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Article

Warming-driven migration of core microbiota indicates soil property changes at continental scale

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ABSTRACT

Terrestrial species are predicted to migrate northward under global warming conditions, yet little is known about the direction and magnitude of change in microbial distribution patterns. In this continental-scale study with more than 1600 forest soil samples, we verify the existence of core microbiota and lump them into a manageable number of eco-clusters based on microbial habitat preferences. By projecting the abundance differences of eco-clusters between future and current climatic conditions, we observed the potential warming-driven migration of the core microbiota under warming, partially verified by a field warming experiment at Southwest China. Specifically, the species that favor low pH are potentially expanding and moving northward to medium-latitudes (25°–45°N), potentially implying that warm temperate forest would be under threat of soil acidification with warming. The eco-cluster of high-pH with high-annual mean temperature (AMT) experienced significant abundance increases at middle- (35°–45°N) to high-latitudes (> 45°N), especially under Representative Concentration Pathway (RCP) 8.5, likely resulting in northward expansion. Furthermore, the eco-cluster that favors low-soil organic carbon (SOC) was projected to increase under warming scenarios at low-latitudes (< 25°N), potentially an indicator of SOC storage accumulation in warmer areas. Meanwhile, at high-latitudes (> 45°N) the changes in relative abundance of this eco-cluster is inversely related with the temperature variation trends, suggesting microbes-mediated soil organic carbon changes are more responsive to temperature variation in colder areas. These results have vital implications for the migration direction of microbial communities and its potential ecological consequences in future warming scenarios.

1. Introduction

The interactions between microorganisms and global climate change have attracted much scientific and social attention: microorganisms are vital in maintaining ecosystem function [1,2] and regulating climate change [3,4] and meanwhile the climate change in turn heavily impacts microbial community composition and function [5]. Despite of the crucial roles of microorganisms in determining the ecological response to current and future climate change [6], their response to climate change is still hard to predict, and changes in microorganisms are barely in the concerns of the policy decision makers [5]. One of the reasons could be the

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tremendous microbial diversity in all ecosystems, especially in soils, that makes it hard to determine the key microorganisms to put into the earth ecosystem model [7]. Besides, the individual microbial taxa showed extremely high spatial heterogeneity and responded to various environmental factors [8–10], making it hard to determine the ecological roles of individual taxa. Therefore, the capability to predict and quantify soil microbial responses to future climate warming has increasingly been challenged [11].

An improved representation of microbial diversity makes it possible to get a more accurate prediction of microbial response and their ecological consequences. It was predicted that the low-temperature adapted species could be replaced by the higher temperature adapted ones in arid soil biocrusts in the coming decades [12], suggesting it is possible to forecast the responses of microbial community to climate change. Recently, there are some emerging evidence that vast soil microbial diversity could be represented by a short list of most abundant and ubiquitous taxa (termed as dominant taxa hereafter) [13], with a total of 511 highly abundant and broadly distributed species displaying very similar patterns in β-diversity as 25 thousands of microbial species observed globally. Although the diversity of the entire microbial community could be represented by 2% of their species, this reduced diversity is still too large to be included in predictive ecosystem models. An alternative way is to further lump these dominant phylotypes into a manageable number of groups. Some trait-based concepts have been proposed in terms of grouping microorganisms, which contribute to link microbial attributes to their ecological roles, such as oligotrophy-copiotrophy [14], competitor-stress tolerator-ruderals (C-S-R) classification, the newly proposed high yield-resource acquisition-stress tolerance (Y-A-S) strategy [15], as well as ecological clusters [13]. The ecological clusters are lumping dominant phylotypes into a limited number of ecologically meaning groups according to the environmental preferences (a kind of microbial trait defined by the favorable habitat where microbial abundance peaks), which take into account the fact that microbial individuals respond differentially to various environmental factors. Given the vital effects of dominants on ecosystem function [16], we proposed that abundance changes of eco-clusters induced by future climate change could be used to forecast environmental processes and subsequent ecological consequences.

Forest has been considered as one of the climate-sensitive soil ecosystems [4]. Here we analyzed high-throughput sequencing datasets of 16S rRNA gene from > 1600 soil samples across over 100 forest sites at continental scale. We propose a scheme to build trait-based continuous distributions to include in the ecosystem models. By integrating with environmental parameters, we build continuous biogeographic distributions of eco-clusters for current climatic condition. Thereafter, we projected the future eco-cluster-based microbial biogeography in 2050s (average across 2040–2069) and 2080s (average across 2070–2099) under two climate scenarios: Representative Concentration Pathway (RCP) 2.6 where the global mean temperature rise to 2 °C by 2100 relative to preindustrial times, and scenario RCP8.5 in which temperature rises with time. Such projection has successfully predicted the northward migration of terrestrial species [17–20] and the abundance increase and habitat expansion of major marine cyanobacterial lineages [21] under global warming. The foundation of these projections is that species occurrence and abundance in future climate scenarios is linked to similar factors as under current climate condition. Our major objectives are (i) to predict the direction or magnitude of changes in soil core microbiota in a warming world; and (ii) to forecast the potential ecological consequences on the basis of climate-change-induced shifts in microbial hotspots. Here, "hotspots" refers to locations where high abundances of an eco-cluster occur. Our methods and current results provided new insights on deciphering microorganism-climate change connections by bridging the climate-change-induced microbial changes with potential ongoing environmental processes and ecological consequences.

2. Materials and methods

2.1. Sampling sites description

A total of 1654 samples collected from 111 sites in China were initially included in this study, along the 15th standard terrestrial transect of the International Geosphere-Biosphere Project (Fig. S1 online). This transect is typically heat-driven, crossing more than 30 latitudes and covering various forest types (evergreen broadleaf forests, evergreen needleleaf forests, broadleaf and needleleaf mixed forests, deciduous broadleaf forests, and deciduous needleleaf forests) and located in different climatic regions (from north to south: cold humid regions, temperate humid and semi-humid regions, temperate semi-arid regions, warm temperate humid and sub-humid regions, north subtropical humid regions, mid-subtropical humid regions, south subtropical humid regions, and tropical humid regions).

2.2. Sequencing data collection and analysis

Information about the data sources, formats and pretreatments were collected and compiled in a summary data file. A subset of raw reads for 885 samples were collected by the China Soil Microbiome Initiative (CSMI) and we also downloaded data which were generated from forest soils in China through "SRA Toolkit 2.9.0" based on their BioProject accession numbers. Only reads that covered the V4 region (515F-806R) of 16S rRNA gene and were generated from Illumina MiSeq sequencing platforms were retained (see Supplementary materials online). After merging and standardizing process, reads were subjected to regular sequence analysis (Fig. S2 online) by using our in-house Galaxy pipeline (http://mem.rcees.ac.cn) [22].

2.3. Statistical analysis

Geographic information (latitude, longitude and elevation) and soil physical and chemical properties (including pH, soil organic carbon (SOC), total nitrogen (TN), moisture %) were recorded and measured, respectively. Climatic parameters were obtained from WorldClim database (version 2.0, http://worldclim.org/version2) [23]. ordinary least squares (OLS) regression models were performed to examine the latitudinal and environmental associations to microbial diversity across those individual samples. Microbial diversities (richness, Shannon, and Faith's phylogenetic diversity (PD)) were quadratic fitted to latitudinal gradient determined by lower Akaike information criterion (AIC) values compared to linear fit. We also performed principal components analysis (PCA) based on Unweighted Unifrac distance and Bray-Curtis dissimilarity to show the community clustering between samples categories or across environmental gradients. Different beta matrices resulted in similar results. Canonical correspondence analysis (CCA) was also performed to determine the most significant environmental variables shaping the microbial community composition. The variables selected by CCA were then used in structural equation modeling (SEM)-based analysis.

SEM was performed to further test direct and indirect effects of geographic, climatic, edaphic, and plant-related variables on microbial distribution and diversity. An *a priori* model was initially established according to empirical data and literature, which was then adjusted by removing non-significant links or variables and adding new links until a lowest χ^2 value was archived with

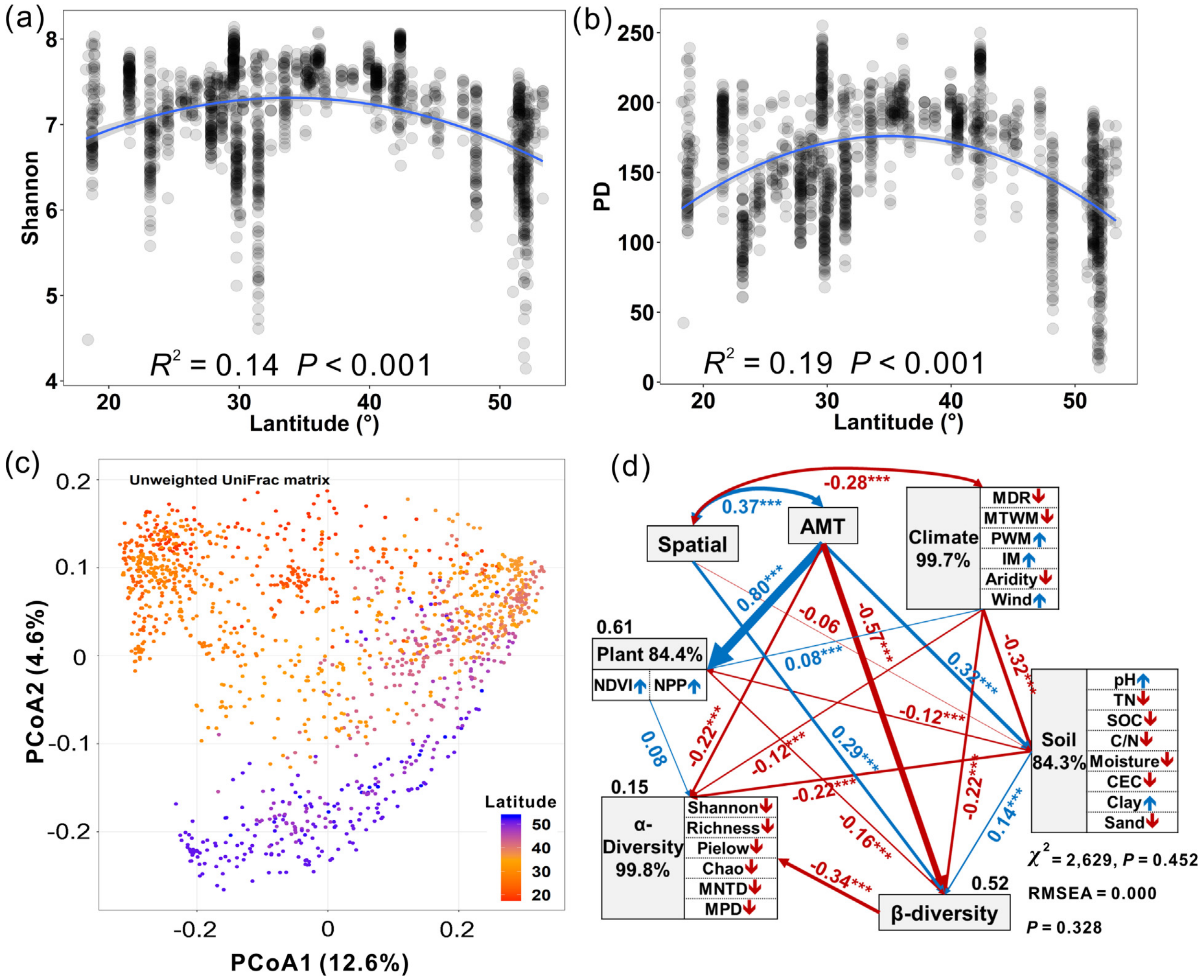

Fig. 1. Overall microbial alpha and beta diversity patterns along latitudinal gradient and the direct and indirect driving forces. Latitudinal distributions of shannon (a) and Faith's phylogenetic diversity (PD) (b) with second order polynomial regression lines. (c) PCoA plot of microbial community based on unweighted unifrac matrix. This plot illustrates that similarity of microbial communities were structured by latitudes. The possible reasons revealed by SEM analysis (d) which shows that AMT, followed by spatial eigenvector, have strong direct effect on microbial community structure.

$P > 0.05$ which means the model fits the observed data. PCA was employed to simplify the vectors subjected to SEM analysis (see Supplementary materials online). The spatial variable was represented by PCNM5 (the most significant Principal Coordinates of Neighbor Matrices (PCNM) eigenvector identified by CCA) and microbial composition was represented by principle coordination analysis (PCoA) 1 axis based on Bray-Curtis dissimilarity. In order to isolate the effect of mean annual temperature (AMT) on microbial community and diversity, it was treated as an independent variable. Most of the statistical tests and graphics were conducted with program R (version 3.5.1) [24] and SEM was performed in Amos 24.0.0 (IBM SPSS Inc, Chicago, USA).

2.4. Identification of core microbiota and ecological clusters

A total of 1411 samples with full environmental parameters were involved in identifying core microbiota. Dominant phylotypes were selected based on two criteria [13,25]: high abundance (phylotypes ranked among top 10% of total abundance) and relative ubiquity (accounting for > 40% occurrence frequency, i.e. > 564 samples). The rank-abundance pattern is plotted. Ecological clusters were identified following the method used by Delgado-Baquerizo et al. [13]. Briefly, the dominant phylotypes were subjected to random forest (RF) analysis to quantify the relative importance of environmental parameters, and address the most significant indicator for each phylotype. The best indicator characterized the environmental preference for a given phylotype with >30% variation explained by the RF model (Supplementary materials online). Semi-partial Spearman correlations were calculated for the selected phylotypes (n = 764) with known environmental preference. These analyses were done in RandomForest [26] and ppcor packages [27] in R. The dominant phylotypes were clustered into various ecological groups by using *hclust* function (with maximum distance clustered by ward.D2 method) and visualized in a heatmap figure by using pheatmap package in R, only showing the correlations with a significance of $P < 0.001$ (Supplementary materials online). Relative abundance of each cluster per sample was calculated by percentage of sequences belonging to that cluster to the sum of total sequences in the whole community.

2.5. Cubist model construction and evaluation

Cubist prediction model is a type of regression tree based tool to explore how to estimate a case's target value by information on explanatory covariates [28]. In this study, it is to relate the measured soil characteristic and current/future climatic data to the abundance of each ecological cluster for a given spatial spot (Fig. S3 online). Cubist committee models for each eco-cluster were first built for 1411 samples, and then predictions for the unsampled locations with the same predictors were made by using *prediction* function based on the created Cubist model fit. The underlying procedures are as follows: first, identifying the rule or rules that cover the new location; second, calculating the relative abundance for that location by the corresponding linear formulas under the rule (s) and finally averaging those results. Three parameters were used to evaluate the Cubist model fits: average error magnitude, relative error magnitude, and correlation coefficient. The relative error magnitude should be less than 1 if this model is to be considered as useful. The correlation coefficient indicates the fitness between the actual relative abundances and those values predicted by the model. RF regression analysis was also performed to predict the relative abundances of eco-clusters and the results were significantly correlated to Cubist prediction ($R^2 > 0.5$, $P < 0.05$). For all the subsequent analyses, only Cubist predictions were used in this study.

The spatial distributions of ecological clusters under current conditions were generated and mapped over the forested region using Kriging interpolation method based on exponential semivariogram (Fig. S3 online). Model construction and map visualization were done in R 3.5.1 with Cubist, gstat, raster, sp, maptools, and ggplot2 packages and the spatial distribution maps were redecorated in ArcMap 10.3 (ESRI, RedLands, USA).

2.6. Projection under future climate scenarios

A similar approach was taken for quantifying and mapping biogeographic patterns of each ecological cluster with the climatic condition under future climate projections (Fig. S3 online). The relative abundances of ecological clusters were predicted based on the previously constructed Cubist model, using climate related parameters derived from climate projections in the year of 2050s and 2080s for the two end-members of representative concentration pathways RCP2.6 and RCP8.5, with soil characteristics constant to current condition. The projected temperature changes for forested regions in China under RCP2.6 is close to the Paris Agreement's aim limiting the temperature increase to 1.5 °C [29] with current condition as baseline, whereas that under RCP8.5 is more approximate to temperature change inferred from the best model simulating today's climate [30]. Future climate projections (same climatic indices with current condition) under RCP2.6 and RCP8.5 in the year of 2050s and 2080s were derived from climate model BCC-CSM1.1 (originated from Beijing Climate Center, China) which was downloaded from the CCAFS-Climate data portal (http://www.ccafs-climate.org/data_spatial_downscaling/). All the spatial data were gridded using bilinear interpolation to the same spatial resolution of 0.1°.

In order to show the spatial effects on temporal variations of biogeographic pattern, we recalculated the overall relative abundances for four latitudinal groups under current and future climate conditions: high-latitudes (> 45°N), higher mid-latitudes (35°–45°N), lower mid-latitudes (25°–35°N), and low-latitudes (< 25°N). Paired *t*-test analysis of cell-to-cell grid data was used to show whether significant differences exist between future projection and current condition for certain latitudinal regions. Raster calculation function in ArcMap 10.3 was used to calculate the projected differences between future and current condition (future-current).

2.7. Field-warming experiment

Global warming induced temporal variations in biogeographic patterns in terms of ecological clusters were tested by using the one-site warming experiment. This warming experiment was established in 2010 at the Ailaoshan Station (24°32′N, 101° 01′E; with elevation of 2480 m) in Jingdong County, Yunnan Province, southwestern China. This station is set up for Subtropical Forest Ecosystem Studies of the Chinese Ecological Research Network. Dominant plants at this area contain *Lithocarpus xylocarpus*, *Lithocarpus hancei*, *Castanopsis rufescens*, *Sinarundinaria nitida*, *Carex teinogyna*, and *Pteridium aquilinum var. latiusclum*. The monthly mean temperature ranged from 15. 3 °C in July to 5.1 °C in January, with annual mean air temperature of 11.0 °C. The average annual rainfall was 1882 mm, with 85.4% occurring in the rainy season (May to October) [31]. Surface soils are characterized by high water permeability and water conservation ability, high organic carbon content, and relatively low pH of 4.5–5.0 [31]. A total of 10 plots (5 under warming and 5 under ambient condition) were set up. An infrared lamp (45 cm in length) and an arch-shaped heat reflector were fixed at a height of 2.3 m above a glass chamber (90 cm in length, 90 cm in width, and 50 cm in height) for each warming plot to achieve a whole ecosystem warming of 2 °C. The samples from this study were collected after warming for 1.5 years. Under each condition (warming vs. ambient), five samples were collected. The sequence data from the warming experiments were processed and grouped into eco-clusters like the data along the latitudinal gradient, but not involved in the Cubist model construction. Student's *t*-tests were performed to assess differences in defined eco-clusters under warming and ambient conditions. Response ratio analysis was used to compare the effects of projected and experimental warming on relative abundance of high-pH with high-AMT eco-cluster with a 95% confidence interval.

3. Results and discussion

3.1. Latitudinal biogeographic patterns of microbial diversity

The soil samples from forest ecosystems in China cover most of the forest types in northern hemisphere with various edaphic and climate conditions (Fig. S1 and Table S1 online) [32]. Apparent latitudinal patterns were obtained in microbial diversity and structure (Fig. 1a–c). Unlike the typical latitudinal diversity gradient (LDG) observed in plants and animals, microbial diversity peaked around the median latitude of 35° (Fig. 1a, b), which was likely favored by the neutral soil pH and moderate climate conditions (Table S1 online). Similar biogeographic pattern has been observed for bacteria in both terrestrial and marine ecosystems over large spatial scales [33–35]. The linear regression analysis showed that soil pH was the most important factor accounting for this variation in microbial diversity (Fig. S4 online). Latitudinal pattern was also detected in microbial community structure (Fig. 1c). CCA analysis showed the variables that had great influence on the microbial community distribution, including climatic, especially temperature-associated factors, soil-related and geographic-related factors (Fig. S5 online), in accordance with previous observations that these parameters impact soil biodiversity and community structure alone or combined [36]. The SEM analysis further partitioned the direct and indirect effects of multiple factors on microbial diversity and community structures. Previous studies showing temperature exerts a direct and indirect effect on soil microbial community structure, diversity and activity [12,37]. Indeed, AMT had significant direct effects on microbial diversity, higher on β-diversity (Bray-Curtis index) than α-diversity (Fig. 1d). In addition, temperature could exert an indirect effect on microbial community via soil chemistry and aboveground vegetation (Fig. 1d). Overall, this finding suggests future global warming will likely be the primary force driving shifts in microbial composition in forest soils at large geographic spatial scale.

3.2. Core microbiota and eco-clusters

Despite this AMT-determined latitudinal biogeographic pattern, the enormous diversity of microorganisms hindered the process to obtain generalizable predictions for spatiotemporal distribution under climate change. To tackle this barrier, we first narrowed down the vast number of phylotypes (OTUs) to a short list of dominant taxa that were both abundant and ubiquitous (Figs. S3 and S6 online). A small number of dominant taxa (827 phylotypes, core microbiota) represented a large fraction of the community (~40% of sequencing reads) and closely mirrored the whole community (Fig. S7 online). Hence, instead of understanding the entire vast diversity of taxa in soils, a handful of species could paint a picture of the community, in agreement with the observations from other ecosystems at global scale [13,38]. Highly abundant taxa have a large impact on community and ecosystem function [16] especially on the broad function such as community-level respiration [39]. To better understand the ecological roles of microbial taxa, we lumped those core microbiota into a number of manageable but meaningful groups by using RF modeling and clustering analysis based on semi-partial spearman correlations. Six well-defined groups have been identified based on habitat preference: high pH with high AMT, high pH with low sand and clay content, high pH, low pH, low pH with high precipitation of wettest month (PWM), and low SOC (Fig. 2a and Fig. S8 online). We found that the relative abundances of phylotypes in eco-clusters dependent on pH alone were monotonically increasing (high pH eco-cluster, peaked around pH = 6–7) or decreasing (low pH eco-cluster, peaked around pH = 3–4) with pH, whereas when combined with other factors, the variation as a function of pH became unimodal and the optimum pH corresponding to the peaked abundance were deviated (peaked around pH = 5–6 for high pH related eco-cluster and pH = 4–5 for low pH related eco-cluster) (Fig. 2a).

To understand if habitat preference was predictable by the phylogeny alone, the taxonomic affiliations in eco-clusters were determined. Even at coarse phylogenetic level (class level for Proteobacteria and phylum for others), each of eco-clusters harbored diverse lineages (Fig. 2b). Some lineages have been reported with apparent life strategies (i.e., oligotrophy-copiotrophy) and could be taken as ecological indicator for nutrient status. [40]. Accordingly, we found Betaproteobacteria and Bacteroidetes (mainly class *Sphingobacteriia*), following copiotrophic lifestyle, which inhabit soils rich in nutrients [14] peaked only in high-pH (around pH 6.0) with low-clay and low-sand eco-cluster (Fig. 2b). In contrast, Verrucomicrobia (mainly *Spartobacteria* and Subdivision3), typically oligotroph which dominate nutrient-limited environments [14] were abundant in low SOC eco-cluster (Fig. 2b). However, not all the taxa within a single phylum could be simply classified as oligotrophic or copiotrophic [14] such as for Acidobacteria habitat preference could be only tracked at a fine phylogenetic level. Indeed, genera Gp1, Gp2, and Gp3 following oligotrophy were abundant in acid and low SOC soils (i.e., low pH eco-cluster, low-pH with high-PWM eco-cluster and low SOC eco-cluster), whereas Gp4 and Gp6 exhibiting copiotrophic lifestyle were abundant in high pH eco-cluster and high-pH with high-AMT eco-cluster (Fig. 2b). Collectively, these findings indicated habitat preferences are conserved at differential phylogenetic depths and not predictable from coarse taxonomic information alone [8,13] and the eco-clusters with habitat preferences together with life strategies provided more comprehensive ecological characteristics besides nutrient availability.

3.3. Specific spatial distributions of eco-clusters at present-day

To further predict and quantify the magnitude of changes of eco-cluster-based microbiota in a warming world, we tracked the prevalence and biogeographic patterns of six eco-clusters under current and future (2050s and 2080s) conditions (Fig. 3). A predictive-oriented model Cubist was used to predict the relative abundance of eco-clusters and good model fit was obtained (Table S3 online). Patched distribution patterns reflected distribution heterogeneity in taxa composition and selection of ecological niches (Fig. 3a), partially due to distinct climate conditions and soil and forest types. For example, current hotspots of low pH eco-cluster (Fig. 3a) that was colored as blue patches, mostly occupied acid soils in south of China (< 25°N). Besides, the low-pH with high-PWM eco-cluster dominated acid soils in north of China (> 45°N). Both of these two eco-clusters roughly matched typical low pH regions in China [41], but were geographically located in the warm-moist and cold-moist climatic zones, respectively. Furthermore, the distribution patterns of eco-clusters (Fig. 3a) were more complex than species diversity which peaked around mid-latitudes (Fig. 1a, b). It has been reported that loss of dominants has more impacts on ecosystem function and community structure [16]. Taken together, stacking of trait-based (i.e., eco-cluster-based) and species-diversity-based biogeographic maps should be more efficient in refining the conservation regions than microbial diversity alone.

3.4. Potential changes in distributions of eco-clusters under warming conditions and the ecological implications

Eco-clusters contained highly abundant and highly impacted species and thus changes in their abundances could be an early indicator of changes in community and related ecosystem functioning [16]. Each eco-cluster harbored geographic regions that experienced fewer and greater changes in abundance (the differences between future and current, Fig. 4). Less change may suggest more buffering capacity of soils or less adaptability of microbes against warming [42,43]. Great changes may indicate poor adaptation (loss in abundance) or well adaptation (gain in abundance) to warming, to some extent dependent on the surrounding community diversity and composition [44]. Paired *t*-test of cell-to-cell grid data demonstrated significant changes of abundance occurred for each latitudinal region in future scenarios compared to present ($P < 0.01$, Table S4 online).

The hotspots of low pH eco-cluster remained in low latitudinal areas (< 25°N), but the average relative abundances in mid-latitudinal areas (25–45°N), covering most of the forested regions (Fig. 4b blue color) were projected to increase under warming conditions (Fig. 3b-II), suggesting it will slightly expand northward in future climate warming. This increase potentially indicates that forest ecosystems across China are under threat of soil acidification caused by the deposition of atmospheric nitrogen and sulfur [41,45]. Similarly, high-pH (peak around pH 6) with high-AMT eco-cluster is the only ecological cluster directly related to temperature, so it was supposed to experience the greatest changes in a warmer world, especially at higher latitudes which suffered higher temperature increasing amplitude [20]. As expected, this eco-cluster experienced significant abundance increases at middle- (35°–45°N) to high-latitudes (> 45°N), especially under RCP8.5 (Fig. 3b-VI and Fig. 4f blue color), likely resulting in northward expansion of hotspots by 2080s. Simultaneously, relative abundance in low-pH (peak around pH 4–5) with high-PWM eco-cluster significantly decreased at high-latitudes (> 45°N) by 2080s under RCP8.5 (Fig. 3b-III and Fig. 4c red color). Together, these changes indicated microbial succession to those preferring relatively higher pH at high-latitudes (> 45°N) in a warming condition. In fact, previous study has shown that afforestation in northeastern China (located at high latitudes) to some extent neutralizes pH from initial acidic condition [46]. This soil pH change well corresponds to our prediction. Collectively, the shift or expansion of

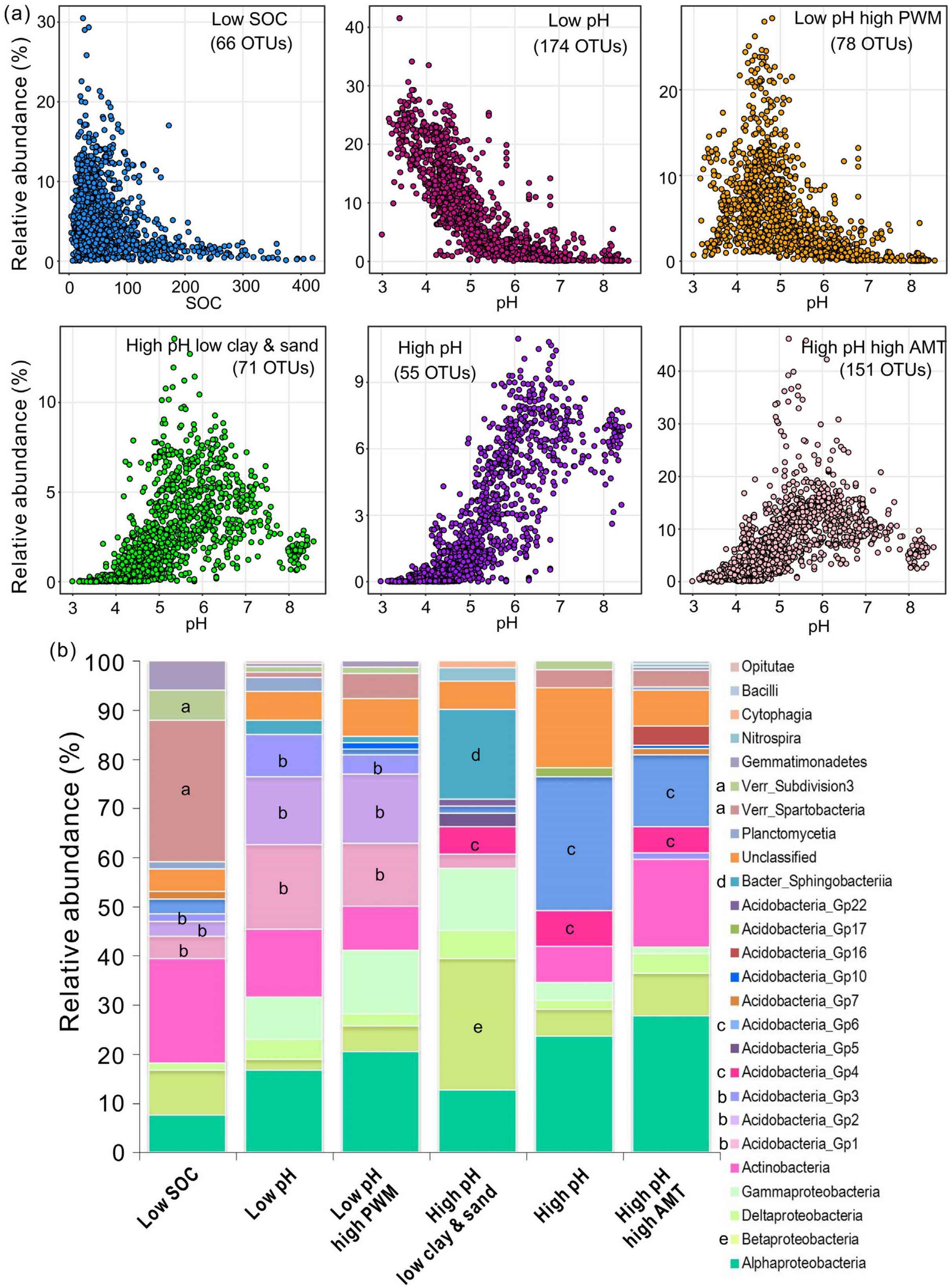

Fig. 2. Abundance and composition of identified ecological clusters. (a) Relationship between relative abundance of phylotypes (percentage of sequences in whole community)within each ecological cluster and primary environmental factor. (b) Taxonomic compositions (percentage of OTUs within each cluster) for eco-clusters at class level. “Verr” is short for Verrumicrobia and “Bacter” for Bacteroidetes. Different labels on each bar indicate the taxa with specific lifestyles (oligotrophy or copiotrophy). Specifically, “a” represents Subdivision3 and Spartobacteria in phylum Verrumicrobia, which are typical oligotroph; “b” and “c” represent oliogotrophic (Gp1, Gp2, and Gp3) and copiotrophic (Gp4 and Gp6) genera in Acidobacteria, respectively; “d” and “e” are for Bacteriodetes (mainly Sphingobacteriia) and Betaproteobacteria, respecitively, and both of them are copiotrophic.

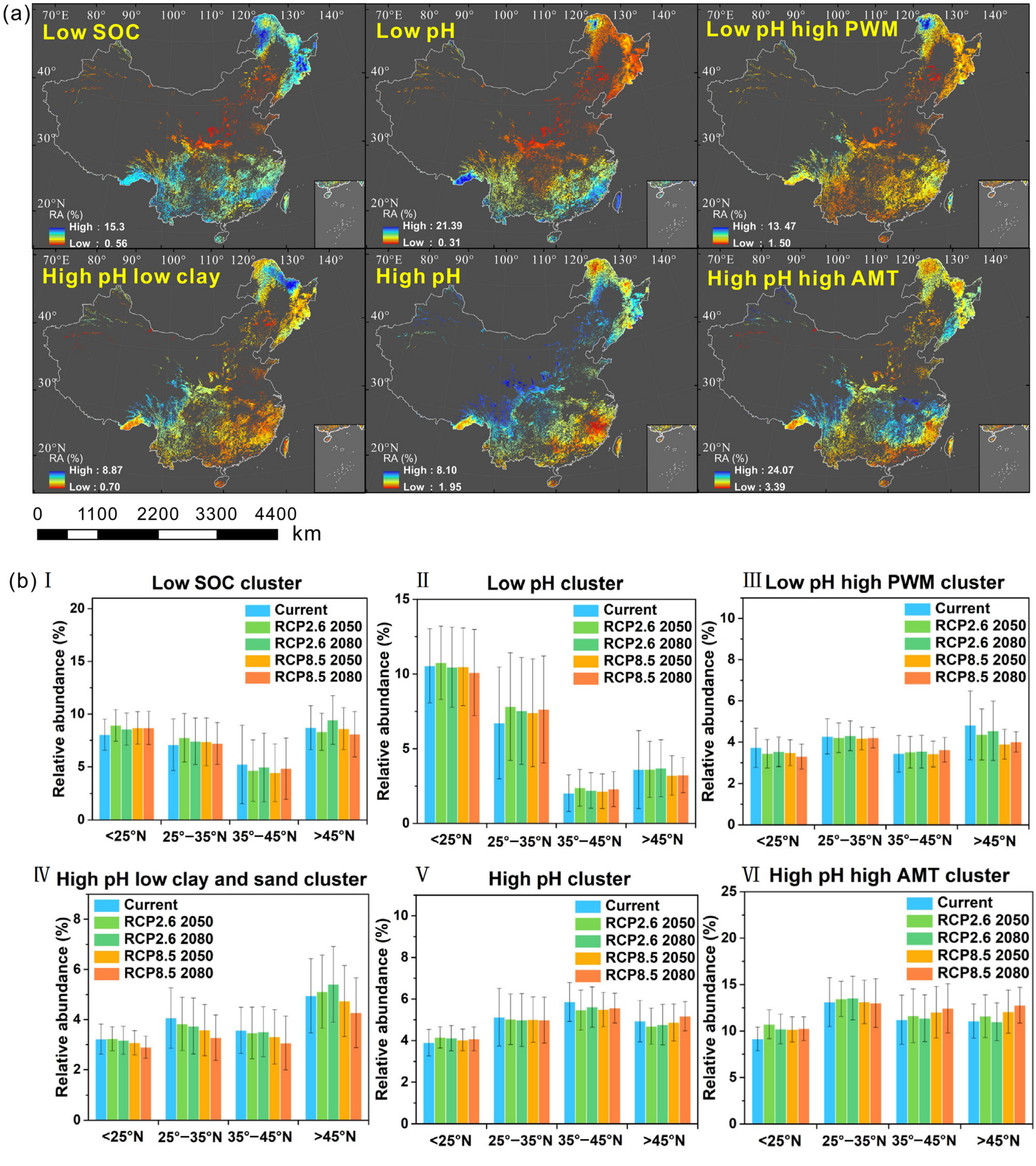

Fig. 3. Biogeographic distributions for present-day and latitudinal variation in average abundance for current and future climatic conditions. (a) Maps showing biogeographic distributions of eco-clusters in present-day. Hotspots for each eco-cluster represented by blue patches were not overlapped. (b) Projected average abundances from low to high-latitudes for current and projected future climatic conditions. The abundance was averaged from the grid cells within each latitudinal range. Large standard deviation was observed due to heterogeneous variation in abundances. However, paired *t*-tests of cell-to-cell gridded data (future scenarios vs. current condition) have shown significant changes ($P < 0.001$).

eco-cluster hotspots under projected future climate conditions indicates the potential warming-driving changes in microbial biogeography (Fig. 3b and Fig. 4), which may have profound implications for ongoing environmental process and the eventual ecological consequences.

The fluctuation in abundance of low SOC eco-cluster is the reflection of abundance changes in nutrient-limited preferring microorganisms (i.e., oligotroph). Most importantly, the relative abundance changes of dominants could infer the changes in broad ecosystem function, such as community-level respiration [39]. Abundance changes in low SOC eco-cluster differed at high- (> 45°N) and low-latitudes (< 25°N) (Fig. 3b-I), possibly suggesting regionally variable responses in soil respiration. At high-latitudes, average abundance initially decreased (from 8.71% in present to 8.33% by 2050s) and subsequently increased (to 9.44% by 2080s) under RCP2.6, but continuous decrease (8.71% to 8.62% to 8.09%)

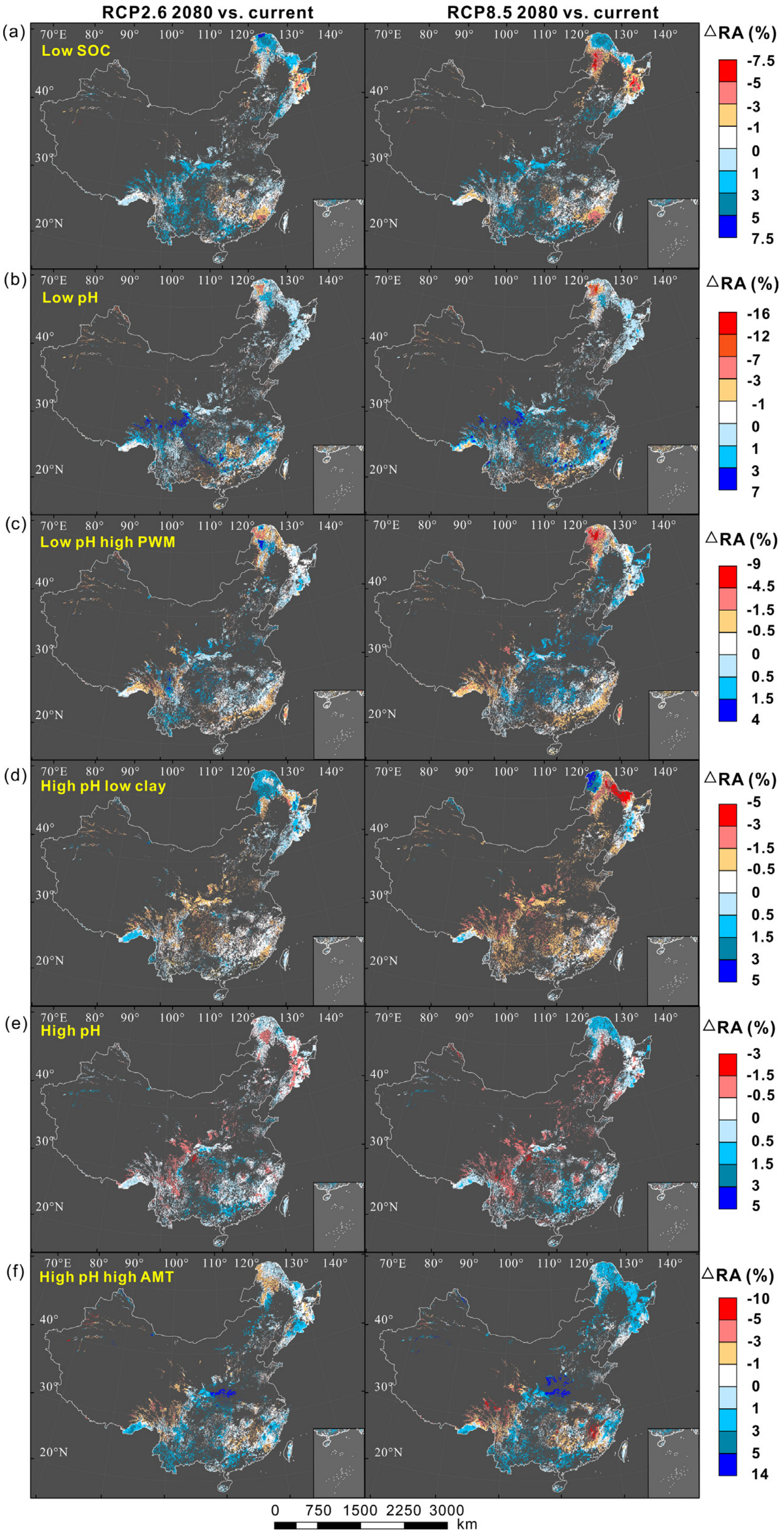

Fig. 4. Projected differences (2080 vs. current) in abundance (ΔRA, %) for identified ecological clusters under two climate scenarios. (a) eco-cluster low SOC; (b) low pH; (c) low pH with high PWM; (d) high pH with low clay content; (e) high pH; (f) high pH with high temperature, respectively. Sub-figures in the first column are for projected differences under RCP2.6 and those in the second column are for projected differences under RCP8.5. Projected increase was colored by light blue-dark blue and decrease by light orange-red.

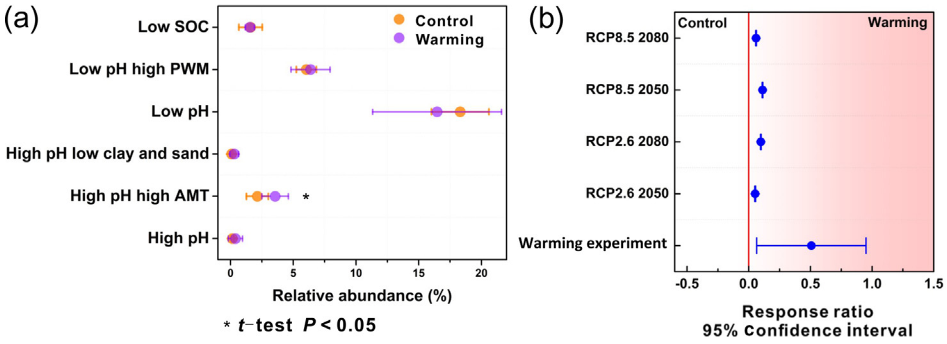

Fig. 5. Cross-validation by using field-warming experiment. (a) Observed abundance variation in the corresponding ecological cluster between warming and ambient conditions for Ailaoshan warming experiment site. Student's *t*-test showed marginally significant changes in high pH high AMT eco-cluster ($P < 0.05$). (b) Response ratio (RR) at 95% confidence interval for high-pH with high-AMT cluster for both experimental and modeled data. Values of response ratio greater than zero with confidence interval not crossing zero indicate projected (future scenarios vs. present-day) or experimental (warming vs. ambient) warming significantly ($P < 0.05$) increase the relative abundance of microorganisms belonging to high-pH with high-AMT eco-cluster at this site. Modeled data were obtained from 53 nearest grid cells around warming experiment site (Global Positioning System (GPS): 101.0167°E/ 24.5333°N).

occurred under RCP8.5 (Fig. 3b-I). We found these changes were exactly opposite to temperature variation trends (Fig. S9 online), suggesting microbes in colder regions were more responsive to temperature changes [42]. However, average abundance of this eco-cluster increases under both scenarios compared to current condition at low-latitudes (8.05% vs. 8.93% vs. 8.58% for present, 2050s and 2080s, respectively under RCP2.6, while 8.05% vs. 8.70% vs. 8.70% under RCP8.5) (Fig. 3b-I). This increase may represent low-SOC preferring microbes well adapted to rising temperature at warmer regions. Given the physiology of oligotrophs, low carbon turnover (that is, limited decomposition), more oligotrophs indicate lower emission of CO_2 and higher carbon sequestration [3]. On the basis of this, increasing abundance of low SOC favorable microorganisms at low-latitudes under warming indicated limited decomposition, which may eventually lead to increase in SOC storage in the coming decades [47]. However, decline in abundance of low-SOC eco-cluster for high-latitudes under RCP8.5 inferred the losses in SOC storage at high-latitudes under warming, probably induced by accelerated decomposition outpacing potential carbon input. These results partially supported previous findings regarding to latitudinal limits of soil carbon losses under warming [47,48] and that soil carbon storage at higher latitudes are more vulnerable to warming [49].

The projected changes in the identified eco-clusters were partially cross-validated by the one-site warming experiment at Ailaoshan Mountain located in Yunnan, southwestern China (< 25°N) (Fig. 5). The significant difference between experimental warming and ambient conditions was only observed in the high-pH with high-AMT eco-cluster (Fig. 5a), suggesting the sensitive regions for other eco-clusters differ from this. Response ratio analysis evidenced a significant increase in the high-pH with high-AMT eco-cluster with warming when compared experimental warming to ambient conditions, as well as projected warming to present conditions (Fig. 5b). In addition, we observed low pH eco-cluster decreased under warming conditions (Fig. 5a), similar to the projection result at low-latitudes (< 25°N) (Fig. 3b).

Understanding how soil microbes respond and adapt to changing climates is a critical question in climate-change-microbes interaction study. Predicting the abundance variation of the eco-clusters to changing climate will also gain important insights into the adaptability of microorganisms to relatively harsh environments (e.g., low pH and oligotrophic conditions) under warming. It has been documented that rate of growth under constant environments and the ability to adapt to changing environments determine the success and evolution of microbes in different ecosystems [50]. Despite greater growth rate was observed at higher temperature [51], our findings of latitudinal-dependent changes in eco-clusters indicated that the adaptability of microbes within different eco-clusters differed and varied with geographic regions under warming. For example, the abundance increase in the low-pH eco-cluster at mid-latitudinal areas (25°–45°N) indicates that warming promotes the adaptability of low-pH favoring microbes in subtropical and warm-temperate climatic zones, but the situation is different at high-latitudes (> 45°N).

One limitation in this study is that model results does not follow closely with the field-warming experiment. A possible reason is the relatively short-warming duration. Previous study has proved discrepancy results from short-term and long-term warming experiments. Another reason is that we only included the dominants in this study, but a number of studies have emphasized the importance of rare biosphere in ecosystem functioning [52]. Therefore, further efforts are needed to address these uncertainties. Additionally, the warming cross-validation is just from single warming site located at subtropical zone, but the coldest regions were more sensitive to climate change according to our projection, so we are eager to call for new studies related to such efforts from different climatic zones, especially in high-latitude regions. A quantitative methodology for assessing the relative response rate of different groups of microorganisms to climate change was proposed in this study. We highlighted the microbial roles in future SOC changes. To confirm this change, one of the promising method is to directly investigate the microbial contribution to SOC by tracing microbial necromass [53] given the importance of microbial anabolism to SOC [54]. Furthermore, we believe this procedure could be applied to other ecosystems, such as grassland and agriculture soils. Since the grassland soils were more sensitive to temperature elevation than forest soils [55], we could propose more intense changes in grassland ecosystem induced by microbes than forest under future climate change conditions.

4. Conclusion

In this study, our prediction indeed paves a new path for quantifying the direction of microbial response to global warming and for the first time projected the eco-cluster-based biogeography in future climate conditions. The latitudinal-dependent changes in eco-clusters under rising temperature potentially indicate that the adaptability of soil microbes to warming was regionally variable. Particularly, regions experienced great projected anomalies (future vs. current) highlight areas that require particular attention under ongoing global climate change, providing valuable information for identifying ecological vulnerable regions in ecological conservation and environmental management. The shifts or expansion in hotspots induced by climate change could be potentially referred as meaningful “ecological indicators” to inform ongoing environmental processes and potential ecological consequences, like soil acidification due to sulfur and nitrogen deposition at mid-latitudes and carbon storage changes at high-latitudes which are useful for decision-making regarding climate change mitigation on ecosystem functions and biodiversity conservation. Collectively, our results provided new insights into deciphering microorganisms-climate change connections by bridging the climate-change-induced microbial changes with potential ongoing environmental processes and ecological consequences.

Conflict of interest

The authors declare that they have no conflict of interest.

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Author contributions

All authors contributed intellectual input of ideas and assistance to this study. The initial concept and analysis were provided by Shang Wang, Ye Deng, and Kai Feng. Sequencing data was merged and processed by Shang Wang, Xuelian Bao, and Kai Feng. The samples belong to CSMI in the charge of Chao Liang, Xingguo Han, and Yongguan Zhu. Field sampling, DNA preparation and sequencing, and soil chemical analysis were carried out by Xuelian Bao, Pengshuai Shao, Tiantian Zheng, Fei Yao, Shan Yang, Shengen Liu, Rongjiu Shi, Zhen Bai, Hongtu Xie, Jinghua Yu, Ying Zhang, Hui Li, Qingkui Wang, and Yuguang Zhang. Field warming experiments were designed and carried out by Wenjun Zhou, Yiping Zhang, Liqing Sha, Qinghai Song, and Yuntong Liu. The manuscript was written by Shang Wang, Kai Feng, Ye Deng, and Chao Liang with insightful inputs from Jizhong Zhou and Yongguan Zhu.

Appendix A. Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.scib.2021.01.021.

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