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Research article

Effects of deterministic assembly of communities caused by global warming on coexistence patterns and ecosystem functions

Wenjing Chen [a,c,1], Huakun Zhou [b,d,1], Yang Wu [a], Jie Wang [a], Ziwen Zhao [a], Yuanze Li [a], Leilei Qiao [e,f], Kelu Chen [b,c], Guobin Liu [a,e], Coen Ritsema [g], Violette Geissen [g], Xue Sha [a,d,e,*]

[a] *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Yangling, 712100, China*
[b] *Qinghai Provincial Key Laboratory of Restoration Ecology in Cold Regions, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, 810000, PR China*
[c] *Moutai Institute, Renhuai, 564500, PR China*
[d] *State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining, 810000, PR China*
[e] *Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, 712100, PR China*
[f] *University of Chinese Academy of Sciences, Beijing, China*
[g] *Wageningen University & Research, Soil Physics and Land Management, POB 47, NL-6700, AA Wageningen, Netherlands*

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ABSTRACT

Seasonal rhythms in biological and ecological dynamics are fundamental in regulating the structuring of microbial communities. Evaluating the seasonal rhythms of microorganisms in response to climate change could provide information on their variability and stability over longer timescales (>20-year). However, information on temporal variability in microorganism responses to medium- and long-term global warming is limited. In this study, we aimed to elucidate the temporal dynamics of microbial communities in response to global warming; to this end, we integrated data on the maintenance of species diversity, community composition, temporal turnover rates (v), and community assembly process in two typical ecosystems (meadows and shrub habitat) on the Qinghai-Tibet Plateau. Our results showed that 21 years of global warming would increase the importance of the deterministic process for microorganisms in both ecosystems across all seasons (R^2 of grassland (GL) control: 0.524, R^2 of GL warming: 0.467; R^2 of shrubland (SL) control: 0.556, R^2 of SL warming: 0.543), reducing species diversity and altering community composition. Due to environmental filtration pressure from 21 years of warming, the low turnover rate (v of warming: −3.13/-2.00, v of control: −2.44/−1.48) of soil microorganisms reduces the resistance and resilience of ecological communities, which could lead to higher community similarity and more clustered taxonomic assemblages occurring across years. Changes to temperature might increase selection pressure on specialist taxa, which directly causes dominant species (v of warming: −1.63, v of control: −2.49) primarily comprising these taxa to be more strongly impacted by changing temperature than conditionally (v of warming: −1.47, v of control: −1.75) or always rare taxa (v of warming: −0.57, v of control: −1.33). Evaluation of the seasonal rhythms of microorganisms in response to global warming revealed that the variability and stability of different microbial communities in different habitats had dissimilar biological and ecological performances when challenged with an external disturbance. The balance of competition and cooperation, because of environmental selection, also influenced ecosystem function in complex terrestrial ecosystems. Overall, our study enriches the limited information on the temporal variability in microorganism responses to 21 years of global warming, and provides a scientific basis for evaluating the impact of climate warming on the temporal stability of soil ecosystems.

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* Corresponding author. Institute of Soil and Water Conservation, Northwest A&F University, Yangling, 712100, PR China
E-mail address: xuesha100@163.com (X. Sha).

[1] These authors contributed equally to this work.

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1. Introduction

Microbial communities change over time, with seasonality as a regular characteristic (Buckley and Schmidt, 2003; Docherty et al., 2015; Žifčáková et al., 2016; Li et al., 2021a). However, the lack of exploration of driving factors microbial dynamics limits our knowledge about their variability and stability under climate change.

Time–decay relationship (TDR) is used to elucidate biological succession dynamics, which quantifies how community similarity changes over time (Shade et al., 2013; Wang et al., 2020). Both stochastic and deterministic assembly processes influence TDR (Martiny et al., 2011; Wang et al., 2017; Xiang et al., 2022), because dispersal limitation and environmental selection are the two major drivers regulating time decay patterns when microbial communities are inspected over extended periods (Hanson et al., 2012; Zhang et al., 2021). Environmental interference pressure is mainly manifested via stochastic rather than deterministic processes (Zhang et al., 2011, 2016; Dang et al., 2022). To describe the temporal distribution patterns of microorganisms, several studies have attempted to unravel the potential processes and mechanisms (Liang et al., 2015a; Guo et al., 2018; Wang et al., 2023). Thus, understanding community assembly rules and defining their roles in regulating community succession, distribution, and diversity is a research topic (Zhou and Ning, 2017; Ning et al., 2020). However, estimating individual ecological processes at the microbial community level is difficult, because the effect-levels of various ecological processes are finer than those of whole communities (Ofiţeru et al., 2010; Caruso et al., 2011; Hanson et al., 2012; Nemergut et al., 2013; Graham et al., 2016). Furthermore, the susceptibility of different microbial taxa to drift, diversification rates, and dispersal ability varies (i.e., dispersal rates depend on body or cell size) (Fenchel, 1993; Chen et al., 2023). Consequently, species within different taxa tend to respond differently to external interference. Thus, shifts in community assembly cannot be identified at the whole community level, rendering it necessary to evaluate assembly processes and other ecological processes at the microbial taxa level.

Information is also limited on temporal variability in microorganism responses to medium- and long-term global warming. Most studies have focused on the influence of short-term warming (i.e., days or weeks) (Zogg et al., 1997; Waldrop and Firestone, 2006; Liang et al., 2015a; Jurburg et al., 2017; Guo et al., 2018; Yan et al., 2022). However, studying how long term warming affect succession is required for climate change research. The long-term models of climate microbial feedback showed that warming usually yields different consequences over long- and short-term periods (Melillo et al., 2017; Metcalfe, 2017). Based on previous studies (Falk et al., 2013; Kim et al., 2013; Shade et al., 2013; Liang et al., 2015a; Xiong et al., 2015; Jiao et al., 2017; Guo et al., 2018), short-term warming cannot accurately reflect the overall microbial community succession law; thus, medium- and long-term field warming experiments must be developed that address this key deficit.

Seasonal influences on the subsurface microbial community might also vary across habitat types and ecosystems (Kuffner et al., 2012; He et al., 2017; Chen et al., 2021; Wang et al., 2021). Consequently, temporal patterns in dynamics might vary with plant type (Korhonen et al., 2010; Han et al., 2021). Thus, to elucidate the temporal patterns in the soil microbiome dynamics under climate change, a 21 year experimental warming was conducted in two typical ecosystems (meadow and shrub habitat) on the Qinghai-Tibet Plateau. Soil samples were collected at August 2018, December 2018, April 2019, August 2019 to represent the four seasons. We tested the following hypotheses: (i) 21 years simulated warming would lead to a more homogenous community due to warmed soil, resulting in fewer stochastic processes and increased adaptability of microorganisms to higher temperatures; (ii) different bacterial taxa or communities in different ecosystems would response differently to seasonal changes under temperature warming and (iii) assembly processes maintain diversity and adjust biogeochemical functionality when faced with environmental filtering from simulated warming.

2. Materials and methods

2.1. Study site and sample collection

This study was conducted at the Haibei Alpine Meadow Ecosystem Research Station (3220 m above sea level [a.s.l.]; 37°36′N, 101°19′E) at the Chinese Academy of Sciences, on the northeastern Tibetan Plateau (Fig. 1). The climate at the station is plateau continental, with an annual mean temperature and precipitation of −2 °C and 500 mm, respectively. Two dominant ecosystems are widely distributed in this region: *Kobresia humilis* meadow habitats (grassland GL) and *Potentilla fruticosa* shrub habitats (shrubland SL). Silty clay loam and clay loam of Mat-Cryic Cambisol are the main soil type of the shrubland and meadow, respectively. Other plant species include *Elymus nutans, Stipa aliena, Kobresia pygmaea,* and *Gentiana straminea* (Zhang et al., 2017).

In two field experimental sites (30 m × 30 m) established in 1997, six plots (2 m buffer zone between each plot) were randomly selected as replicates for each treatment (warming/control). The warming experiment was designed with open-top chambers (OTCs) (0.4 m height and 1.5 m diameter) using Sun-Lite HP fiberglass (Solar Components Corporation, Manchester, NH, USA, 1.0 mm thick) to simulate climate warming (Fig. S1). The mean temperatures of the soil and air increased by 0.3–1.9 °C and 1.0–2.0 °C, respectively, while the soil moisture content declined by 3% between May and September in the warming site (see (Klein et al., 2004; Zhang et al., 2017)). The effect of OTCs on temperature varied depending on ecosystem type. For instance, generally, the impact of warming was greater in GL than in SL (Klein et al., 2004).

Soil samples were collected in August and December 2018, and April and August 2019 from two sites. Four soil cores from each plot (50 cm × 50 cm area) were collected at each event, resulting in 96 samples overall (2 ecosystems × 4 seasons × 2 treatments × 6 replicates). Samples from the same plot were mixed and sieved (2.0 mm) to remove stones, debris, and roots. The sieved sample was separated into two sub-samples and stored in a freezer (−20 °C for <1 week) before analyzing microorganisms.

2.2. DNA extraction, amplification, and sequencing

Total bacterial DNA was extracted from 0.25 g frozen soil samples using a Power Soil DNA Isolation Kit (MO BIO Laboratories). Microbial communities were profiled by targeting a region of the 16S rRNA gene for bacteria. Corresponding polymerase chain reaction (PCR) assays were performed using 338F/806R primer pairs (Wang et al., 2019). The internal transcribed spacer amplification procedures are shown in Appendix S1. High-throughput sequencing analysis was performed using the Illumina Hiseq 2500 platform (2 × 250 paired ends).

2.3. Processing of sequencing data

To obtain clean tags, sequences were filtered using QIIME quality control (Bokulich et al., 2013) and sorted by barcode using the UCHIME algorithm. Chimeric sequences were removed (Edgar et al., 2011). Using UPARSE software, sequences were clustered and assigned to operational taxonomic units (OTUs) with a 97% similarity cutoff. Bacterial representative sequences were then assigned to taxonomic lineages within the SILVA database using RDP Classifier, BLAST, and QIIME2 software. QIIME2 software was used to calculate the OTU richness, Chao1 estimator (Chao1), Shannon, Simpson, abundance-based coverage estimator (ACE) indices and phylogenetic diversity (PD). Shannon, Simpson, OTU richness, Chao1and ACE were used as taxonomic diversity parameters, phylogenetic diversity as phylogenetic diversity parameters.

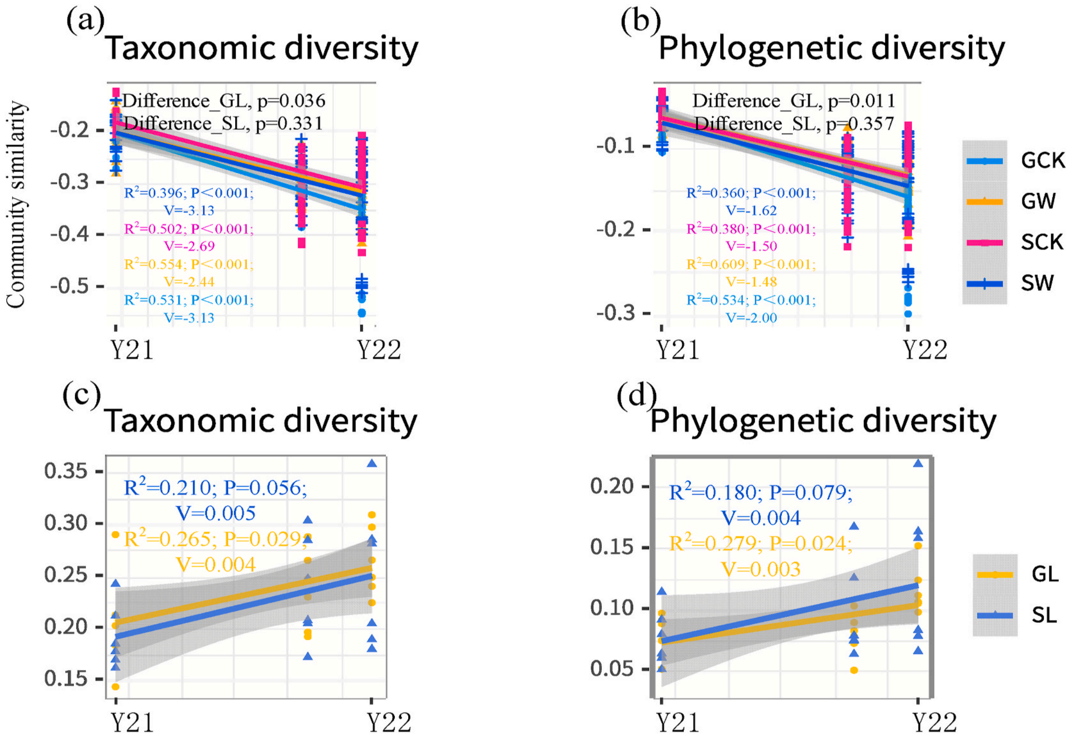

Fig. 1. | The TDRs based on taxonomic diversity measured by Bray–Curtis (a) and phylogenetic diversity measured by Weighted UniFrac (b) of bacterial communities under warming and control conditions. Temporal change in community differences based on Bray–Curtis dissimilarity metrics (c) and Weighted UniFrac dissimilarity metrics (d) between warming and control conditions. The shaded area around the lines covers 95% confidence interval of the correlations.
GW, Grass Land warming; GCK, Grass Land-control; SW, Shrub Land-Warming; SCK, Shrub Land-control.

2.4. *Definition of abundant, rare taxa and generalists, specialists*

In this study, we separated the whole community into subcommunities based on relative abundance thresholds (0.5% for abundant taxa and 0.05% for rare taxa). We then classified the subcommunities into six groups based on published studies (Liu et al., 2015; Dai et al., 2016; Chen et al., 2017; Xue et al., 2018) (Table S1). The six groups were: CRAT, conditionally rare and abundant taxa; CAT, conditionally abundant taxa; AAT, always abundant taxa; CRT, conditionally rare taxa; ART, always rare taxa; and MT, moderate taxa. We defined CRAT, AAT, and CAT as dominant taxa to conduct further study (Chen et al., 2017) (Table S1). Moreover, we distinguished the OTUs as generalists or specialists based on their occurrence, and by using permutation algorithms as implemented in “EcolUtils” (Salazar, 2018).

2.5. *Network analysis*

Network analyses were implemented to evaluate the patterns of coexistence among the bacterial community using the Python module “SparCC” (Friedman and Alm, 2012). SparCC correlations and p-values among bacterial communities were obtained based on 999 permutations of random selections (correlations ≥ 0.8 and $P < 0.05$). Then, the visualization of networks and property measurements of calculations were realized in Gephi (Bastian et al., 2009). By measuring the positive pairwise correlations with positive cohesion, it was possible to describe the degree of cooperative behavior among microorganism community members. In contrast, the degree of competitive behavior among microorganism community members was measured with negative cohesion.

2.6. *Time–decay relationship*

We evaluated TDRs of soil bacteria based on phylogenetic and taxonomic diversity, using linear regressions between temporal distance and community similarity to perceive the influence of warming on the temporal turnover of bacteria (Chen et al., 2015). Bray–Curtis distance was used as the taxonomic-based metric of difference in community composition based on the resampled OTU tables in R using the vegan package. Weighted UniFrac was used as the phylogenetic-based metrics of differences in community composition in R using the *phyloseq* package. The Arrhenius (log–log) plot was used to model the species–time relationship as:

$$\ln (Ss) = \text{constant} - v \ln (T)$$

where Ss is the pairwise similarity of community structure, T is temporal span, and v is the evaluation of the rate of species turnover over time.

The weighted UniFrac distances and Bray–Curtis dissimilarity metrics were computed to measure the diversity of phylogenetic and taxonomic-based metrics in R via the “phyloseq” and “vegan” package using the resampled OTU tables (Dixon, 2003; McMurdie and Holmes, 2013). We then tested whether differences in the slopes of TDRs were statistically significant using a permutation-based linear regression approach in the function of diffslope within the package of “simba” (Nekola and White, 1999).

2.7. *Community assembly*

The null model was used to evaluate the importance of deterministic mechanisms versus stochastic mechanisms underlying bacterial assembly processes. To evaluate the relative importance of stochastic processes in shaping community structure, the stochastic ratio was calculated using a modified method, which is detailed in a previous study, via the function of “ses.mntd” within the R package of “picante” (Zhou et al., 2014). Firstly, quantify the degree of phylogenetic turnover for each paired community ($\beta\text{MNTD}_{\text{obs}}$) and zero distribution ($\beta\text{MNTD}_{\text{null}}$) for comparison, βNTI value characterization $\beta\text{MNTD}_{\text{obs}}$ and β the size of the deviation between $\text{MNTD}_{\text{null}}$. Significant βNTI value (|

βNTI | > 2) is the result of the selection, $\beta NTI < -2$ and $\beta NTI > 2$ refers to homogeneous selection and heterogeneous selection, respectively. For non-significant βNTI values (| βNTI | < 2) refers to dispersal limitation ($RC_{Bray} > 0.95$), homogenizing dispersal ($RC_{Bray} < -0.95$) and ecological drift ($| RC_{Bray} | \leq 0.95$).

The neutral community model (NCM) was used to analyze the dominance of stochastic processes on community assembly by predicting the correlation between relative abundance and OTU detection frequency (Sloan et al., 2006). In this model, immigration rate was defined by m, the overall fit to the neutral model was defined by R^2 (Sloan et al., 2006). The 95% confidence intervals around all fitting statistics were calculated by bootstrapping with 1000 bootstrap replicates.

2.8. Statistical analysis

PICRUSt was used to construct the bacterial metabolic pathways in a previous study (Langille et al., 2013) based on the Kyoto Encyclopedia of Genes and Genomes database (KEGG database, https://www.kegg.jp/kegg/) and NCBI NR database (https://www.ncbi.nlm.nih.gov/) (Zheng et al., 2019).

Statistical analyses were performed with the *vegan* package in R software 3.1.1, unless otherwise stated. The effects of warming on soil variables, plant characteristics, and ecosystem function were tested by repeated-measures analysis of variance (ANOVA). Temporal patterns in bacterial communities under different treatments were estimated by principal coordinate analysis (PCoA) based on the Bray–Curtis dissimilarity. Non-parametric multivariate analysis of variance (Adonis) was used to detect the effects of warming on soil bacterial communities via the function Adonis within the R package *vegan* (Zhou et al., 2012). Linear mixed-effects models (function lmer from the *lme4* package), in which warming (or season) was regarded as a fixed factor and block, treated as a random factor, were used to detect the effect of warming on microbial responses (diversity, cohesion and network properties).

3. Results

3.1. Responses of bacterial community alpha diversity and community structure to 21 years of simulated warming across seasons

After 21 years of simulated warming, bacterial OTU richness, ACE, Chao1, and PD significantly decreased in GL ($P < 0.05$). In contrast, the bacteria of each index (except for Simpson) remained unchanged under warming in SL ($P > 0.05$) (Fig. S1). The diversity of bacteria decreased in GL in spring, summer, and fall, but not winter based on the analysis of ACE, Chao1 index ($P < 0.05$). However, diversity did not alter between the warming and control treatments across all four seasons in SL ($P > 0.05$) (Fig. S2). The variance in plant community and soil variables in response to climate warming and seasonal variations could induce shifts in microbial communities. The structure of the bacterial community was altered by warming, as shown in the PCoA (Bray-Curtis dissimilarity), both in GL and SL (Fig. S3). For example, the relative abundance of Acidobacteria, Actinobacteria, Chloroflexi, Verrucomicrobia, Rokubacteria, Gemmatimonadetes and Nitrospirae between the warming and control site of GL (Fig. S4) and the Proteobacteria, Acidobacteria, Bacteroidetes, Chloroflexi, Verrucomicrobia, Nitrospirae and Firmicutes in SL were different.

To quantify temporal dynamics in the community, we classified all OTUs into abundant and rare taxa (Fig. S5). A small portion of the whole community was classified as dominant (5.252–6.521% OTU richness), and accounted for 37.676–40.232% of the total abundance. However, OTUs that were CRT encompassed a huge proportion of taxa (64.234–67.318% OTU richness), accounting for 50.862–51.302% of total abundance. OTUs that were ART also encompassed a large proportion of taxa (25.261–29.202% OTU richness), accounting for 5.487–6.524% of total abundance (Table S1).

Climate warming had a significant effect on both the composition of abundant and rare subcommunities in both GL and SL. The structure of each bacterial subcommunity was altered by climate warming and seasonal variations, as shown in the PCoA (Bray–Curtis dissimilarity), in both GL and SL (Fig. S6). Adonis showed that the structure of each bacterial subcommunity in warmed plots significantly differed from that of subcommunities in control plots ($P < 0.05$) (Table S2). The structure of each bacterial subcommunity also differed among seasons, as shown in the PCoA based on Bray-Curtis dissimilarity in both GL and SL (Fig. S6). Adonis also showed that season led to differences in the structure of each bacterial subcommunity ($P < 0.05$) (Table S2).

3.2. Changes in microbial temporal turnover under 21 years simulated warming

The GL and SL microbiomes exhibited significant TDRs, under both warming and ambient temperature, based on taxonomic diversity ($P < 0.001$) (Fig. 1a). Bacteria in GL and SL also exhibited significant TDRs both under warming and ambient temperature, based on phylogenetic diversity ($P < 0.001$) (Fig. 1b). The slopes of TDRs in GL based on both diversity metrics (weighted UniFrac and Bray–Curtis) were significantly shallower under warming than the control for bacteria (Bray–Curtis: $v = -3.1$ to -2.44, $P = 0.036$; weighted UniFrac: $v = -1.48$ to -2.00, $P < 0.011$) (Fig. 1a and b). However, there was no difference between the warming and control treatments for the slopes of TDRs in SL ($P = 0.4331$; $P = 0.357$) (Fig. 1a and b).

The bacterial subcommunities in GL and SL had significant TDRs under both warming and ambient temperature based on taxonomic and phylogenetic diversity ($P < 0.05$) (Fig. 2, S7). The slopes of ART and dominant taxa TDRs in GL based on the diversity metrics (weighted UniFrac and Bray–Curtis) were significantly less steep under warming than the control for bacteria ($P < 0.05$) (Fig. 2 and S7a–c). However, there was no difference between warming and control treatments for the slopes of TDRs in SL based on the two diversity metrics ($P > 0.05$) (Fig. 2 and S7d–f). Thus, the continuous changes induced by warming in each subsurface GL subcommunity over time differed from those under ambient temperature, but were the same as those in SL.

Our results further revealed that the differences of microbiome GL structure between warming and control increased linearly with time (weighted UniFrac and Bray–Curtis) diversity metrics (slope = 0.004, $P = 0.029$; slope = 0.003, $P = 0.024$), however, the increases of SL were not significant (slope = 0.005, $P = 0.056$; slope = 0.004, $P = 0.079$) (Fig. 1c and d). Moreover, the distinctions of bacterial subcommunity structure in GL between control and warming all increased linearly with time based on the Bray–Curtis and weighted UniFrac diversity metrics (but not for ART) ($P < 0.05$), nonetheless, the increases of SL were not significant (apart from dominant taxa) ($P > 0.05$) (Fig. 3a–d). In general, the response sensitivity (the high slope of the community differences) of dominant species to warming was higher than that of CRT and ART (Fig. 3a–d).

3.3. Fit to the neutral model and null model of community assembly

The NCM successfully estimated much of the relationship between the occurrence frequency of OTUs and variation in their relative abundance (Fig. 4), with 52.4% and 55.6% of explained overall microbiome variance for GL and SL, respectively, under ambient temperature (Fig. 4). For any treatment or site, there were several bacterial subcommunities that occurred more or less (below (yellow: lower dispersal ability) or above (red: higher migration ability) neutral prediction) frequently than predicted by NCM (Fig. 4). However, the NCM of bacterial community showed large explained community variance for overall bacterial community (GL range: 52.4–46.7%, SL range: 55.6–52.2%), particularly at each subcommunity level: dominant taxa (GL range: 43.6–37.5%, but not for SL), CRT (GL range: 56.6–48.3%, SL range: 54.8–54.3%), and ART (GL range: 64.0–59.3%, SL range:

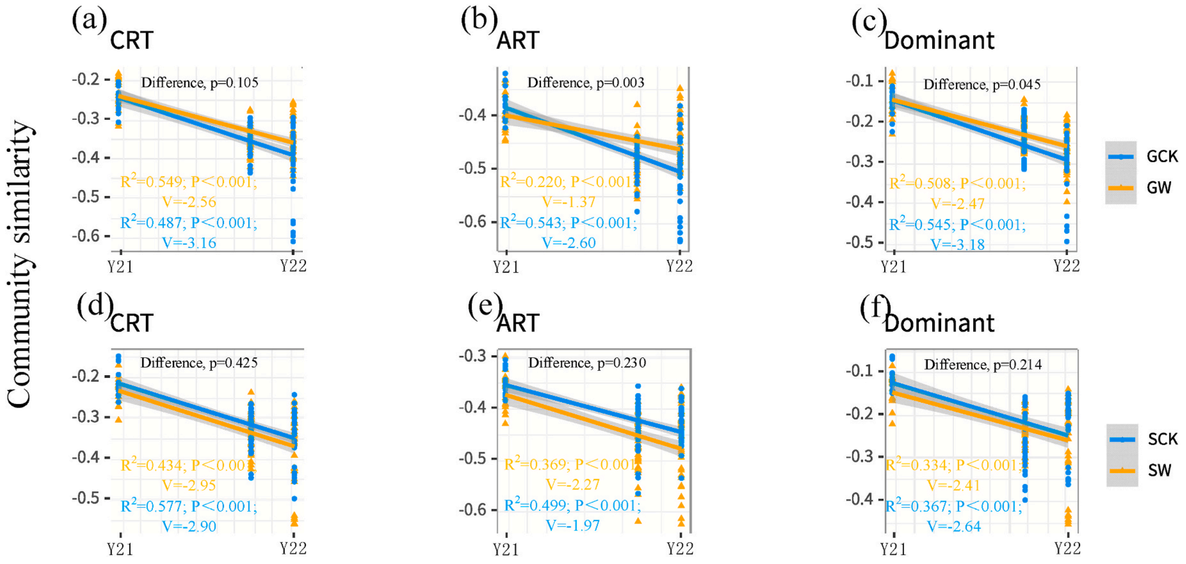

Fig. 2. | The TDRs based on taxonomic diversity (measured by Bray–Curtis) of bacterial subcommunities under warming and control conditions in Grassland (a, b, c) and in Shrubland (d, e, f).
The shaded area around the lines covers 95% confidence interval of the correlations.
Dominant represents taxa including three categories of abundant taxa including AAT (always-abundant taxa), CAT (conditionally abundant taxa) and CRAT (conditionally rare and abundant taxa), CRT, conditionally rare taxa; ART, always-rare taxa.
GW, Grass Land warming; GCK, Grass Land-control; SW, Shrub Land-Warming; SCK, Shrub Land-control.

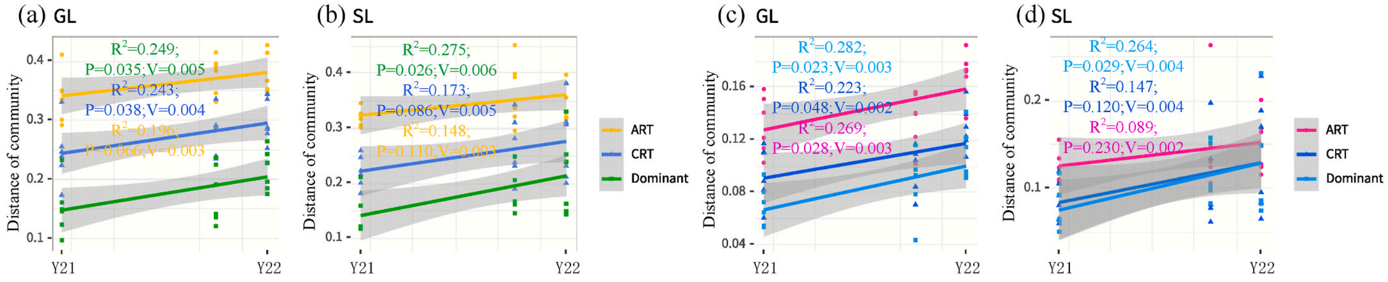

Fig. 3. | Temporal change in subcommunity differences based on Bray–Curtis dissimilarity metrics(a, b) and weighted UniFrac dissimilarity metrics (c, d) between warming and control conditions. The shaded area around the lines covers 95% confidence interval of the correlations. a,c Grassland. b,d Shrubland.
Dominant represents taxa including three categories of abundant taxa including AAT (always-abundant taxa), CAT (conditionally abundant taxa) and CRAT (conditionally rare and abundant taxa), CRT, conditionally rare taxa; ART, always-rare taxa.
GL, Grass Land; SL, Shrub Land-Warming.

65.1–60.6%) (Fig. 4). The high temperature decreases the dispersal limitation with the increase in undominated process in the various subcommunities in GL based on quantifying the deviation of phylogenetic turnover, however, the phenomenon in SL is just the opposite (Fig. S8). Moreover, the species dispersal of ART was higher than CRT and dominant taxa under both warming and ambient temperature of GL and SL (Fig. 4). These results suggest that the essential characteristics of bacterial taxonomy determine the characteristics of their community assembly processes to some extent.

The dominant taxa included a relatively high proportion of non-neutral taxa and a low proportion of neutral taxa. CRT included a more balanced ratio of neutral and non-neutral taxa. ART were composed of a relatively high proportion of neutral taxa (Table 1). The dominant taxa also included a relatively high proportion of specialist taxa, and lacked generalist taxa. CRT comprised a more balanced combination of specialist and generalist taxa. ART comprised a relatively high proportion of generalist taxa (Table 1).

Climate warming significantly affected both neutral and non-neutral fractions of community composition in both GL and SL. The community structures of both GL and SL were altered by warming, as shown in the PCoA (Bray–Curtis dissimilarity) (Fig. S9). Adonis also showed that each fraction of community composition in the control plots differed significantly from the warming plots ($P < 0.05$) (Table S2).

The neutral and non-neutral fractions of the bacterial communities in GL and SL had significant TDRs under both warming and ambient temperature based on phylogenetic and taxonomic diversity ($P < 0.05$) (Figs. S10 and S11). The slopes of each TDR fraction (neutral and non-neutral) in GL were gentler under warming than the control for bacteria ($P < 0.05$), based on the diversity metrics (weighted UniFrac and Bray–Curtis) (Fig. S10 and S11a–b). However, there was no difference between the warming and control plots for the slopes of TDRs in SL based on the two diversity metrics ($P > 0.05$) (Fig. S10 and S11c–d).

Differences to the neutral and non-neutral fractions in the composition of the bacterial community in GL increased linearly with time in both the control and warming plots based on weighted UniFrac and Bray–Curtis diversity metrics ($P < 0.05$). SL also showed a significant increase ($P < 0.05$), but not for neutral taxa ($P > 0.05$) (Figs. S12a–d). Thus, the neutral fractions of bacteria appeared to be more stable than those of non-neutral fractions.

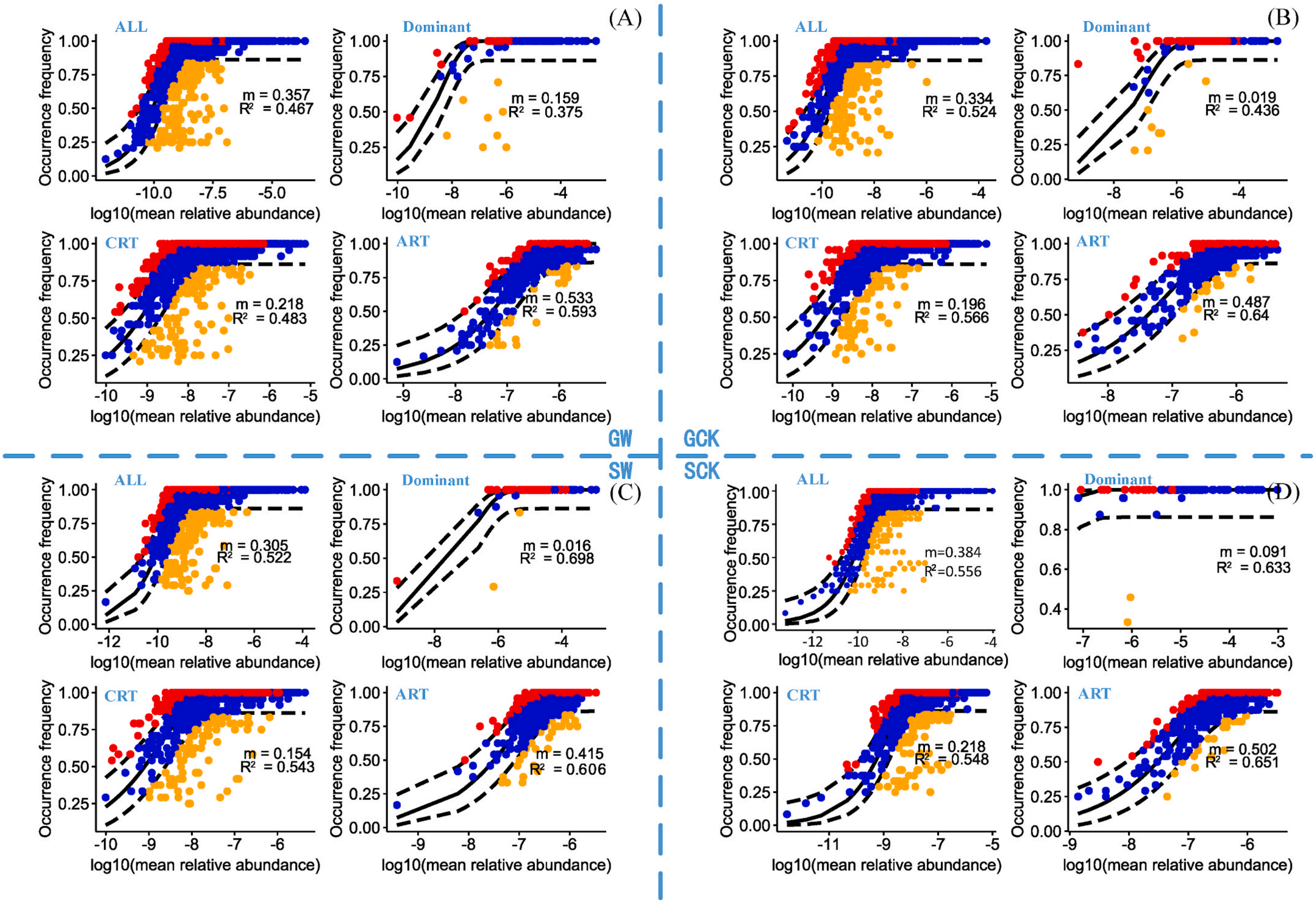

Fig. 4. Fit of the neutral community model (NCM) of community assembly. The solid blue lines indicate the best fit to the NCM, and the dashed black lines represent 95% confidence intervals around the model prediction. OTUs that occur more(Red) or less(Yellow) frequently than predicted by the NCM. Values of m indicate the estimates of dispersal rate between communities, R^2indicates the fit to this model.

Dominant represents taxa including three categories of abundant taxa including AAT (always-abundant taxa), CAT (conditionally abundant taxa) and CRAT (conditionally rare and abundant taxa), CRT, conditionally rare taxa; ART, always-rare taxa.

GW, Grass Land warming; GCK, Grass Land-control; SW, Shrub Land-Warming; SCK, Shrub Land-control.

Table 1

| Species composition of different subcommunities.

Category	Dominant(%)		CRT(%)		ART(%)	
	GL	SL	GL	SL	GL	SL
Neutral	12.195	5.102	44.058	40.991	57.699	58.251
Non-neutral	87.805	94.898	55.942	59.009	42.301	41.749
Specialist	11.382	5.102	13.248	13.690	10.575	9.076
Generalist	0.000	0.000	12.869	9.205	20.408	20.297
Non significant	88.618	94.898	73.883	77.105	69.017	70.627

Dominant represents taxa including three categories of abundant taxa including AAT (always-abundant taxa), CAT (conditionally abundant taxa) and CRAT (conditionally rare and abundant taxa), CRT, conditionally rare taxa; ART, always-rare taxa.

3.4. *Co-occurrence patterns of bacteria and mechanism of ecosystem functions*

Positive and negative cohesion was significantly higher in the warming plot than in the control plot GL, due to ART and CRT having higher cohesion ($P < 0.05$) (Fig. S13). Thus, climate warming might enhance biotic interactions by increasing connectedness between species. The ratio of negative cohesion to positive cohesion significantly decreased in the warming plots of SL ($P < 0.05$) (Fig. S14), but not for that in GL. In short, under 21 years pressure of climate warming, the dominant position of positive cohesion in molecular networks was strengthened in SL. The lower modularity in the warming plot was significantly lower than that of the control in GL and SL ($P < 0.05$) (Fig. S15).

Warming temperature significantly increased the average degree, average path length, connectance, global clustering coefficient, centralization closeness and centralization betweenness in SL ($P < 0.05$). In comparison, warming temperature caused average path length, centralization betweenness, centralization closeness and global clustering coefficient to decrease in GL ($P < 0.05$ (Fig. S15). Overall, the responses of molecular ecological networks to warming temperature differed substantially between the two habitats. Pairwise comparisons of βNTI values for the bacterial community were significantly and positively correlated with the positive/negative cohesion of dominant taxa, CRT, and ART (Fig. 5a), with a shift from stochastic processes to deterministic processes increasing cohesion within each subcommunity. The ratio of negative to positive cohesion created a stronger correlation with community functions associated with plant polymer degradation and nitrogen and phosphorus cycling than other network characteristics and species diversity (Shannon, ACE, Chao1, OTU richness) (Fig. 5b).

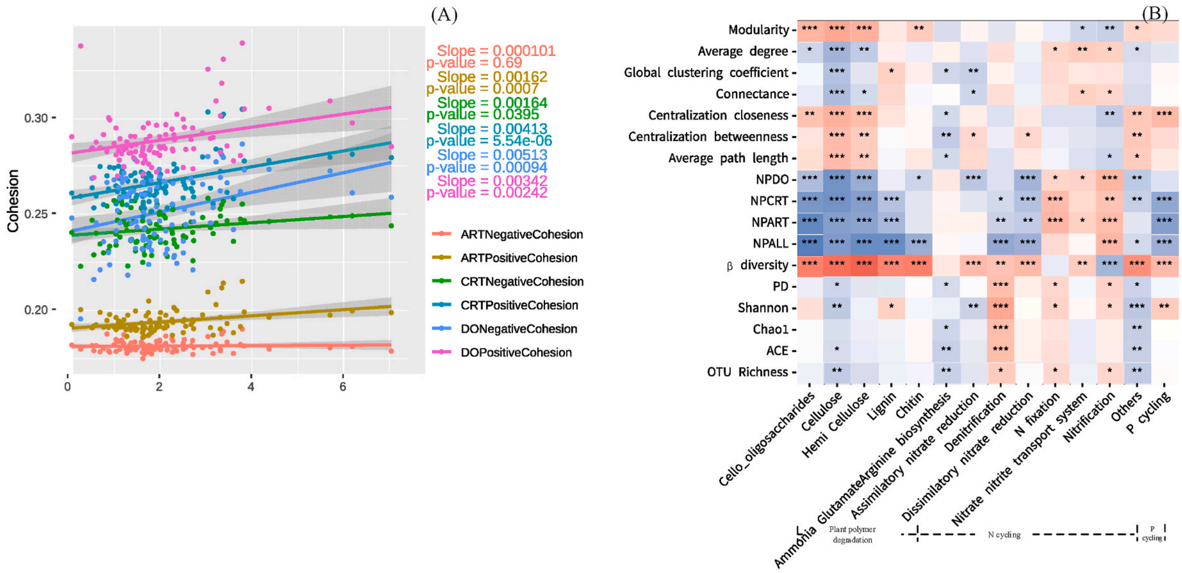

Fig. 5. | Relationships between the bacterial cohesion and β-nearest taxon index (βNTI), network properties and community functional traits under warming. a, Linear regressions models and associated correlation coefficients are provided on each panel.
b, Pearson correlations of network properties and relative abundances of predicted functional gene. For significant ($P \leq 0.05$) correlations, positive correlation coefficients are highlighted in red, while negative correlation coefficients are highlighted in blue.

4. Discussion

4.1. Simulated warming disturbance drives seasonal variability in bacterial communities

Our results revealing that climate warming interferes with seasonal dynamics in microbial community composition and community assembly processes, creating new and uncertain consequences regarding community structure and species diversity. As expected, PCoA showed that each bacterial subcommunity in the warming sites was distinct to the control community in both SL and GL ecosystems. Twenty-one years of warming promotes deterministic over stochastic processes in controlling community composition in all four seasons, resulting in a determinism-dominated assembly (except for winter in GL). Strong environmental pressure deterministically selects species, reducing neutrality and historic contingency. Environmental filtering from deterministic processes only selects individuals with high environmental tolerance or other beneficial characteristics to survive (Gamez-Virues et al., 2015), which results in biotic homogenization, with the same β-diversity each summer (Mori et al., 2015). When environmental filtering pressure was lacking after 1 year of warming, the stochastic assembly process of the community led to the higher β-diversity of the community than the previous year, as observed in the control sites of GL and SL.

Shifts in community structure generally alter species diversity; however, the bacterial diversity of shrub sites might have recovered through a combination of colonization/re-establishment (through dispersal and seed banks) and/or competitive release (transfer of dominant species) after simulated warming (21 years in our study), similar to the restoration of diversity in above-ground vegetation (Zhang et al., 2017). Twenty-one years of observations of increasing temperature in the Plateau meadow showed that the decline in diversity was permanent, or that the negative impact of high temperature on diversity was still in progress, because warming strongly altered the balance of community diversity in this ecosystem. Except for winter, the negative effects of warming on soil bacterial diversity in the plateau meadow ecosystems appeared to be stable in all seasons.

4.2. Warming disturbed the dominant role of stochastic processes in controlling community structure

We found that 21 years of simulated warming reduced stochasticity in the turnover of community structure. There was a significant linear decline in the similarity of the bacterial community and subcommunities across the 1-year warming experiment; however, v values were low. Furthermore, control plots had considerably steeper slopes for TDRs within the bacteria community (Bray–Curtis and/or weighted UniFrac metrics) than did warming plots. The shift in TDRs was strongly correlated with the decline in stochastic assembly. Twenty-one years of simulated warming increased determinacy, reducing stochasticity in the microbial community, selecting for temperature adaptive advantages. This phenomenon led to greater community similarity as the consequence of a gentler turnover pattern. Due to the continuation of 21 years simulated warming effects, the soil environments of GL and SL were subjected to stress during periodic high summer temperatures, which enhanced environmental filtration pressure in warming plots compared to the control. This pressure prevented species lacking certain physiological characteristics from appearing in local communities (Kraft et al., 2015). In a population system of a species exposed to large environmental changes, deterministic processes overwhelm stochastic processes (Wang et al., 2013). The warming climate might also indirectly strengthen the selection of the subsurface community by altering the plant community (Yuan et al., 2016) or through more regular inputs of organic accessible C and N from plants influencing plant community composition (Liang et al., 2015b; Huang et al., 2019). Thus, a more specialized habitat would promote the dominance of important deterministic processes for shaping the bacterial community structure in our findings (Robinson et al., 2010; Valyi et al., 2016). However, our results are contradictory to those of a previous study, which showed that 6 years of simulated warming significantly increased the rates of temporal soil microbial turnover (Guo et al., 2018). This difference might be attributed to higher microbial activity during dispersal, reproduction, extinction, and colonization caused by faster metabolic kinetics under warmer circumstances at the earlier stage of global warming (Allen et al., 2002; Brown et al., 2004). Based on results from one unusually long time series of global warming (26 years), the microbiome passed through four main stages characterized by different structural and functional properties (Melillo et al., 2017). Hence, the warming climate likely influences microbial assembly processes and associated underlying mechanisms differently at different stages.

4.3. Different successional patterns of dominant, always-rare, and conditionally rare subcommunities

We found that CRT were more resistant to disturbance caused by climate warming than dominant taxa and ART, which was reflected in the lack of significant differences in CRT temporal turnover slopes between warming and control plots. Temporal turnover in microbes tends to be lower than that of large organisms (Shade et al., 2013), due to the specific biological characteristics of microbes (massive population sizes, high dispersal rates, rapid asexual reproduction, and resistance to extinction). Thus, different microbial subcommunities with various biological traits (body and cell size (Fenchel, 1993) and the existence of spores or cysts (Hanson et al., 2012)) exhibited different slopes for time-decay relationships in response to a warming climate, which resulted in varying sensitivity and resilience to disturbance. Thus, comparing the resilience and resistance of different microbial taxa could be measured using temporal turnover when challenged by outside disturbances (Shade et al., 2011, 2012).

Variation in the dominant bacterial taxa composition between the control and warming plots increased gradually with time. Dominant species included a greater percentage of habitat specialists than habitat generalists, whereas CRT and ART were composed of a balanced percentage of the two groups. Habitat generalists can occupy a wider range of habitats, and so are more ubiquitous. In contrast, specialists have very limited environmental tolerances, and are more susceptible to changes in temperature (Pandit et al., 2009; Vazquez et al., 2017). A previous study suggested that there is stronger filtration pressure from deterministic processes on specialists than generalists (Mo et al., 2021). The process of selection generally differentiates microbial composition among locations. The environment selects for taxa that are relatively better adapted to the conditions at a given moment, based on the different responses of microbes to environmental conditions (Vellend, 2010). As selective factors have a continuous temporal effect, higher degrees of selection tend to produce a more frequent temporal turnover in the TDR. In particular, the distance–decay relationship of dominant taxa subjected to the stress of global warming should be stronger when dispersal is more limited, such as across disconnected freshwater bodies (Barberán and Casamayor, 2010). Overall, our findings revealed the multiple significant influences of experimental warming on the succession of soil bacterial subcommunities. In summary, the influence of global warming on the bacterial TDR varied with respect to time-scale, habitat, and taxon resolution in our study. Therefore, the interaction among these factors likely shapes the distinct succession sequences in community composition, leading to temporally changing patterns in ecological functional processes (Fierer et al., 2007; Strickland et al., 2009).

4.4. Impact of community assembly on interaction patterns and ecosystem function

Our results showed that the interactions among taxa are driven by environmental selection. Previous studies confirmed that the interaction pattern of microbes is correlated to assembly processes in subsurface ecosystems (Plerou et al., 1999) and river systems (Aitchison, 1982). Our study showed that higher temperatures induced more bacterial associations (both negative and positive) in the GL warming plot, with the ratio of negative to positive cohesion significantly decreasing in the SL warming plot. Negative/positive cohesion also increased with the importance of deterministic processes and was induced by high temperatures. This result indicated that the interaction model became more complex when the community was increasingly dominated (controlled) by deterministic processes. This phenomenon might be attributed to more cooperative behaviors that provide direct benefits to other community members, offsetting pressures on environmental selection. Alternatively, environmental filtering might be more intense in the subsurface community when the temperature is higher, causing a higher degree of negative cohesion among bacteria, due to multiple antagonistic interspecific behaviors arising under the pressures of environmental selection. Overall, a higher negative/positive cohesion or a decrease in the ratio of negative to positive biotic cohesion appeared to affect bacterial responses to temperature stress in our study.

Biodiversity is a vital driver of ecosystem functioning, because the major loss of biodiversity is expected to negatively impact ecosystem functions and services (Cardinale, 2011). However, the network properties typically exhibit stronger correlations with the abundance of genes related to plant polymer degradation and nitrogen and phosphorus cycling, particularly the ratio of negative and positive cohesion, when compared to other network properties and other indices like alpha-diversity. The weak correlation between diversity and ecosystem function might be influenced by functional redundancy, complementarity (Becker et al., 2012; Liang et al., 2016; Maynard et al., 2017), or species competition based on our results. Functional variation in the ecosystem might arise because adaptation to environmental stress induced from global warming might enhance interspecific environmental selection pressure, resulting in competitive and cooperative behaviors (Ma et al., 2020), which are further mediated by changes to community functions (Li et al., 2021b). Thus, our results confirm prior observations that the balance between negative and positive cohesion among the bacterial community determines the comprehensive performance of functional processes in the ecosystem (Bardgett and Van Der Putten, 2014). Overall, intrinsic linkages between community assembly and microbial interactions are regarded as the mechanism of deterministic (niche-based) assembly shaping community composition (Nazir et al., 2009; Chase and Myers, 2011; Zhou and Ning, 2017) and related functional processes.

5. Conclusion

Our study found that global warming affects the seasonal dynamics of bacterial communities, and this is due to stronger selective pressure from deterministic processes. This impacts the community structure and related functions under climate warming. The succession dynamics of bacteria were notably affected by simulated warming, and dominant specialist species were subjected to higher impact under such conditions. The study showed that 21 years of warming regulated the rhythm of seasonal turnover and coexistence relationships of microbes, and contributed to maintaining ecosystem services. This study enhances our knowledge about the temporal variability in microorganism responses to global warming, and provides a scientific foundation for assessing the influence of climate warming on soil ecosystems.

Credit author statement

WJC, HKZ, GBL, CJ Ritsema, V Geissen and SX design the experiments. WJC, YW, YZL, LLQ, ZWZ and KLC contributed to sample collection. WJC, YW performed the experiments. WJC, YW, JWC analyzed the data. WJC and HKZ wrote the manuscript. All authors reviewed the manuscript. All authors read and approved the final manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that might have influenced the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.118912.

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