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Negative effects of multiple global change factors on soil microbial diversity

Yang Yang [a,b,c], Ting Li [d], Yunqiang Wang [a,b,*], Huan Cheng [e], Scott X. Chang [f], Chao Liang [g], Shaoshan An [c,**]

[a] State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an, 710061, China
[b] CAS Center for Excellence in Quaternary Science and Global Change, Xi'an, 710061, China
[c] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling, 712100, China
[d] Guangzhou Academy of Forestry and Landscape Architecture, Guangzhou, 510405, China
[e] College of Forestry, Sichuan Agricultural University, Chengdu, 611130, China
[f] Department of Renewable Resources, University of Alberta, Edmonton, T6G 2E3, Canada
[g] Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, China

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ABSTRACT

Soil microbial diversity is one of the key factors affecting the structure and function of the belowground ecosystem; yet, little is known about the response of microbial diversity to multiple global change factors. Here, we conducted a global meta-analysis based on data collected from 237 published papers to explore the effect of multiple global change factors (elevated carbon dioxide (eCO_2), warming, elevated nitrogen addition (eN), wetting–drying cycle, drought, decreased precipitation (precipitation(−)), and increased precipitation (precipitation(+))) on microbial diversity (Shannon index) across different ecosystems (cropland, grassland, forest, shrubland, desert, wetland, and tundra). Global change decreased soil bacterial and fungal diversity by an average of 2.9% and 3.5%, respectively. For each global change factor, the effect sizes of precipitation(−), eN, wetting–drying cycle, and drought on soil microbial diversity were negative, whereas the effect sizes of eCO_2, warming, and precipitation(+) were positive. This phenomenon was driven by changes in mean annual temperature (MAT) and edaphic factors (especially soil pH, bulk density and organic carbon content) rather than mean annual precipitation. Moreover, the effect size of soil microbial diversity linearly declined with increasing MAT, suggesting that microbial diversity was highly dependent on climate conditions at the global scale. In addition, two- and three-way interactions of global change factors aggravated the negative effects of individual effects. We suggest that it is essential to conduct long-term, multiple-factor experiments to assess the response of soil microbial diversity to global change because multiple global change factors often occur simultaneously.

1. Introduction

Global change (including elevated atmospheric carbon dioxide concentration (eCO_2), warming, alterations in precipitation, wetting–-drying cycle, drought, and elevated atmospheric nitrogen deposition (eN)) induced by human activities are major drivers of biodiversity loss from local to global scales (Crowther et al., 2015; Chen et al., 2019; Engelhardt et al., 2018; Rillig et al., 2019; Zhou et al., 2020). Soil microorganisms, dominated by bacteria and fungi, play a vital role in maintaining the function of belowground ecosystem (Lloyd-Price et al., 2017; De Nijs et al., 2019). The diverse microbial communities mineralize soil organic matter, and regulate nutrient cycling and carbon (C) sequestration (Romero-Olivares et al., 2017). Because of the key roles played by microorganisms in soil organic matter mineralization and other C cycling processes, identifying microbial responses to global change can greatly improve our understanding of C cycling-climate change feedback mechanisms (Liang et al., 2017; Delgado-Baquerizo et al., 2017a).

Based on our knowledge of the response of soil microbial communities and ecological processes to global change (Crowther et al., 2015;

* Corresponding author. State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an, 710061, China.
** Corresponding author. State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Shaanxi, 712100, China.
E-mail addresses: wangyq@ieecas.cn (Y. Wang), shan@ms.iswc.ac.cn (S. An).

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Delgado-Baquerizo et al., 2018; Zhou et al., 2020), we developed a conceptual model that presents the effects of multiple global change factors on soil microbial communities (Fig. 1). Global change factors, such as eCO_2, warming, eN, alterations in precipitation, wetting–drying cycle and drought, have strong effects on microbial communities by changing soil properties and conditions for plant performance (Sulman et al., 2014; Toju et al., 2018). For example, global warming could stimulate plant productivity and a series of enzymatic reactions (Guo et al., 2018, 2019), and then the increased organic matter input from plant production promotes soil organic C (SOC) decomposition as the increased substrate availability enhances the activities of microorganisms (Tylianakis et al., 2008; Allison et al., 2010). As a result, global warming would enhance microbial activities, and their nutrient metabolism rates (Sheik and Beasley, 2011), and some microorganisms excrete large amounts of organic acids, degradable sugars, and amino acids that help to maintain the balance of microbial diversity (Romero-Olivares et al., 2017; Xiao et al., 2018). Atmospheric N deposition is estimated to increase by 2–3 times in the next century (Yu et al., 2019). It is widely accepted that increasing N deposition rates will cause soil acidification and change soil nutrient availability and the composition of microbial communities (Dai et al., 2018; Yang et al., 2020; Zhou et al., 2020). This would decrease soil microbial diversity and biomass at regional and global scales (Chen et al., 2019; Yang et al., 2020). In addition, soil microorganisms have a wide range of physiological tolerance to alterations in precipitation, wetting–drying cycle and drought to maintain their diversity under extreme climate conditions.

When terrestrial ecosystems are experiencing higher atmospheric CO_2 concentrations, alterations in precipitation or climate warming may occur at the same time (Sheik and Beasley, 2011; Ware et al., 2019). However, most previous studies are focused on the effect of individual global change factors on soil microbial diversity, while a combination of these global change factors often regulates microbial diversity (Delgado-Baquerizo et al., 2017b; Zhou et al., 2020). For example, combined eCO_2 and altered precipitation increased soil microbial diversity, yet such an increase can be offset by climate warming, which ultimately decreases soil microbial diversity (Rodriguez-Caballero et al., 2018; Delgado-Baquerizo et al., 2018). Similarly, warming can enhance microbial activity and diversity, but such positive effects can be negated by altered precipitation (Engelhardt et al., 2018). Thus, it is crucial that we investigate whether multiple global change factors have additive or antagonistic effects on soil microbial diversity (Delgado-Baquerizo et al., 2016; Fox, 2018; Chen et al., 2019; Zhou et al., 2020). Here, we collected soil microbial diversity data associated with multiple global change factors, including eCO_2, warming, alterations in precipitation, eN, wetting–drying cycle and drought, from 237 published papers (up to August 2020). Our objective was to address two important questions: 1.) how do the individual and combined global change factors influence soil microbial diversity? and 2.) what are the potential factors driving these individual and combined effects of global change factors on soil microbial diversity?

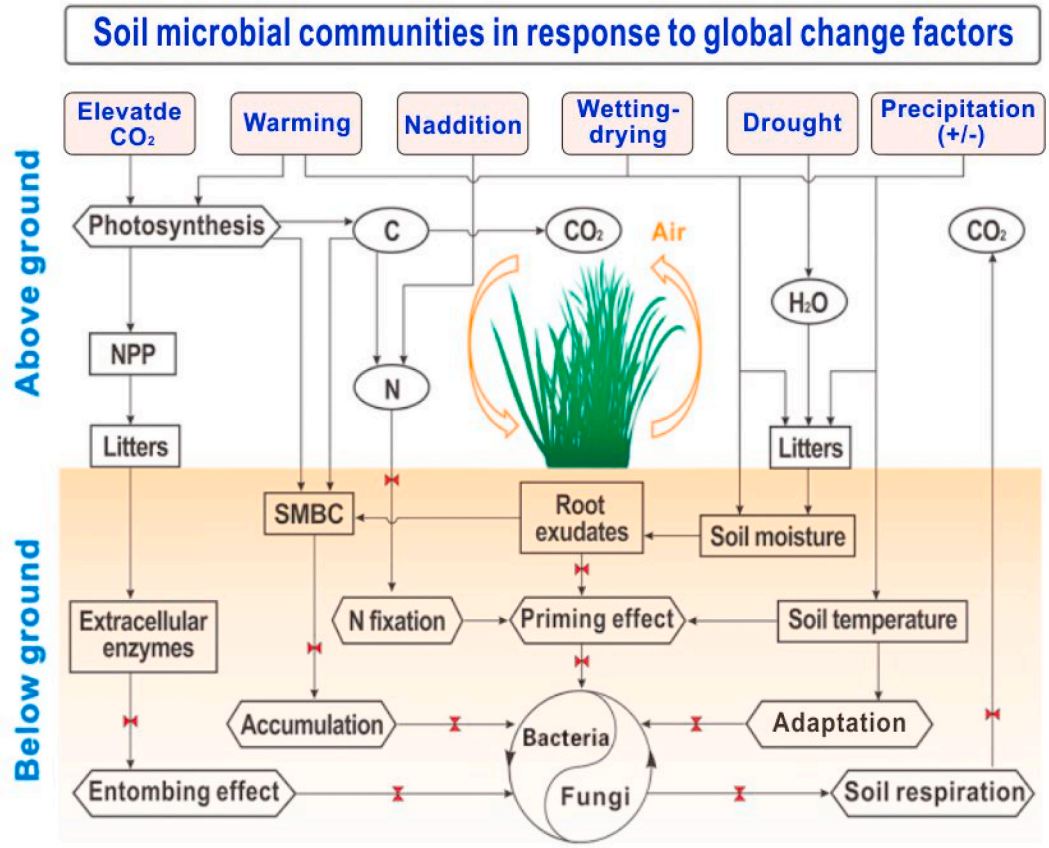

Fig. 1. Conceptual model of the effect of global change factors on soil microbial communities, highlighting the microbial metabolic processes involved in carbon (C), nitrogen (N), and water (H_2O) cycling in terrestrial ecosystems. Yellow arrows around the plants indicate air exchange (carbon dioxide (CO_2) and H_2O) in processes such as photosynthesis, transpiration, and respiration; black arrows indicate flows of energy and elements or an effect of one process on another; ellipses indicate atmospheric pools of nutrients and H_2O; rectangles are nutrient pools; and hexagons indicate soil processes that are controlled by soil microbial communities, as indicated by the red valves. The taiji symbol is used to create a sense of changing microbial processes and illustrate that microbial processes are driven differently by bacteria and fungi with different trophic relationships. The microbial driven processes, such as the priming effect, entombing effect and soil respiration, highlight the importance of global change effects on soil microbial communities. This figure was modified from Yuan et al. and Liang et al. (2017). The plant illustration is from a PPT gallery (http://www.58pic.com/tupian/pptzhiwu.html). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2. Materials and methods

2.1. Data collection

Soil microbial diversity (Shannon index) data associated with global change factors were retrieved from the Google Scholar (https://scholar.google.com/), CNKI (http://www.cnki.net/), and Web of Science (http://apps.webofknowledge.com/) databases.

The following keywords were used for the literature search: global change factors (elevated CO_2, warming, alterations in precipitation [increased and decreased precipitation], N addition/deposition, wetting–drying cycle [periods of prolonged drying interspersed with relatively rapid rewetting events], drought [soil drought]), soil microbial diversity, richness, and microbial communities. The following criteria were used to narrow down our search: (1) when considering the multiple effects of global change factors on soil microbial diversity, at least two of the global change factors were studied in the publication; (2) the global change experiments were conducted in terrestrial ecosystems in the field but not in the laboratory; (3) when a publication included several experiments under different global change factors, such as different treatments, locations, soil layers, and ecosystems, we considered them different observations; (4) when different publications included the same data from one study, we recorded the data only once. When a study included two or more global change factors, we considered them distinct observations; and (5) all data were obtained from 0 to 20 cm soil layer in different ecosystems: cropland, grassland, forest, shrubland, desert, wetland, and tundra.

The numeric data were extracted directly from tables and supplementary files, and data presented in graphs were extracted using the Engauge Digitizer v 11.1 software (http://www.zdfans.com/html/).

Based on the above criteria, 237 published papers were identified, including a total of 1374 observations in the following categories: eCO_2 (212 observations from 43 published papers), warming (259 observations from 44 published papers), alterations in precipitation (138 observations from 26 published papers), eN (392 observations from 89 published papers), wetting–drying cycle (86 observations from 17 published papers), and drought (287 observations from 20 published papers). The global distribution of these sites is presented in Fig. 2. In addition, the edaphic factors (soil pH, bulk density (BD), SOC, total N, and microbial biomass C data of each site were recorded from these publications. The mean annual temperature (MAT), mean annual precipitation (MAP) were recorded from these publications or derived from the WorldClim database (https://www.worldclim.org/) using the latitude and longitude information for each site.

2.2. Calculation of the treatment effect size

To identify how global change factors affect soil microbial diversity, this meta-analysis used natural log-transformed effect size (ln RR) as the index ("effect size"), and the method in Hedges et al. (1999) was utilized to calculate the effect sizes for individual observations (d*ij*):

$$dij = \ln RRij = \ln (Yt/Yc) = \ln Yt - \ln Yc \quad \text{Eq. 1}$$

where d*ij* represents the effect size of an individual observation, Yt represents the average value in the treatment, and Yc represents the average value in the control.

The variance (v) of the effect size of individual observations was calculated according to Hedges et al. (2010):

$$v = \frac{St^2}{NtXt^2} + \frac{Sc^2}{NcXc^2} \quad \text{Eq. 2}$$

where *Nt* represents the sample number of the treatment, *Nc* represents the sample number of the control, Sc represents the standard deviation of the control, St represents the standard deviation of the treatment, *Xc* represents the average value of the control, and *Xt* represents the average value of the treatment.

The weight factor (w*ij*) was calculated according to the following equation:

$$wij = 1/v \quad \text{Eq. 3}$$

The weighted average effect size (RR_{++}) was calculated with ln RR*ij*:

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} wij \cdot \ln RRij}{\sum_{i=1}^{m}\sum_{j=1}^{k} wij} \quad \text{Eq. 4}$$

The effect sizes were calculated using the METAWIN 2.1 software (https://en.freedownloadmanager.org/Windows-PC/MetaWin.html). The effect sizes (ln RR) of all observations were treated as random variations, and all individual observations were weighted based on the mixed-model variance reciprocal (Lajeunesse, 2011; Limpens et al.,

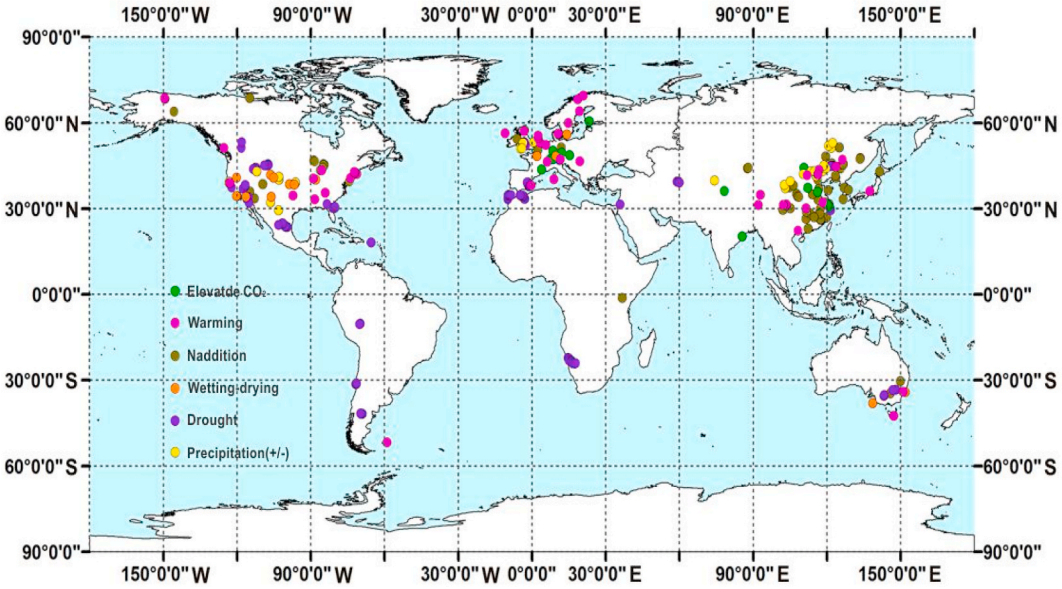

Fig. 2. Global distribution of study sites included in this meta-analysis of global change effects on soil microbial diversity. Global change factors included elevated carbon dioxide (eCO_2), warming, elevated nitrogen addition (eN), wetting–drying, drought, precipitation(−), and precipitation(+).

2011). We assessed heterogeneity by formal Cochran's Q-test tests (Q_E), which test whether the variability in the observed effect sizes is larger than would be expected based on sampling variability alone, and the heterogeneity of each independent meta-regression was assessed with omnibus tests (Q_M). The *p*-values were adjusted for multiple hypothesis testing using Bonferroni corrections. Moreover, the 95% confidence interval (CI) for each effect was generated by bootstrapping tests with 999 iterations, and effects were significant ($p < 0.05$) if the 95% CI did not overlap with 0 (Hedges et al., 1999).

2.3. Statistical analyses

The two- and three-way interaction effects of global change factors on soil microbial diversity were explored using multiple regression analysis, and *p*-values were determined by permutational multivariate analysis of variance (PERMANOVA), with the "Adonis" function in R 3.4.2 software (https://cran.r-project.org/bin/windows/base/old/3.4.2/). Further, the impact of ecosystem type on soil microbial diversity was also tested. Thereafter, we checked the linear regression relationship between microbial diversity and MAT, MAP, and the goodness-of-fit of these models was assessed using R^2 and significance (*p*-value).

The "pca" package in R was used to conduct the principal component analysis (PCA) by Monte Carlo permutation tests (n = 999), for displaying relationships among the driving factors for soil microbial diversity. Then, the relative contributions of the driving factors were determined by random forest analyses using the "rfPermute" package. Finally, the impact of global change factors on soil microbial diversity was analyzed using structural equation modeling (SEM), and mantel R-values were used to build these models in AMOS v 21.0 (http://www.3322.cc/soft/27372.html).

3. Results

3.1. Effects of multiple global change factors on soil microbial diversity

The Cochran's Q-test results indicated that only soil fungal diversity under the wetting–drying cycle had potential publication bias (Table 1); meanwhile, the relative frequency of soil microbial diversity was normally distributed (Fig. S1). Further, the residual error (Q_E) and the total heterogeneity (Q_M) of all observations followed χ^2 distributions (Tables S1-3), indicating that global change factors significantly affected microbial diversity.

Across all sites, the effect of global change on soil microbial diversity was negative, and global change decreased soil bacterial and fungal diversity by an average of 2.9% (95% confidence interval, −0.8 to −5.0%) and 3.5% (95% CI, −1.6 to −5.4) (Fig. 3). For each global change factor, the effect sizes of precipitation(−), eN, wetting–drying cycle, and drought on soil microbial diversity were negative, whereas the effect sizes of eCO_2, warming, and precipitation(+) were positive.

For multiple global change factors, the effect sizes of eCO_2 × warming, warming × precipitation(+), and eN × precipitation(+) on bacterial diversity were significantly negative, whereas the effect size of eCO_2 × precipitation(+) was significantly positive. The effect sizes of eCO_2 × precipitation(+), warming × eN, warming × precipitation(+), and eN × precipitation(+) on fungal diversity were significantly negative, whereas eCO_2 × eN had no significant effect. Notably, the three-way interaction terms of global change factors (Table 2; Fig. 4) had stronger negative effects than the individual or two-way effects.

Table 1
Publication bias tests for soil microbial diversity based on the rank correlation test of the funnel plot asymmetry. Publication bias was detected when $p < 0.05$.

Global change factors	Bacterial diversity		Fungal diversity	
	Kendall's tau	*p*-value	Kendall's tau	*p*-value
Elevated CO_2 (eCO_2)	0.06	0.35	0.15	0.26
Warming	−0.12	0.43	0.32	0.19
N addition (eN)	0.19	0.52	0.16	0.08
Wetting–drying	0.32	0.51	**0.24**	**0.03**
Drought	0.18	0.49	−0.18	0.17
Precipitation(−)	−0.24	0.44	−0.14	0.35
Precipitation(+)	−0.08	0.48	0.31	0.27

Bold type indicates significance at $p < 0.05$.

3.2. Factors driving soil microbial diversity

Soil microbial diversity varied among different ecosystem types. The strongest effects were found in cropland (95% CI, −0.053 to −0.017 to bacterial diversity, and −0.055 to −0.023 to fungal diversity) and grassland (95% CI, −0.043 to −0.021 to bacterial diversity, and −0.047 to −0.025 to fungal diversity); whereas there were no significant effects in the desert ($p > 0.05$) and tundra ($p > 0.05$) (Fig. S2). Moreover, soil microbial diversity declined linearly with MAT ($p < 0.01$, Fig. S3). Edaphic factors (soil pH, BD and SOC) strongly affected soil microbial diversity (Fig. 5A and B, with details in Tables S4-5). Additionally, random forest analyses showed that edaphic factors (especially soil pH, BD and SOC) and MAT had strong impacts on soil microbial diversity (Fig. 5C and D).

The SEM models had a strong comparative fit index (CFI, >0.90), a small Akaike information criterion (AIC), a small chi-square (χ^2) value, and a small root mean square error of approximation (RMSEA, <0.05), and thus met the application conditions of the models. The SEM models showed that edaphic factors ($p < 0.05$) and MAT ($p < 0.05$) had negative effects on bacterial and fungal diversity, while ecosystem type had no effect ($p > 0.05$) on soil microbial diversity (Fig. 6A, C). Thus, we removed ecosystem type in the models. Edaphic factors, MAT and MAP explained 76.4% of the variance in soil bacterial diversity (Fig. 6A, $p = 0.603$, $\chi^2 = 7.169$, CFI = 0.961, AIC = 7.163, RMSEA = 0.002) and 83.3% of the variance in fungal diversity (Fig. 6C, $p = 0.689$, $\chi^2 = 8.155$, CFI = 0.972, AIC = 6.154, RMSEA = 0.001). The standardized effects (both direct and indirect pathway effects) are presented in Fig. 6B, D, indicating that global change indirectly affected microbial diversity through changes in edaphic factors (especially soil pH, BD and SOC) and MAT, supporting the results from PCA and random forest analyses.

4. Discussion

Soil bacterial and fungal diversity play key roles in the structure and function of ecosystems; yet, our understanding of their response to global change is lagging behind that of other organisms (Singh et al., 2010; Delgado-Baquerizo et al., 2017a). Empirical evidence and meta-analyses indicate that soil microbial diversity has variable responses to global change (Zhou et al., 2018, 2020; Delgado-Baquerizo et al., 2016; Yang et al., 2020). However, most past studies focused on the effect of a single global change factor on microbial diversity and few have evaluated the combined effects of multiple global change factors. By using data with a large sample size, our meta-analysis found negative effect of global change on soil microbial diversity, and two- and three-factor global change had stronger negative effects than single-factor. Those effects were predominantly linked to soil pH, BD and SOC, supporting results from other studies at local and global scales (Ren et al., 2018; Delgado-Baquerizo et al., 2018; Yang et al., 2020). Below, we discuss the potential mechanisms of microbial diversity responses to global change.

4.1. Individual effects of global change factors on soil microbial diversity

4.1.1. Effects of alterations in precipitation on soil microbial diversity

Changes in precipitation can alter the abundance and composition of soil microorganisms directly by changing soil water availability or indirectly by altering the composition and productivity of plant communities (Luo et al., 2017; Ren et al., 2018). Recently, Knapp et al.

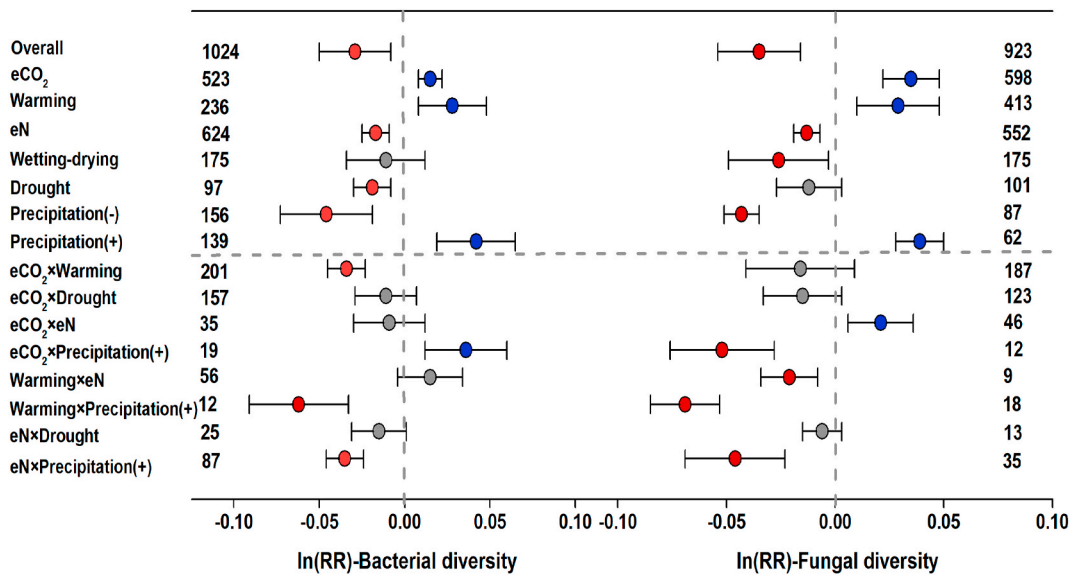

Fig. 3. The response of effect size (ln RR) of soil bacterial (left) and fungal (right) diversity to global change factors (elevated carbon dioxide (eCO_2), warming, elevated nitrogen addition (eN), wetting–drying cycle, drought, precipitation(−), and precipitation(+)), including two-way interactions between global change factors (eCO_2 × warming, eCO_2 × drought, eCO_2 × eN, eCO_2 × precipitation(+), warming × eN, warming × precipitation(+), eN × drought, and eN × precipitation (+)). The numbers on the right (bacteria) and left (fungi) of the graph indicate the sample size of a single term or interaction. The error bars represent 95% confidence intervals (CI) and indicate a significant ($p < 0.05$) effect when not overlapping with 0. Red symbols indicate a significant negative response in microbial diversity, and blue symbols indicate a significant positive response. Gray symbols indicate no significant ($p > 0.05$) difference between the effect size and zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Multiple regression analysis of soil microbial diversity with two-way and three-way interaction terms in relation to global change factors. The *p*-values were determined by permutational multivariate analysis of variance (PERMANOVA). "ns" means no significance ($p > 0.05$).

Global change factors	Bacterial diversity		Fungal diversity	
	r	*p*-value	r	*p*-value
Elevated CO_2 (eCO_2)	0.495	<0.05	0.512	<0.05
Warming	0.509	<0.05	0.621	<0.01
N addition (eN)	0.612	<0.01	0.603	<0.01
Wetting–drying	0.312	ns	0.714	<0.01
Drought	0.512	<0.05	0.356	ns
Precipitation(−)	0.659	<0.01	0.712	<0.01
Precipitation(+)	0.678	<0.01	0.736	<0.01
eCO_2 × warming	0.705	<0.01	0.166	ns
eCO_2 × drought	0.278	ns	0.278	ns
eCO_2 × eN	0.301	ns	0.754	<0.01
eCO_2 × precipitation(+)	0.698	<0.01	0.657	<0.01
Warming × eN	0.378	ns	0.598	<0.01
Warming × precipitation(+)	0.716	<0.01	0.769	<0.01
eN × drought	0.412	ns	0.324	ns
eN × precipitation(+)	0.723	<0.01	0.803	<0.01
eCO_2 × warming × eN	0.759	<0.01	0.812	<0.01
eCO_2 × warming × recipitation(+)	0.716	<0.01	0.756	<0.01
eCO_2 × warming × drought	0.558	<0.05	0.703	<0.01
eCO_2 × eN × drought	0.697	<0.01	0.685	<0.01
eCO_2 × eN × precipitation(+)	0.269	ns	0.325	ns
eCO_2 × drought × precipitation(+)	0.254	ns	0.657	<0.01
Warming × eN × drought	0.801	<0.01	0.187	ns
Warming × eN × precipitation(+)	0.734	<0.01	0.651	<0.01

(2017) introduced the double asymmetric model for revealing the association between aboveground net primary productivity (ANPP) and alterations in precipitation (Luo et al., 2017). However, there is no consensus about the response of soil microbial diversity to alterations in precipitation (Knapp et al., 2017; Luo et al., 2017; Zhou et al., 2018). In the present meta-analysis, precipitation(+) had positive effects, and precipitation(−) had negative effects on soil microbial diversity (Fig. 3), with the negative effects greater than the positive effects, leading to a net negative effect; this indicates that the response of soil microbial diversity to altered precipitation may also follow the double asymmetric model, which should be verified by controlled experiments. This result is consistent with previous findings that microbial diversity was higher in wet than in dry soils (Ren et al., 2018; Du et al., 2020). Reduced precipitation decreases soil water availability and substrate supply to microorganisms and consequently decreases microbial diversity (Manzoni et al., 2012; Rodriguez-Caballero et al., 2018). In contrast, increased precipitation enhances soil water availability, plant productivity and SOC accumulation, promoting microbial growth, and ultimately increasing soil microbial diversity (Maestre et al., 2015; Dacal et al., 2019).

4.1.2. *Effects of wetting–drying cycle on soil microbial diversity*

One aspect of global change is the intensification of hydrological cycling, as represented by changes in the intensity of evaporation and precipitation (Evans and Wallenstein, 2014). Such changes could affect both the intensity and frequency of soil wetting–drying cycles. However, the effect of wetting–drying cycle on fungal and bacterial communities is variable. For example, in contrast to bacteria, fungi could remain active in soils at very low water potential (Ochoa-Hueso et al., 2018). Engelhardt et al. (2018) reported that soil fungi were more sensitive to the wetting–drying cycle than bacteria in a temperate grassland. However, Scheu and Parkinson (1994) found that the susceptibility of bacteria and fungi to wetting–drying cycle was not different. This meta-analysis showed that the drying–rewetting cycle decreased soil microbial diversity (Fig. 3), consistent with Luo et al. (2017) and Ren et al. (2018). To survive in drought conditions, soil microorganisms are more likely to aggregate to avoid dehydration or death (Ren et al., 2018). When the soil water potential goes below a certain threshold, soil microbial population size and diversity would substantially decrease (Liu et al., 2018; Ochoa-Hueso et al., 2018). On rewetting, soil water will flood microbial cells, and could potentially rupture and kill these microorganisms, which can decrease microbial metabolism and diversity (Rodriguez-Caballero et al., 2018; Engelhardt et al., 2018).

In addition, frequent wetting–drying cycle may alter the composition of specific microbial groups, for example, by favoring the copiotrophic

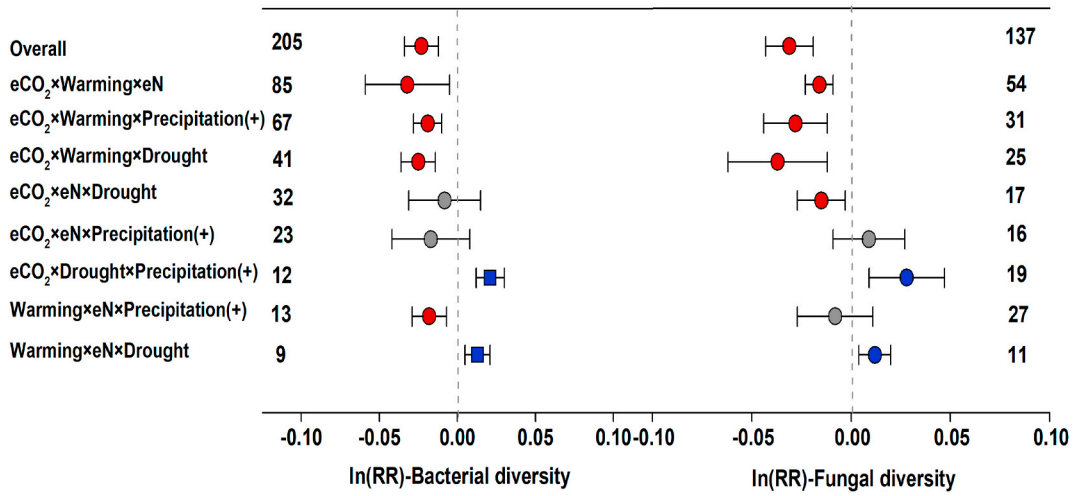

Fig. 4. Comparison of the effect size (ln RR) of soil bacterial (left) and fungal (right) diversity in response to three-way interactions of global change factors, including elevated carbon dioxide (eCO_2) × warming × nitrogen addition (eN), eCO_2 × warming × precipitation(+), eCO_2 × warming × drought, eCO_2 × eN × drought, eCO_2 × eN × precipitation(+), eCO_2 × drought × precipitation(+), warming × eN × precipitation(+), and warming × eN × drought). The numbers on the right (bacteria) and left (fungi) of the graph indicate the sample size of each interaction among global change factors. The error bars represent 95% confidence intervals (CI) and indicate a significant ($p < 0.05$) effect when not overlapping with 0. Red symbols indicate a significant negative response in microbial diversity, and blue symbols indicate a significant positive response. Gray symbols indicate no significant ($p > 0.05$) difference between the effect size and zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

microorganisms with rapidly grow rates (Rodriguez-Caballero et al., 2018), and altering the microbial community composition by promoting groups that are adapted to frequent alterations in the soil water potential. Thus, it is necessary to identify microbial groups that are adapted to wetting–drying cycle in future studies.

4.1.3. *Effects of warming on soil microbial diversity*

The Earth's surface temperature will increase by 1.0–3.7 °C in the 21st century due to the increasing concentration of greenhouse gases (e.g., CO_2, methane and nitrous oxide) in the atmosphere (IPCC et al.,). Several studies suggested that warming accelerated the decline of soil microbial diversity at the regional level (Pritchard, 2011; Brito-Morales et al., 2018). Similar, warming can increase the microbial population but decrease its diversity as compared with the unwarmed control (Guo et al., 2018, 2019). However, our meta-analysis found positive effects of warming on soil microbial diversity on a global level (Fig. 3). The majority of ecological models predict that climate warming increases surface soil temperature, enzyme activities and soil respiration rate, and stimulates SOC decomposition (Zhou et al., 2012; Frey et al., 2013). Warming increases plant productivity and plant-derived C input to the soil, leading to shifts in the structure and diversity of soil microbial communities (Allison et al., 2010; Fang et al., 2018; Brito-Morales et al., 2018). In addition, warming induced increases in organic matter decomposition enhance the availability of nutrients for microbial growth, and ultimately promoting microbial diversity (Chapin et al., 2009; Guo et al., 2018; Guo et al., 2019).

4.1.4. *Effects of elevated carbon dioxide (eCO_2) on soil microbial diversity*

Increased atmosphere CO_2 concentration (to up to 450–600 ppm) is predicted for 2050 (IPCC et al.,). Microbial biomass or diversity has been reported to decrease (Luo et al., 2017), increase (Hu et al., 2001), or remain unchanged (Gorissen et al., 1995) in response to eCO_2. In this meta-analysis, we found that eCO_2 enhanced both soil bacteria and fungal diversity (Fig. 3). The increased CO_2 has been shown to increase the abundance of C-fixing microbial groups (Kuypers et al., 2018) and enhance photosynthetic C production and input to the soil (Gorissen et al., 1995; Hu et al., 2001; Sulman et al., 2014); these changes can result in concomitant increases in soil microbial respiration and SOC turnover (Liang et al., 2017). In addition, eCO_2 is conducive to enhancing the accumulation of SOC and providing resources for microbial growth, which can alter the ecological strategies of microorganisms (Hu et al., 2014). For example, the slow-growing (k-selection species) microbial groups that dominate temperate grasslands under ambient conditions can be replaced by fast-growing microbial groups (r-selection species) under eCO_2, because of the abundant availability of substrates (Sulman et al., 2014; Hu et al., 2001). Despite the positive effects of eCO_2 on soil microbial diversity that have been reported, there is a lack of understanding of the mechanisms involved and further research is needed to improve our understanding of the eCO_2-soil microbial diversity relationship.

4.1.5. *Effects of drought on soil microbial diversity*

For microorganism to survive a drought, they must accumulate high concentrations of solutes (osmolytes) to retain water inside the cell and prevent dehydration (Sherlynette et al., 2019). Under drought stress, more than 10% of the microbial biomass might be tied up in osmolytes to deal with the low soil water potential (Rodriguez-Caballero et al., 2018). Therefore, the response of microorganisms to drought depends on their metabolic flexibility and physiological condition (Fang et al., 2018; Field and Pressel, 2018). In the present meta-analysis, we found that drought decreases soil microbial diversity at the global scale (Fig. 3), supporting previous meta-analyses (Maestre et al., 2015; Zhou et al., 2020). This result is related to 1) drought lowering plant productivity, cover and litter quality, reducing soil nutrient availability and limiting microbial reproduction (Crowther et al., 2015; Field and Pressel, 2018), and 2) the lower water content under a drought decreases the mobility of soil nutrients but increases soil aeration; both of those effects would decrease microbial diversity (Kerfeld et al., 2010; Manzoni et al., 2012; Rodriguez-Caballero et al., 2018; Meyer et al., 2018).

Our meta-analysis also found that drought has a greater negative effect on fungal than bacterial diversity (Fig. 3). This is supported by fungi being able to remain active under lower water potentials than bacteria (Maestre et al., 2015). Generally, fungi are thought to be more tolerant to drought than bacteria because they are able to create large hyphal networks that facilitate water transfer over long distances, allowing them to explore water-filled soil pores not accessible to plant roots (Rodriguez-Caballero et al., 20189), or accessing water from small soil pores (Kerfeld et al., 2010; Manzoni et al., 2012). Although many bacteria species have an osmotic regulation mechanism, they are

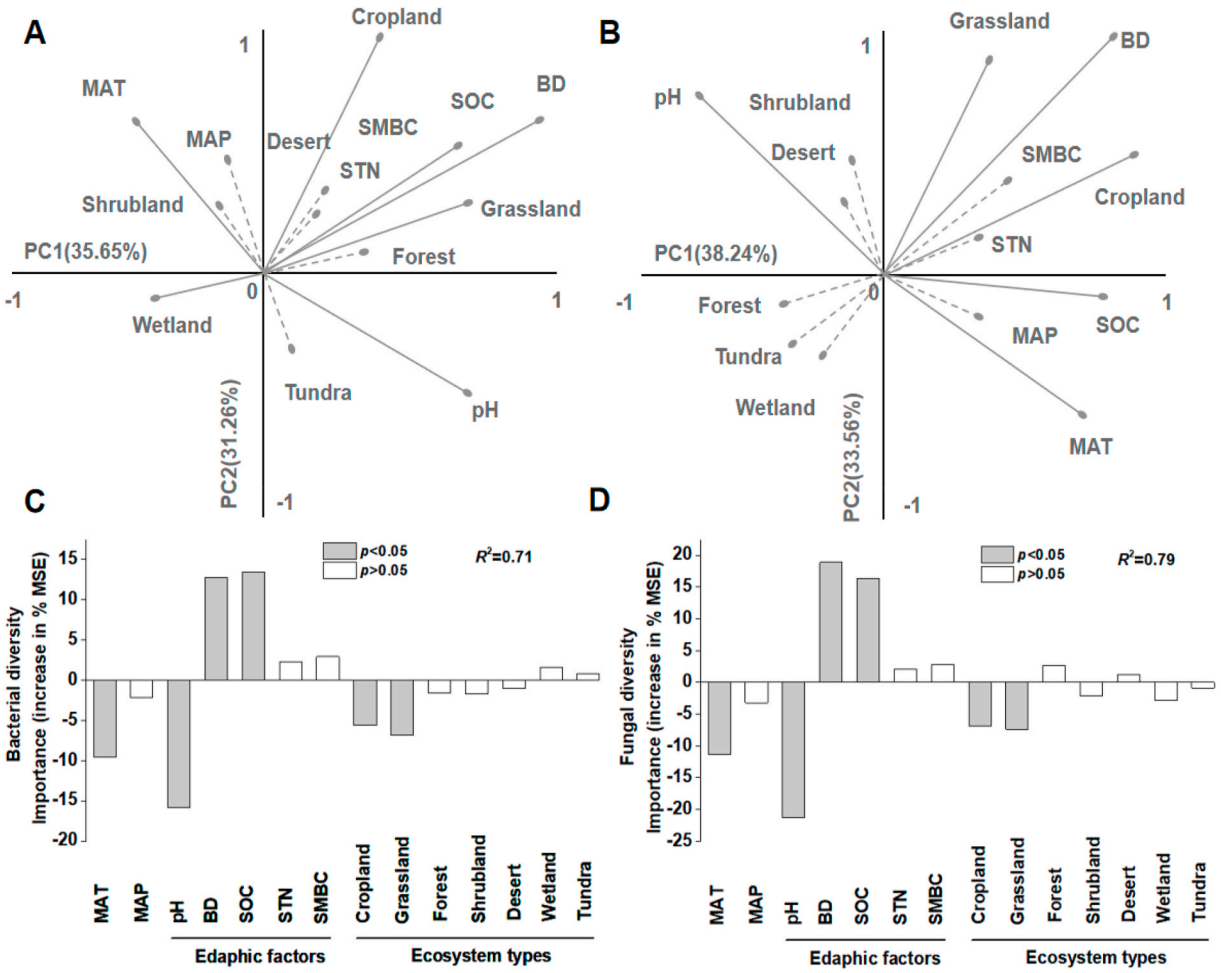

Fig. 5. Principal component analysis (PCA) ordination of the distribution of soil microbial diversity across ecosystem types. (A) Soil bacterial diversity. (B) Soil fungal diversity. The details of Intra-set correlations are presented in Tables S4 and S5. Random forest analysis was used to identify the best individual predictors for soil microbial diversity. (C) Soil bacterial diversity. (D) Soil fungal diversity. The predictors included mean annual temperature (MAT), mean annual precipitation (MAP), and the edaphic factors included soil pH, bulk density (BD), organic carbon (SOC), total nitrogen (STN), and microbial biomass carbon (SMBC), and the ecosystem types included cropland, grassland, forest, shrubland, desert, wetland, and tundra. MSE, mean square error.

typically more susceptible to drought because they require water films within soil aggregates and on soil surfaces for dispersion and substrate diffusion (Kerfeld et al., 2010; Manzoni et al., 2012).

4.1.6. *Effects of N addition on soil microbial diversity*

A large body of evidence has demonstrated that global eN could directly alter soil microbial biomass and composition or indirectly affect them by decreasing soil pH or organic C availability (Chen et al., 2019; Li et al., 2019; Yang et al., 2020). This is due to high levels of eN having direct toxic effects on some saprophytic microorganisms and ultimately decreasing microbial diversity (Ye et al., 2018; Li et al., 2019). As expected, we found consistent negative eN effects on soil microbial diversity across different ecosystem types (Fig. 3), supporting findings in previous studies (Finn et al., 2017; Ye et al., 2018; Chen et al., 2019; Li et al., 2019; Yang et al., 2020). The eN effect is related to N input enhancing soil N availability and soil acidification, and then increasing nitrosative or nitrifying stress and competition for non-N nutrients, thereby inhibiting soil microbial activities (Singh et al., 2004; Zhou et al., 2017; Wagg et al., 2018). On the other hand, soil microbial activities also benefit from eN, as the increase in nutrient availability improves microbial nutrient utilization strategies (Philippot et al., 2013). If the rate of N deposition continues to increase, effective measures need to be developed to mitigate the eN effect on the global decline of microbial diversity.

4.2. *Factors driving soil microbial diversity under global change*

In this meta-analysis, multiple global change factors interactively affected soil microbial diversity (Fig. 3; Table 2). The responses of microbial communities to multiple global change factors are very complex because these global change factors are temporally and spatially complex and often occur simultaneously (IPCC et al.,). Interactions among two or more global change factors may result in additive or antagonistic effects (Engelhardt et al., 2018; Rillig et al., 2019). For example, eCO_2 and warming often synchronously occur and lead to drought at the regional scale (Kuypers et al., 2018). As a consequence, eCO_2 and warming combined can result in additive effects on soil microbial diversity (Hu et al., 2014). Further, eCO_2 and eN can have offsetting impacts on fungal diversity (Gorissen et al., 1995; Hu et al., 2001; Sulman et al., 2014). These results indicate that multiple global change factors could combine to modulate soil microbial diversity. However, soil microbial diversity data are primarily based on short-term experiments, and there have been few long-term studies on the effect of multiple global change factors on soil microbial diversity. Therefore, we caution readers that conclusions from this meta-analysis should be further evaluated through long-term studies. Long-term experiments with multiple global change factors are essential to assess their interactive effects on microbial processes and diversity.

Our SEM models showed that global change factors indirectly

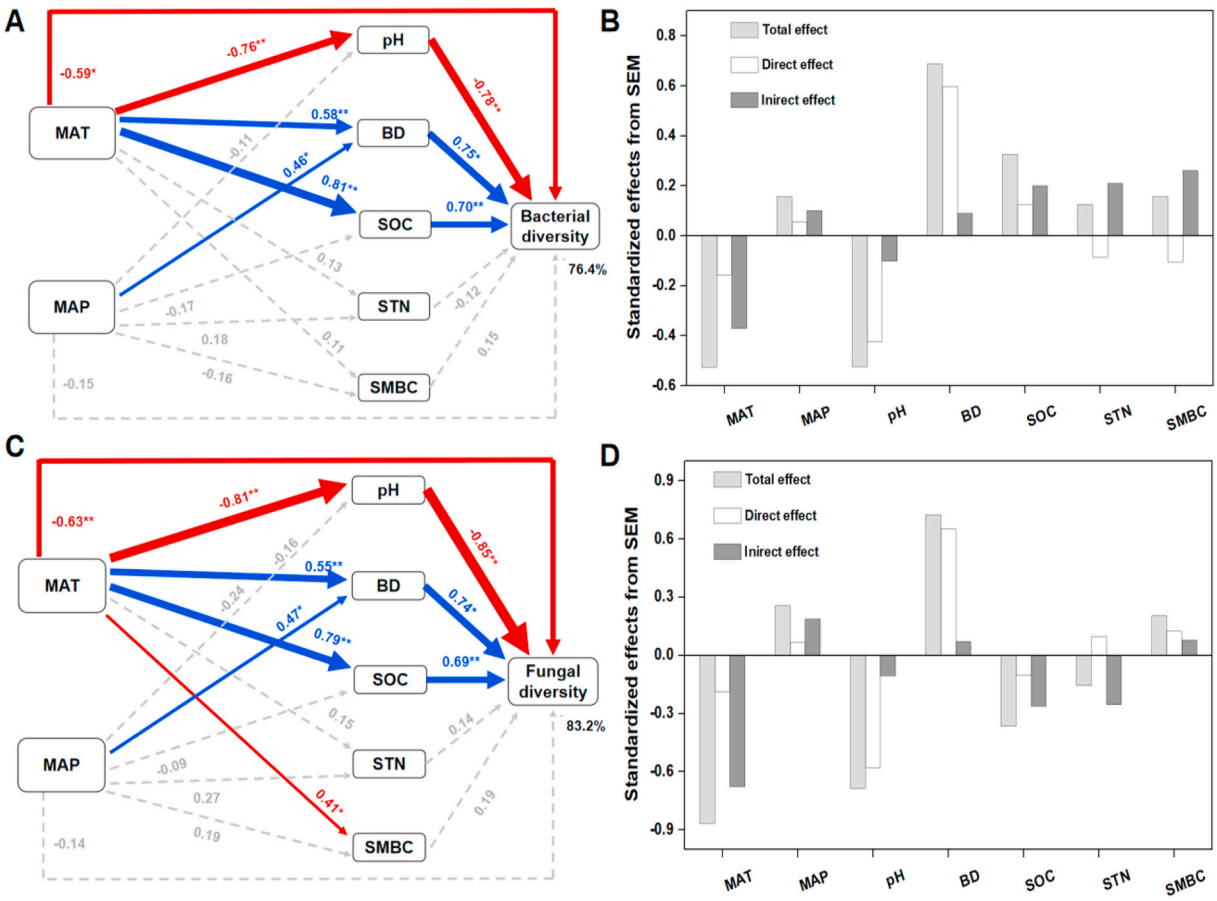

Fig. 6. Structural equation models (SEMs) describing the effects of global change factors on soil microbial diversity. (A) Soil bacterial diversity: $p = 0.603$, df = 20, $\chi^2 = 7.169$, comparative fit index = 0.961, Akaike information criteria = 7.163, root square mean error of approximation = 0.002. (C) Soil fungal diversity: $p = 0.689$, df = 20, $\chi^2 = 8.155$, comparative fit index = 0.972, Akaike information criteria = 6.154, root square mean error of approximation = 0.001. (B) Total and direct and indirect standardized effects from the SEMs on soil bacterial diversity. (D) Total and direct and indirect standardized effects from the SEMs on soil fungal diversity. Red and blue arrows represent significant negative and positive pathways, respectively, while the gray dashed arrows represent no significant pathways. Numbers adjacent to the arrows are standardized path coefficients, analogous to relative regression weights and indicative of the effect size of the relation. The thickness of the arrows is proportional to the magnitude of the standardized path coefficient s. The arrow width is proportional to the strength of the relationship. $^*p < 0.05$, $^{**}p < 0.01$, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

affected soil microbial diversity through changing edaphic factors (especially soil pH, BD, and SOC) and MAT, with soil pH being negatively correlated with bacterial and fungal diversity, in line with previous findings and highlighting soil pH as a major predictor of microbial diversity on a global scale (Delgado-Baquerizo et al., 2016; Zhalnina et al., 2018; Yang et al., 2020; Zhou et al., 2020). Both SOC and soil bulk density (BD) were positively correlated with bacterial and fungal diversity after accounting for the effects of other edaphic factors. These findings indicate that global change factors indirectly impacted microbial diversity by strongly influencing soil pH, soil organic C content, and soil BD.

5. Conclusions

In summary, responses of microbial diversity to multiple global change factors are potentially important but rarely studied. This meta-analysis provides new insights on how soil microbial diversity responds to multiple global change factors. We conclude that eCO_2 and warming had positive effects, while eN, wetting-drying cycle and drought had negative effects on soil microbial diversity. Importantly, the effect of global change on soil microbial diversity was negative; soil microbial diversity linearly declined with mean annual temperature (MAT) and was highly dependent on climatic conditions. In particular, the combined effects of multiple global change factors on soil microbial diversity were greater than that of individual effects. Overall, this study improved our knowledge of factors driving changes in soil microbial diversity under global change; such improved understanding is critical for the implementation of the Global Earth Microbiome Project (https://www.earthmicrobiome.org/).

Authors' contributions

All authors contributed intellectual input and assistance to this study. Y.Y. and S.A. developed the original framework. T.L. and C.H. collected the data. Y.Y. wrote the paper with the help from C.L., S.X.C., and Y.W.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108229.

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