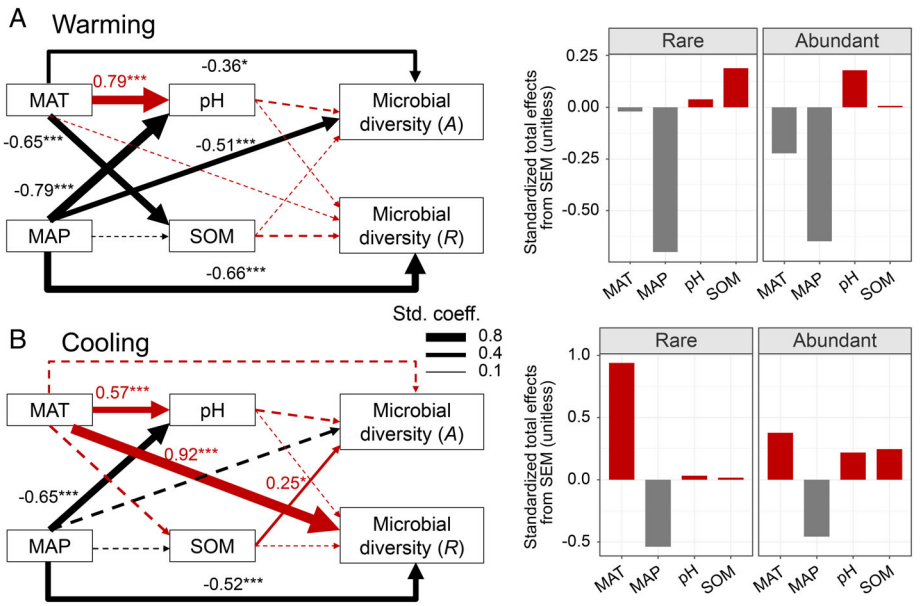

Fig. 3. Structural equation model (SEM) to illustrate the direct and indirect effects of climatic and soil attributes on the microbial diversity of rare and abundant taxa under climate warming and (B) cooling. Red and black arrows indicate positive and negative path coefficients respectively. Dotted arrows represent non-significant paths ($p > 0.05$). Path widths are scaled proportionally to the path coefficient. Numbers adjacent to arrows are significant standardized path coefficients. Standardized total effects bar graph (direct plus indirect effects) derived from the SEM depicted above. MAT, mean annual temperature; MAP, mean annual precipitation; SOM, soil organic matter; R, rare; A, abundant.

altered by climatic attributes, they exerted little effect on rare and abundant microbial diversity. According to the standardized total effects, changes in MAP were a predominant factor that directly and negatively influenced the microbial diversity of rare and abundant taxa under the warming climatic regime.

With respect to climate cooling, both MAT and MAP exerted significant direct effects on rare microbial diversity (MAT: $r = 0.92$, $p < 0.001$; MAP: $r = -0.52$, $p < 0.001$). However, no significant linkage between soil attributes and rare microbial diversity was observed. Abundant microbial diversity was poorly predicted by both climatic and soil attributes, except the direct positive effects of OM ($r = 0.25$, $p < 0.05$). According to the standardized total effects, both MAT and MAP were important factors impacting rare microbial diversity under cooling, with positive effects of MAT and negative effects of MAP.

Microbial N transformation under changing climatic regimes

Soil N cycling is tightly coupled to plant growth. To further understand the microbial N transformation under changing climatic regimes, the variations of key functional genes involved in N cycling carried by rare and abundant taxa were studied by matching the taxonomic annotations of both sequencing and GeoChip data at the genus level (Fig. 5). N functional diversity in the rare taxa was higher compared with the abundant taxa (Additional file 1: Table S3). Some N cycling genes, including *amoA*, *napA*, *nifH*, *nirK*, *nirS*, *norB* and *nrfA*, were detected only in the rare taxa. Changing climatic regimes significantly decreased several functional genes carried by rare taxa, especially for the denitrification processes (*narG*, *nirS/K* and *nosZ*) and dissimilatory N reduction (*napA*) ($p < 0.05$). Maize is a crop that favours the use of a nitrate-based source of nutrition (Engels and Marschner, 1993). Thus, the reduction of denitrification genes carried by rare taxa may benefit plant growth by reducing N loss. In addition, the cooling climatic regime also resulted in a significant decrease in the functional process of ammonification (*gdh*) in both rare and abundant taxa.

Linking the rare and abundant microbial taxa to potential community functions

Random forest modelling was used to predict the crop yield with rare and abundant taxa; in this model, the importance of a variable is determined by removing it from the model and quantifying subsequent increases in the model's mean square error (MSE) (Fig. 5A and B). Our results indicated that microbial communities were potentially more important to crop yield under climate cooling than warming, which explained 45.7% and 12.3% ($p = 0.01$) respectively. Interestingly, despite their lower relative abundance, the ART and CRT contributed more to crop yield than the abundant taxa. It is notable that rare taxa were possibly more important to crop yield under climate cooling, with a 30.5% increase in the MSE in predicting crop yield when removing the ART and CRT. Rare members of Acidobacteria (10.9%) and Bacteroidetes (8.0%) might contribute most to the crop under climate cooling (Fig. 5D). In addition, some abundant taxa were found to potentially influence the maize yield, such as abundant Actinobacteria under warming (13.4%) and Verrucomicrobia under cooling (10.9%) (Fig. 5C and D).

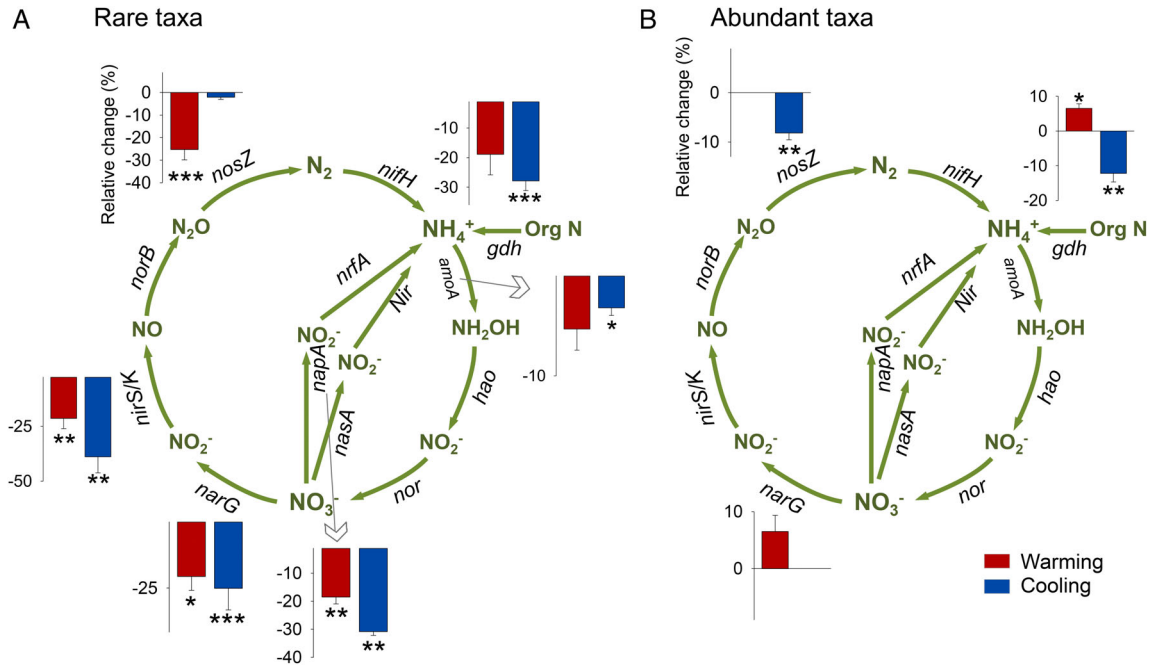

Fig. 4. Changes of nitrogen cycling genes. Significantly changed functional gene numbers in the nitrogen cycle carried by (A) rare and (B) abundant taxa in response to changing climatic regimes. The N cycling genes include *nifH* (nitrogenase reductase), *amoA* (ammonia monooxygenase), *hao* (hydroxyacid oxidase), *narG* (nitrate reductase subunit alpha), *nirK*/*S*, *Nir* (nitrite reductase), *norB* (nitric oxide reductase), *nosZ* (nitrous oxide reductase), *napA*/*nasA* (nitrate reductase) and *nrfA* (c-type cytochrome nitrite reductase).

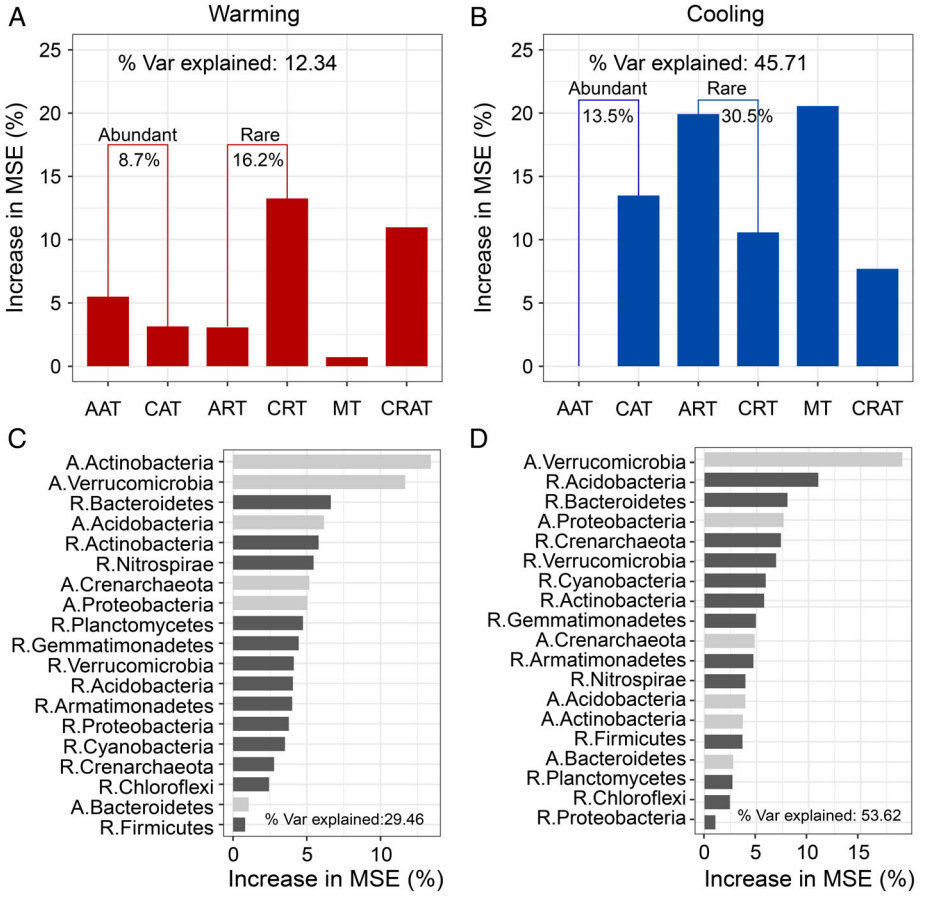

Fig. 5. Mean predictor importance of the relative abundances of abundant and rare taxa on aboveground yield. A, C. Climate warming; (B, D) climate cooling. The contribution (% of increased mean square error) is calculated based on random forest analyses. AAT, always abundant taxa; CAT, conditionally abundant taxa; ART, always rare taxa; CRT, conditionally rare taxa; MT, moderate taxa; CRAT, conditionally rare and abundant taxa. A, abundant taxa; R, rare taxa. Light grey indicates the abundant taxa, and dark grey indicates the rare taxa.

Discussion

Changing the climatic regime by soil transplantation significantly altered both the α- and β-diversity of the bacterial communities. Consistent with previous studies, climatic factors (e.g., temperature and precipitation) were the main drivers of the distribution patterns of soil microbial communities (Jing *et al*., 2015; Delgado-Baquerizo *et al*., 2016). Recent climate change experiments also suggested that climatic factors profoundly influence belowground communities, resulting in a loss of microbial biomass and changes in microbial abundance and community structure in response to the warmer climate (Vanhala *et al*., 2011; DeAngelis *et al*., 2015). Climatic factors can have strong effects on the physiological rates of microorganisms, including metabolic rates, life history strategies, growth and even rates of nucleotide substitution in molecular evolution (Woodward *et al*., 2010). In addition, species interactions may pose a great contribution to the overall community assembly (Datta *et al*., 2016).

Similar to the overall communities, changing climatic regime change also led to a continuous succession of both rare and abundant communities over time (temporal turnover of rare taxa varied between 0.04 and 0.21; and the abundant taxa varied between 0.001 and 0.28). Pronounced alterations of MAP and MAT under warming posed negative effects of on soil abundant or rare microbial diversity, which indicated significant microbial taxonomic diversity losses when faced with environmental stress or disturbance as previously reported (Atlas *et al*., 1991; Maestre *et al*., 2015). The exposure of soil microbes outside the range of their life history might significantly lower the growth rates of these organisms (Wertz *et al*., 2007), which override the positive role of warming in metabolic rate (Woodward *et al*., 2010). Comparisons of the biogeography patterns of these two microbial taxa also indicated that rare members of the community followed a similar distribution pattern to that of the abundant members (Logares *et al*., 2014). These results indicated that similar ecological processes structured rare and abundant communities, such as speciation, extinction, dispersal, or species interactions underlying both of these two major groups (Galand *et al*., 2009). However, the changes in succession rates for abundant communities were higher than those in the rare communities under both warming and cooling conditions, indicating more stable rare microbial communities under environmental pressure. Higher average resistance ratio and constancy of the rare taxa further supported the conclusion. Despite the strong influences of climatic factors on the rare taxa, the relatively stable rare taxa were the results of the combined effects of various exogenous factors (such as climatic factors and soil geochemical properties), as well as the endogenous dynamics (such as biological interactions in microbial communities) (Hastings, 2010). One evidence of the biological interactions is that rare members are protected from active loss by both viral lysis and predation because of their low abundance (Galand *et al*., 2009). Interestingly, even small variations of rare taxa were important to the overall dissimilarity of microbial communities induced by changing climatic regimes compared with the abundant taxa, which highlights the disproportionate roles of the rare taxa in the overall communities. Thus, we speculated that stable rare members can contribute to the overall community stability by acting as a reservoir that can rapidly respond to environmental changes (Shade *et al*., 2014), as the CRT are members of a seed bank that may become active under favourable conditions (Lynch and Neufeld, 2015).

The functional diversity of rare and abundant taxa was also different, with the rare taxa containing more diverse N cycling functional genes than the abundant members. Some N cycling genes were carried only by the rare members, including *amoA*, *napA*, *nifH*, *nirK*, *nirS*, *norB* and *nrfA*. Rare species probably offer the required gene pool to catalyse complex N cycling processes, such as diazotrophs (LaRoche and Breitbarth, 2005), ammonia oxidizers (Hermansson and Lindgren, 2001; Leininger *et al*., 2006) and some denitrifiers (Philippot *et al*., 2013), which are rare members with extremely low relative abundance. The variations of functional gene numbers of the rare taxa under changing climatic regimes seem to have positive roles in terms of plant yield, as denitrification gene numbers of the rare taxa decreased under climate cooling, which increased the nitrate contents in soils and improved the nutrient utilization efficiency. As most of the taxonomic and functional diversity in a community is composed of rare species, our study suggests that the stability of the rare taxa is meaningful for the stability of the overall community, further implying the potentially important role of rare members in maintaining ecological functions.

Several recent studies have shown that microbial diversity and ecosystem productivity are tightly related. For example, a recent study revealed that soil bacterial and fungal α-diversity is positively related to plant productivity on a global scale and is as important as the soil pH, climate and spatial predictors, latitude and altitude as a driver of variation in ecosystem multifunctionality (Delgado-Baquerizo *et al*., 2016). Rare taxa together with the abundant members constitute an active community that is essential for ecosystem function (Galand *et al*., 2009). Here, we found that rare members had potentially more important roles in relation to maize yield under changing climatic regimes. This may be attributable to the following factors. First, a changing climate might potentially promote some of the low-abundance or

dormant members to become active (Jones and Lennon, 2010), which might be important for maintaining ecosystem function. The rare communities acting as a microbial seed bank then function as a valuable insurance source during changing climatic regimes, known as the insurance effect (Yachi and Loreau, 1999) on community functions, in which at least one species will perform a given process under a given environmental condition. Second, stable rare taxa might provide diverse functions, as a previous study indicated that a substantial amount of metabolically active lineages was found to belong to the rare biosphere (Logares *et al*., 2014). Rare taxa were also found to be tightly linked to the temporal stability of maize yield under changing climatic regimes. Previous studies suggest that rare species are likely to offer complementary, or unique, metabolic pathways to support ecosystem functioning (Helliwell *et al*., 2013; Jousset *et al*., 2017), such as the secretion of certain vitamins or amino acids by the rare species that are needed by other organisms or plants. Consequently, with a wide variety of diversity in the rare biosphere, rare species might be able to increase functional redundancy and enhance the resistance of the soil microbiota to counteract the environmental disturbance and maintain community function.

Conclusions

Together, our results indicated that changing the climatic regime could lead to continuous succession of both rare and abundant communities over time, but rare taxa were generally more stable in terms of microbial diversity and community composition, as they may be protected from active loss by both viral lysis and predation due to their low abundance (Galand *et al*., 2009). In addition, rare microbes may represent the hidden backbone of microbial communities, as the rare biosphere is taxonomically and functionally diverse, which has the potential to increase functional redundancy and enhance the ability of soil communities to counteract environmental disturbances (Jiao *et al*., 2017). Serving as large reservoirs of genetic and functional diversity, rare microbial communities are potentially important for community stability and functions, which is highly related to the sustainable development of the ecosystem in response to changing climate.

Methods

Field sites and reciprocal soil transplant experiment

The SRTE was established in October 2005 at three long-term agricultural experimental stations of the Chinese Academy of Sciences: Hailun station (126°38′E and 47°26′N) is located in Heilongjiang Province of northeastern China and has a cold temperate monsoon climate with a MAT and precipitation of 1.5°C and 500 mm respectively; Fengqiu station (114°24′E and 35°00′N) is located in Henan Province of central China and has a warm temperate monsoon climate with MAT and precipitation of 13.9°C and 605 mm respectively; and Yingtan station (site S, 116°55′E and 28°15′N) is located in Jiangxi Province of southern China and has a middle subtropical monsoon climate with MAT and precipitation of 17.6°C and 1795 mm respectively. Three typical types of agricultural soils, Phaeozem, Cambisol and Acrisol based on the FAO soil classification system (IUSS Working Group WRB, 2006), obtained from the local area of each of the three experimental stations, were reciprocally transplanted in triplicate based on a plot size of $1.2 \times 1.4 \times 1.0$ m (Fig. 1A). The Phaeozem soil, occupying approximately 5.9×10^5 km^2 in China, which is one of the three zonal Phaeozem areas in the world, is the most fertile soil, with a high organic matter content and a pH of 6.0. The Cambisol soil, which covers an area of approximately 1.3×10^5 km^2, was derived from alluvial sediments of the Yellow River, the second largest river in China. This is a sandy loam soil with a pH of 7.7. The Acrisol soil, accounting for approximately 2.0×10^6 km^2 of southern China, was derived from quaternary red clay and has a low pH of 5.0 and a low organic matter content.

Maize was planted in 2006 at all three sites and was fertilized with typical rates of N 150 kg/hm^2, P 75 kg/hm^2 and K 60 kg/hm^2. No irrigation was applied. Maize was sown and harvested once per year. A total of 162 soil samples were collected annually in August to September from 2006 to 2011 in triplicate. In addition, original soil samples transported to each site were also collected in 2005. Ten soil cores were composited from surface soil (0–20 cm) within each plot and were sealed in a polythene wrapper, then stored on ice and transported to the laboratory. The soil was then divided into two subsamples and stored at either 4 °C for soil geochemical variable measurements or at −80°C for microbial community analysis. Soil pH and OM were measured. MAT and MAP data were obtained from the experimental stations' meteorological observation database. Aboveground maize biomass, grain weight, and nutrients in the stem and grain were measured immediately after harvest.

Sequencing of 16S rRNA gene amplicons

Microbial genomic DNA was extracted from 5 g of well-mixed soil of each sample by combining freeze-grinding and sodium dodecyl sulfate for cell lysis and purification by agarose gel electrophoresis, followed by phenol–chloroform–butanol extraction as previously described (Zhou *et al*., 1996). DNA was amplified for the V4 region of 16S rRNA genes using the primer set 515F and 806R (Caporaso *et al*., 2012). Both 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 multiple samples in one run of MiSeq sequencing. Detailed PCR amplification, quantification and sequencing procedures were reported previously (Liang *et al*., 2015). After assigning each sequence to its sample according to its barcode, the sequences were then trimmed based on quality scores using Btrim (Kong, 2011), and pair-end reads were merged into longer reads by FLASH (Magoč and Salzberg, 2011). To test trimming strategies, different sizes of trimming windows and cutoffs were used. Unqualified sequences were removed if they were too short or contained ambiguous residues. Chimeric sequences were discarded based on a prediction by UPARSE (Edgar, 2013). OTUs were clustered at the 97% similarity level. Final OTUs were generated based on the clustering results, and taxonomic annotations were assigned to each OTU's representative sequence by RDP's 16S Classifier (Wang *et al*., 2007).

GeoChip analysis of microbial functional genes

GeoChip 4.0 (Tu *et al*., 2014) was used to target soil microbial functional genes involved in N cycling. An aliquot of 1 μg of DNA from each sample was directly labelled with the fluorescent dye Cy-3 (GE Healthcare, CA, USA), purified, resuspended in 27.5 μl of DNase/RNase-free distilled water and then mixed completely with 42 μl of hybridization solution, containing 1× Acgh blocking, 1× HI-RPM hybridization buffer, 10 pM universal standard DNA (Liang *et al*., 2010), 0.05 μg μl^{-1} Cot-1 DNA and 10% formamide (final concentrations). Subsequently, the solution was denatured at 95°C for 3 min, incubated at 37°C for 30 min, and then hybridized with GeoChip 4.0. The hybridizations were carried out at 42°C with 40% formamide for 16 h with an MAUI hybridization station (BioMicro, Salt Lake City, UT, USA). Then, the arrays were scanned at 633 nm using a laser power of 100% and a photomultiplier tube gain of 75% with a NimbleGen MS200 Microarray Scanner (Roche NimbleGen, Madison, WI, USA). The image data were extracted using the Agilent Feature Extraction program. The microarray data were preprocessed in the Microarray Data Manager system on the Institute for Environmental Genomics website (http://ieg.ou.edu/microarray) as previously described (Liang *et al*., 2015). Spots with signal-to-noise ratios lower than 2.0 were removed before statistical analysis.

Definition of abundant and rare taxa

To depict the responses of both rare and abundant communities to changing climatic regimes, we classified all OTUs into six categories following recent studies (Dai *et al*., 2016; Xue *et al*., 2018): AAT, with a relative abundance ≥1% in all samples; CAT, with a relative abundance ≥0.01% in all samples and ≥1% in some samples; ART, with a relative abundance <0.01% in all samples; CRT, with a relative abundance <0.01% in some samples but never ≥1% in any sample; moderate taxa with a relative abundance between 0.01% and 1% in all samples (MT); and conditionally rare and abundant taxa, with a relative abundance ranging from rare (<0.01%) to abundant (≥1%). For the comparative study of abundant and rare taxa, AAT and CAT were collectively referred to as abundant taxa, and ART and CAT were collectively referred to as rare taxa. N cycling genes carried by rare or abundant taxa were matched based on the taxonomic annotations of both sequencing and GeoChip data at the genus level. Genes carried by rare and abundant taxa are listed in Table S1 (Additional file 1).

Statistical analysis

Both rare and abundant bacterial community taxonomic distribution patterns under long-term soil transplanting were determined by non-metric multidimensional scaling (NMDS). A dissimilarity test of the microbial community was performed using non-parametric multivariate statistical tests and ANOSIM. The ANOSIM statistic R is based on the difference in mean ranks between groups and within groups and is calculated as follows:

$$R = \frac{r_b - r_w}{\frac{1}{4}[n(n-1)]} \quad (1)$$

where r_b is the mean rank of between-group dissimilarities, r_w is the mean rank of within-group dissimilarities, and n is the total number. According to the ranks of the dissimilarities, the statistic R ranges from −1 to +1. Ecological communities rarely achieve $R < 0$. Thus, $R \approx 0$ indicates no difference among groups, and $R > 0$ shows that groups differ in community composition. SIMPER was used to assess which subcommunity was primarily responsible for an observed difference between groups of samples (Clarke, 1993). All of the above analyses were performed in R (version 3.0.3; http://www.r-project.org/) using the package 'vegan' (Oksanen *et al*., 2013). To link the variations of crop yields to the abundant and rare communities, random forest analysis was used to evaluate the importance of each predictor by examining at how much the MSE increased when the data for that predictor were permuted randomly while others remained unchanged. Random forest analyses were performed with the 'randomforest' package (Liaw and Wiener, 2002) in R.

The stability of maize yields and microbial diversity in response to changing climatic regimes were estimated by the index of constancy, which represents the temporal stability of yield and microbial diversity (Tilman *et al*., 2006). The constancy of maize yield/microbial diversity measures the degree of invariability in seed weight/microbial diversity relative to its mean. The constancy is defined as μ/σ, where μ is the mean value of seed weight/microbial diversity for a time period and σ is its standard deviation over the same interval. Here, the constancy was calculated both for the 6-year duration (2006–2011) and 2-year durations (2006–2007, 2007–2008, 2008–2009, 2009–2010 and 2010–2011). Greater constancy indicates higher stability in the maize yield/microbial diversity in response to changing climatic regimes.

The temporal turnover rate of the rare and abundant communities across time was measured as the slope of the microbial time–decay relationship. The time–decay relationship was evaluated using a linear regression between logarithmic β-similarities and logarithmic temporal distance in the following form: ln (S_s) = constant − w ln (T), where S_s is the pairwise similarity in the community, T is the time interval and w is a measure of the rate of species turnover across time. The temporal turnover rates of both rare and abundant communities for three soil systems under both climate warming and cooling were estimated. The deviations of temporal turnover under changing climatic regimes *in situ*, hereafter Δ temporal turnover, were further evaluated to compare the stability of microbial communities.

The stability of rare and abundant microbial communities in response to changing climatic regimes was estimated by both the index of resistance, the property of communities to withstand disturbance (Orwin and Wardle, 2004) and the index of constancy. The resistance (Rs) of microbial communities was calculated by comparing the α-diversity (Shannon index) between transplanted and *in situ* samples during 6 years of soil transplantation. We selected the Shannon diversity index as our metric of α-diversity because it is highly recommended and commonly used when analysing microbial diversity and has been shown to reduce the bias in relation to other diversity metrics, such as the number of OTUs, when comparing data from multiple sources (He *et al*., 2013). The index of resistance of community Shannon diversity was calculated as follows:

$$Rs = 1 - \frac{2|D_0|}{(C_0 + |D_0|)} \quad (2)$$

where D_0 is the difference in the community Shannon diversity between the control (C_0) (samples *in situ*) and the transplanted samples. RS is bounded by −1 and +1, with a value of +1 showing that the disturbance exerted no effect (maximal resistance), whereas low values indicate strong effects (less resistance). Similar to the constancy of maize yield, the constancy of microbial communities was also calculated by evaluating the degree of invariability in α-diversity (Shannon index) relative to its mean.

The significance of differences in plant biomass, yield, soil geochemical attributes, taxonomic and functional richness, and stability of α-diversity was tested using Duncan's multiple range test at $p < 0.05$ after one-way analysis of variance. SEM (Grace, 2006) was used to assess the direct and indirect relationships between climatic attributes (MAT and MAP), soil pH, SOM and rare/abundant microbial taxonomic diversity (16S sequence data). Data manipulation was performed before modelling, and MAT, MAP, soil attributes and microbial taxonomic diversity were log-transformed to improve normality. First, all soil attributes were included in the model, but only soil pH and SOM were found to have significant correlations with other factors. Thus, only pH and SOM were included in the final model. The *priori* SEM is shown in Fig. S7 (Additional file 1). The overall goodness of fit of the composite model was tested as follows: the χ^2-test (the model has a good fit when $p > 0.05$), goodness of fit index (GFI; the model has a good fit when GFI > 0.9), the Bollen–Stine bootstrap test (the model has a good fit when the bootstrap $p > 0.10$) and the root MSE of approximation (RMSEA; the model has a good fit when RMSEA <0.05 and $p > 0.05$) (Schermelleh-Engel *et al*., 2003). With a reasonable model fit, the path coefficients of the model and the associated P values were interpreted. The standardized total effects (calculated by summing all direct and indirect pathways between the two variables) of climatic and soil attributes on microbial taxonomic diversity were also calculated.

To evaluate the potential relative importance of the constancy of rare and abundant microbial diversity and abundance to the maize yield constancy with changing climatic regimes, we used ROC analysis (Fawcett, 2006) to calculate the area under the curve (AUC) for each index. The threshold for more stable or less stable maize yield under climate warming and cooling depends on the median of the constancy datasets of maize yield. All SEM analyses and ROC analyses were conducted using IBM® SPSS® Amos 20.0 (AMOS, IBM, USA).

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Author contributions

All authors contributed intellectual input and assistance to this study and manuscript. B.S., J.Z., and Y. L. developed the original framework. Y.L., X.X., N.Z., K.X. and M.Y. contributed reagents and data analysis. Y.L. and K.X. did GeoChip analysis. Y.L., X.X., E.E.N. and F.C. wrote the paper.

Data availability statement

The raw sequencing data were deposited in the National Center for Biotechnology Information (NCBI) under the project accession: SRP069263. Nitrogen cycling gene data are available at Figshare, DOI: 10.6084/m9.figshare.7410986. Other datasets used and analysed during the current study are available from the corresponding author on reasonable request.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1 Impacts of changing climatic regimes on (a) aboveground biomass and yield and (b) belowground taxonomic and nitrogen functional richness. Changes of the aboveground biomass and maize yield (seed weight) and belowground taxonomic and functional richness in situ (black bars), with climate warming (red bars), and with climate cooling (blue bars).

Fig. S2 Effects of changing climatic regimes on soil attributes. Changes in soil geochemical attributes in the three soil systems (Phaeozem, Cambisol and Acrisol) in situ and under changing climatic regimes.

Fig. S3 Effects of changing climatic regimes on nutrient utilization efficiency (NUE). (a) Climate warming, and (b) climate cooling.

Fig. S4 Soil microbial composition of rare and abundant communities in the Phaeozem, Cambisol and Acrisol soils under changing climatic regimes.

Fig. S5 Changes of soil microbial taxonomic diversity of both rare and abundant taxa in situ (black bars), with climate warming (red bars), and with climate cooling (blue bars).

Fig. S6 The deviation of temporal turnover (exponent of time–decay relationship) of rare and abundant microbial communities under changing climatic regimes from in situ. Red bars represent climate warming, and blue bars represent climate cooling.

Fig. S7 A priori structural equation model (SEM) including climate and soil attributes as predictors of microbial diversity. MAT, mean annual temperature; MAP, mean annual precipitation; SOM, soil organic matter; R = rare taxa; A = abundant taxa.

Table S1 Dissimilarity test of microbial community structures in response to changing climatic regimes simulated by soil transplant via ANOSIM analysis. The ANOSIM statistic R is based on the difference of mean ranks between groups.

Table S2 The effect of climatic factors and soil properties on rare and abundant microbial composition by canonical correspondence analysis (CCA)

Table S3 Nitrogen cycling genes carried by rare and abundant taxa.