Nitrogen deposition does not change stochastic processes of soil microbial community assembly under climate warming in primary forest

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ABSTRACT

Soil microbial communities are essential for ensuring forest health, however, the influences of global change on soil microbial communities and their ecosystem functions remain unclear. Here, we explored the influences of experimental warming (3 °C above average soil temperature) and nitrogen addition (5 g N m^{-2} year^{-1}) on soil microbial biodiversity, community composition, and community assembly in an old-growth subtropical forest. Our findings showed that when the temperature was increased experimentally, there was a decrease in microbial alpha diversity, along with a decline in soil moisture and an elevation in soil temperature. The experimental treatments had not significantly influence microbial beta diversity and community composition relative to the control. Stochastic processes governed fungal and bacterial community assembly in all treatments. In addition, nitrogen addition and warming increased stochastic processes, and warming plus nitrogen addition decreased stochastic processes in bacterial community assembly. Nitrogen addition increased stochastic processes, while warming and warming plus nitrogen addition decreased stochastic processes in fungal community assembly. Overall, microbial beta diversity, community composition, and community assembly were less altered under warming and nitrogen addition, indicating that microbial communities could be resistant to short term global climate changes in an old-growth subtropical forest.

1. Introduction

Climate warming and the rise of nitrogen levels are two significant components of global change and exert a significant impact on forest ecosystems, influencing their processes and functions (Gao et al., 2022). Climate warming and nitrogen deposition are interdependent from each other (Sun et al., 2021). Climate warming can increase reactive nitrogen emissions to atmosphere, resulting in relatively inefficient nitrogen use and atmosphere pollution (Sun et al., 2021). However, increased reactive nitrogen emissions to atmosphere can directly and indirectly exacerbate climate warming (Ma et al., 2022). Forests are vital ecosystems that offer humans a range of economic and ecological functions, including preserving agricultural lands, and supplying wood for bioenergy (Nepal et al., 2018), decreasing the seriousness of floods and droughts (Rudel et al., 2020), and storing carbon dioxide (Beugnon et al., 2023). The tropical and subtropical forests stand out for its diverse forest types, complex forest structure, and high biodiversity compared to other forest ecosystems. It is estimated that the carbon storage of

subtropical ecosystems accounts for an important part of the carbon storage of the total terrestrial ecosystem (Yu et al., 2014). Notably, subtropical old-growth forests are irreplaceable and have greater carbon sequestration and resilience to disturbance than other forests (Watson et al., 2018). According to the IPCC (2021) report, it is predicted that the land surface in subtropical regions will warm by 3–5℃ over the course of this century (IPCC, 2021). Although subtropical regions may experience less warming compared to higher latitudes, the limited seasonal temperature fluctuation in subtropical climates could still have significant consequences (Nottingham et al., 2022a). In the future, it's expected that subtropical regions will have a notable rise in nitrogen deposition (Galloway et al., 2004). As a result, it's crucial to study how subtropical forests will respond to both warming and nitrogen deposition. However, there have been limited experiments conducted on the influence of climate warming, nitrogen deposition and their interactions in subtropical old-growth forests.

Soil biodiversity, one of Earth's greatest reservoirs of biodiversity, is vital for maintaining various functions of terrestrial ecosystems

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(Delgado-Baquerizo et al., 2020). Soil microbial diversity is under threat due to global changes, which have raised concerns about their potential consequences (Niu et al., 2016; Nottingham et al., 2022b; Philippot et al., 2013; Wu et al., 2022; Yang et al., 2022). For instance, it has been revealed that warming decreases soil microbial diversity, such as in tropical forest (Nottingham et al., 2022b) and temperate forest (Anthony et al., 2021). Furthermore, various terrestrial ecosystems are reported to have experienced a decline in soil microbial diversity due to nitrogen deposition, as revealed by previous studies (Niu et al., 2016; Yang et al., 2022). Increased soil nitrogen could enhance proton release, and mobilize toxic ions, resulting in a decrease in microbial diversity (Zhu et al., 2018). Even though our current knowledge of the effects of nitrogen enrichment and warming on other forest ecosystems, there is still limited understanding of how these factors interactively affect the soil microbial biodiversity in old-growth subtropical forests.

Alterations to soil microbial community composition can have an effect on soil nutrient dynamics (Chen et al., 2021; Trivedi et al., 2013). Microorganisms possess unique capabilities and techniques for making use of soil organic matter, so alterations in soil microbial community composition can impact degradation procedures and emission of carbon dioxide (Pec et al., 2021). Global warming dramatically changes soil temperature and moisture, resulting in varies in the composition of plant communities and the amount of ecosystem biomass (Yu et al., 2021). This alteration could affect the quality and amount of soil organic matter, thereby influencing the microbial community composition (DeAngelis et al., 2015). Nitrogen addition may alter microbial community composition in soil directly or indirectly, through decreasing soil pH and organic carbon availability (Chen et al., 2019; Yang et al., 2021). The comprehension of how microbial community composition responds to global change factors is of great important for predicting alterations in ecosystem functions under future global change scenarios; however, there has been limited research on how warming and nitrogen addition, two global change factors, may impact the composition of soil microbial community in field conditions when they interact with each other.

The purpose of research on community assembly is to illuminate how evolutionary and ecological mechanisms control the community composition (Barnett et al., 2019). Community assembly consists of two processes such as stochastic and deterministic processes (Barnett et al., 2019). Deterministic processes, like biotic interactions and environmental filtering govern the composition of communities, whereas stochastic processes, like ecological drift or dispersal limitation, are responsible for explaining a diverse array of patterns of biodiversity in the environment (Zhou and Ning, 2017). Microbial communities are determined by both deterministic and stochastic processes that are necessary to link their composition to the ecosystem functions that they contribute (Liu et al., 2020).

Soil microbial community assembly may be affected by warming, leading to more homogeneous selection (Ning et al., 2020). Nitrogen addition enhanced soil nutrients, expanded niche width of microbial community habitats, and cause a larger relative significance of stochastic event on community composition (He et al., 2021). Elucidating microbial community assembly under global change can assist in prediction of how microbial community respond to climate shifts. Understanding the extent to which stochastic and deterministic processes govern microbial communities is vital for projecting the capacity of microbial communities to acclimate future climate change (Zheng et al., 2022). Even so, there have been few studies that specifically evaluate the impacts of these two global change drivers on microbial community assembly in soil, especially in old-growth forests, where a large proportion of the terrestrial biodiversity is sheltered.

A field experiment of simulating warming ($+3$ °C) and nitrogen addition (5 g N m^{-2} $year^{-1}$) in a primary subtropical forest to explore the underlying mechanisms and examine their influence on microbial diversity, community composition, and community assembly in soil. Subtropical forests are nitrogen-rich but phosphorus-deficient (Lu et al., 2018). Warming increases soil temperature and decreases soil moisture.

Thus, we proposed that warming and nitrogen addition would decline microbial diversity (Hypothesis 1) and alter microbial community composition (Hypothesis 2). Zhou et al. (2014) hypothesized that nutrient input would lead to an increase in stochasticity within ecosystems. This is because the addition of nutrients enhances stochastic processes, weakens niche selection, and promotes priority effects. In addition, in an ecosystem with a non-nutrient disturbance, stochasticity will reduce once a non-nutrient disturbance is applicable because the disturbance would decrease stochastic processes, increase niche selection, and decrease priority effects (Zhou et al., 2014). Therefore, our prediction is that as a result of warming, there will be a decline in the significance of stochastic processes in microbial community assembly. Conversely, we expect an enhancement in the significance of microbial stochastic processes due to nitrogen addition (Hypothesis 3).

2. Materials and methods

2.1. Site description

The experiment was completed at the Chinese Ecological Research Network's Ailaoshan Station for Subtropical Forest Ecosystem Studies, Yunnan Province, Southwest China (101°01′E, 24°32′N; 2480 m above sea level). The study area is characterized by a well-protected primary subtropical evergreen broadleaved forest, with trees older than 300 years (Tan et al., 2011). The forest type in our study area is widely spread and is dominated by: *Manglietia insignsis, Sinarundinaria nitida, Hartia sinensis, Schima noronhae, Vaccinium duclouxii, Castanopsis wattii, Lithocarpus chintungensis, Lithocarpus xylocarpus*, and *Rhododendron leptothrium*. The region has a subtropical monsoon climate, where mean annual temperature and rainfall are 11.11 ± 0.07 °C and 1883.98 ± 30.61 mm from 1982 to 2021, respectively, and the soils are loamy Alfisols.

2.2. Experimental design

In the experiment, the main treatments were warming and nitrogen addition, which were designed as a 2 × 2 factorial design. Twelve 2 m × 2 m plots were set up and at random divided into four combinations of the two factors, each with three replications: control, nitrogen addition, warming, and warming plus nitrogen addition. In the warming and the warming plus nitrogen addition treatments, carbonizing infrared radiator was used as a heat source, and three 400-watt carbon infrared radiant heating lamps were arranged in a triangular pattern about 1.0 m above the floor in each plot. Nitrogen was supplied with NH_4NO_3 at a dose of 5 g N m^{-2} $year^{-1}$ in both the nitrogen addition and warming plus nitrogen addition treatments according to the similar experiment (Lu et al., 2018). The total quantity of nitrogen is divided evenly into twelve applications, with each application occurring in the middle of each month of each year. For each application, each plot was sprayed with a solution of NH_4NO_3. At the same time, we provided the same amount of distilled water (300 mL) to the warming and control plots. Through these treatments, the plots received a total quantity of water that was equivalent to <1 mm of additional annual precipitation. Soil nitrogen addition and warming started on January 1, 2018.

2.3. Field sampling and measurements

Soil respiration were monthly measured from January 2018 to December 2020. A polyvinyl chloride (PVC) collar (20 cm in diameter) was put into the soil with a depth of 2 cm in the central region of each plot; the Li-820 (Li-820; Li-Cor, Lincoln, NE, USA) was applied to determine soil respiration in the collar. Soil temperature (at 5 cm depth) was determined with a digital thermometer (6310; Spectrum, Illinois, USA), and soil moisture (Vol%, at 10 cm depth) was determined with time domain reflectometry (MP-KIT; Beijing Channel, China) concomitantly with respiration measurements. All soil moisture, respiration, and

temperature measurements were conducted at morning during 09:00–12:00.

Considering the effect of seasonality on the experimental results, sampling was conducted four times, i.e. April 2019 (spring), July 2019 (summer), October 2019 (autumn), and January 2020 (winter). To avoid the influence of spatial heterogeneity, we combined three soil cores from each plot into a composite sample using a soil borer with10 cm in depth and 5 cm in diameter. After cooling with ice blocks, soils were transferred to the laboratory and were screened (2-mm pore size) to exclude rocks and roots for further analysis. The fresh soil samples were immediately applied for analyzing soil water content, soil extracellular enzyme, dissolved inorganic carbon, dissolved organic carbon, and DNA extraction. Soil pH, total carbon, available phosphorus, NH_4^+-N, and NO_3^--N were analyzed from air-dried soil samples at room temperature. See supplementary information for more detailed information on soil variables analysis, DNA extraction, amplification, and sequencing.

2.4. Bioinformatics analysis

To obtain clean and high-quality reads, the raw reads were subjected to quality filtering by applying the quality control process in the Cutadapt (Martin, 2011). The UCHIME (Edgar et al., 2011) was used to identify and exclude chimera sequences from the reads. Sequences with a similarity of at least 97 % were clustered to the same operational taxonomic units (OTUs) by applying the UPARSE software (Edgar, 2013). The representative sequences of the bacterial OTUs were annotated to taxa via the Silva 132 (Quast et al., 2012). The representative sequences of the fungal OTUs were annotated to taxa via the UNITE 7.2 (Nilsson et al., 2018). We aligned the representative sequences via MUSCLE (Edgar, 2004), and generated approximately maximum-likelihood trees with FastTree software (Price et al., 2010) using a midpoint root. DNA sequences contained in this research were deposited in the NCBI with the Sequence Read Archive (SRA) database with the BioProject accession number PRJNA979823.

2.5. Statistical analyses

Null model analysis was applied to evaluate the assembly of microbial community (Stegen et al., 2013). Null model-based taxonomic β-diversity (Bray-Curtis-based Raup-Crick, RCbray) and phylogenetic (β nearest taxon index, βNTI) metrics were utilized to quantify the alterations in taxonomic and phylogenetic diversity. The results of the RCbray and βNTI analysis were combined to assess the proportion of community assembly influenced by stochastic and deterministic processes in each treatment. Further details on the division of microbial community assembly processes can be found in the supplementary information.

For each sample, we determined the phylogenetic diversity that best represented microbial alpha diversity. The beta diversity between samples was computed using Bray-Curtis distance (taxonomic beta diversity) and weighted UniFrac distance (phylogenetic beta diversity). The beta mean nearest taxon distance (βMNTD), a null model-based beta diversity, was also computed to measure the pairwise phylogenetic distance between communities. Linear mixed-effects models were performed to determine the influences of experimental treatments on microbial alpha diversity. In the model, warming, nitrogen, and their interactions were treated as fixed effects, whereas seasons and plots were considered as random intercept effects. The effect size (β) in these models is represented by the regression coefficient, which indicates the magnitude and direction of the effect (Wu et al., 2022). To associate the soil factors to microbial biodiversity, we examined the correlations between each soil factor and microbial biodiversity using linear mixed-effects models with seasons and plots as random effects, as described by Wu et al. (2022). Permutational multivariate analysis of variance was utilized to analyze the main and interactive effects of nitrogen addition

and warming on microbial beta diversity. If soil variables exert an influence on beta diversity and assembly processes, we would expect a correlation between microbial beta diversity and βNTI with dissimilarity in soil variables. Partial mantel tests were conducted to determine whether microbial beta diversity and βNTI had associations with differences (represented Euclidian distance) in soil variables. Additionally, the variations in microbial alpha diversity, beta diversity, and βNTI among treatments and seasons were explored employing one-way analysis of variance (ANOVA). The significant difference were explored by Tukey's Honestly Significant Difference (HSD) test. Before running the ANOVA, the assumptions of homogeneity and normality were evaluated by applying the Levene tests and Shapiro-Wilk, respectively.

To more clearly distinguish the indirect and direct impacts of soil factors drivers on microbial biodiversity under warming and nitrogen addition, we implemented piecewise structural equation models (Lefcheck, 2016) to identify the associations among experimental treatments, soil factors, and microbial biodiversity. Initial consideration was given to an assumed conceptual model (Fig. S1) that incorporated all plausible pathways. We then gradually removed pathways that were not significant except for they had biological meaning. The procedure was replicated until the model was perfectly fitted when Fisher's C is not statistically significant ($P > 0.05$) (Lefcheck, 2016). All statistical analysis was conducted using R (v4.2.1; https://www.r-project.org/). Details of the R packages used can be seen in our Supplementary information.

3. Results
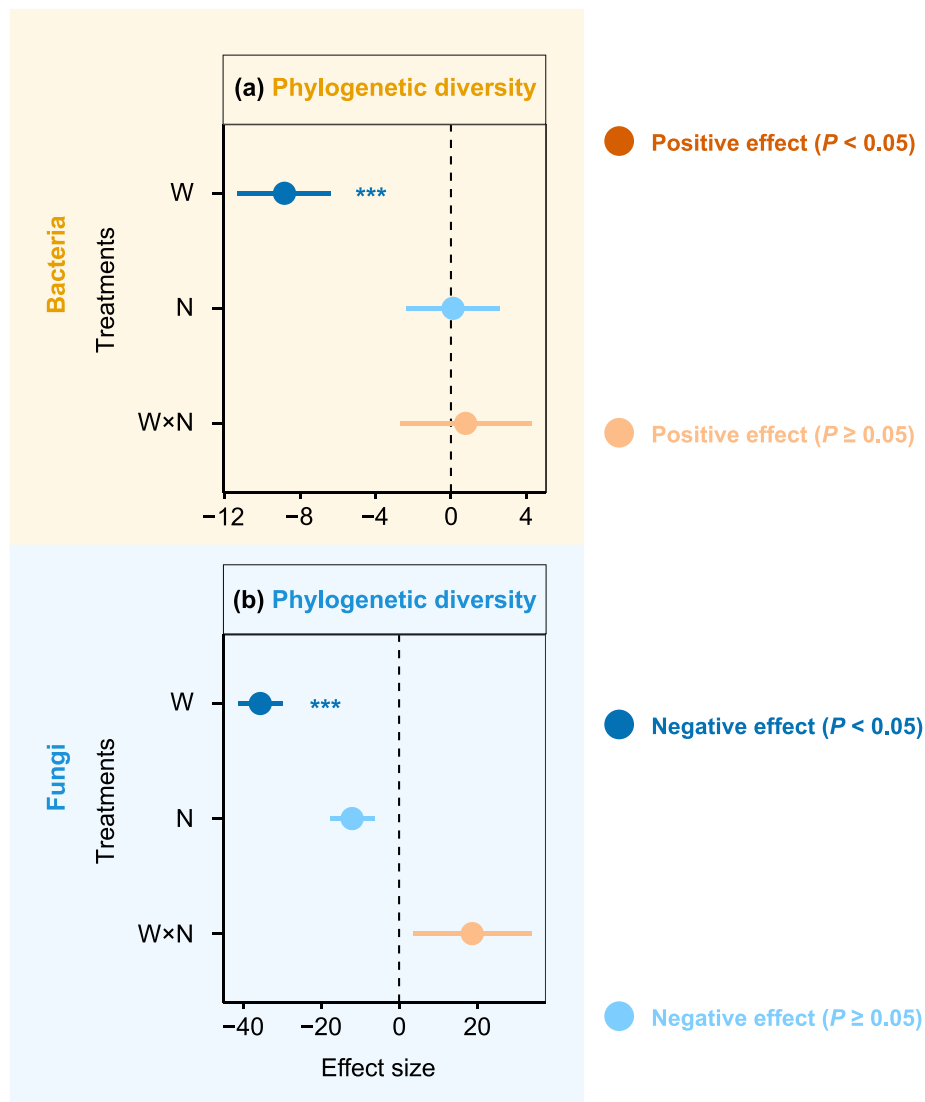
3.1. Responses of soil microbial alpha diversity

Overall, warming had strong adverse influences on bacterial and fungal phylogenetic diversity (β = −8.841, $P < 0.001$; β = −35.589, $P < 0.001$; respectively) (Fig. 1). Additionally, one-way ANOVA results revealed that both warming and warming plus nitrogen addition significantly decreased fungal and bacterial phylogenetic diversity ($P < 0.05$) compared with the control (Fig. S2). Altogether, all these findings imply that experimental warming resulted in a significant decrease in microbial alpha diversity. Moreover, the microbial alpha diversity varies with the seasons (Fig. S3).

3.2. Responses of soil microbial community composition and beta diversity

The relative abundance of bacteria and fungi at the phyla level (Top 10) and order level (Top 10) for different treatments were shown in Fig. 2. The main bacterial phyla were Proteobacteria, Acidobacterial, and Firmicute (Fig. 2a); and the main fungal phyla were Basidiomycota, Mortierellomycota, and Ascomycota (Fig. 2b). The main bacterial order were Rhizobiales, Acidobacteriales, and Lactobacillales (Fig. 2c); and the main fungal order were Mortierellales, Russulales, and Agaricales (Fig. 2d). One-way ANOVA results indicated no significant differences among treatments for each phylum and each order (Fig. 2). Nitrogen addition, warming, and warming plus nitrogen addition did not produce any significant alterations in microbial beta diversity, as shown in Table 1 and Fig. 3. But there were seasonal fluctuations in microbial beta diversity (Figs. S4 and S5).

3.3. Microbial community assembly processes

By coupling βNTI and RCbray metrics, it was indicated that stochastic processes primarily controlled bacterial and fungal community dynamics in all treatments (Fig. 4). Compared with the control, in bacterial community assembly, stochastic processes were increased by nitrogen addition (16.667 %) and warming (25.000 %), whereas warming plus nitrogen addition treatment (8.333 %) marginally

Fig. 1. Effects of experimental treatments on soil microbial alpha diversity. The effect sizes of warming and nitrogen addition on bacterial (a) and fungal (b) phylogenetic diversity. Linear mixed-effects models were applied to calculate the estimated effect size. The estimated effect sizes are represented as mean values ± standard errors. Wald type II χ^2 tests are applied to determine statistical significance. Asterisks are used to show significant effects: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. W stands for warming, N is the nitrogen addition, and W × N is the interaction effects of warming and nitrogen addition.

reduced it (Fig. 4b). Yet, in fungal community assembly, stochastic processes were decreased by nitrogen addition (16.667 %), while it was slightly increased by warming (8.333 %) and warming plus nitrogen addition (8.333 %) (Fig. 4d). Seasonality was decisive in balancing microbial stochastic and deterministic processes (Fig. S6).

3.4. Soil variables impact microbial diversity and community assembly

According to the results of structural equation models, soil temperature, which was positively impacted by warming, and soil moisture, which was negatively impacted by warming, exerted the strongest impact on microbial alpha diversity (Fig. 5a). Soil temperature had a highly negative correlation with bacterial and fungal phylogenetic diversity (LMM's r = −0.761, P = 0.003; LMM's r = −0.764, P = 0.004; respectively) (Fig. 5b). Soil moisture had a strong positive correlation with bacterial and fungal phylogenetic diversity (LMM's r = 0.664, P = 0.005; LMM's r = 0.711, P = 0.002; respectively) (Fig. 5b). In addition, we found no soil variables that significantly affected microbial beta diversity (Fig. 5). Overall, microbial phylogenetic diversity was also significantly correlated with some soil extracellular enzyme activities

(Fig. S7).

We performed a partial mantel test on the associations among different beta diversity, βNTI and soil factors (Fig. 6). Soil dissolved inorganic carbon, NH_4^+-N, and pH showed significant correlations with bacterial Bray-Curtis dissimilarity ($P < 0.05$) (Fig. 6a). Soil temperature and moisture were significantly correlated with bacterial βNTI (Fig. 6a). Bacterial weighted UniFrac dissimilarity and βMNTD were not, however, significantly correlated with all soil variables (Fig. 6a). Soil temperature and dissolved inorganic carbon showed significant correlations with fungal Bray-Curtis dissimilarity ($P < 0.05$), whereas soil temperature and soil respiration exhibited significant correlations with fungal weighted UniFrac dissimilarity ($P < 0.05$) (Fig. 6b). Soil available phosphorus was found to have a strong correlation with fungal βNTI ($P < 0.05$) (Fig. 6b). However, fungal βMNTD exhibited no significant correlation with any of the soil variables (Fig. 6b). Various microbial beta diversity, βNTI and several soil extracellular enzyme activities also showed significant correlations (Figs. S8–S11).
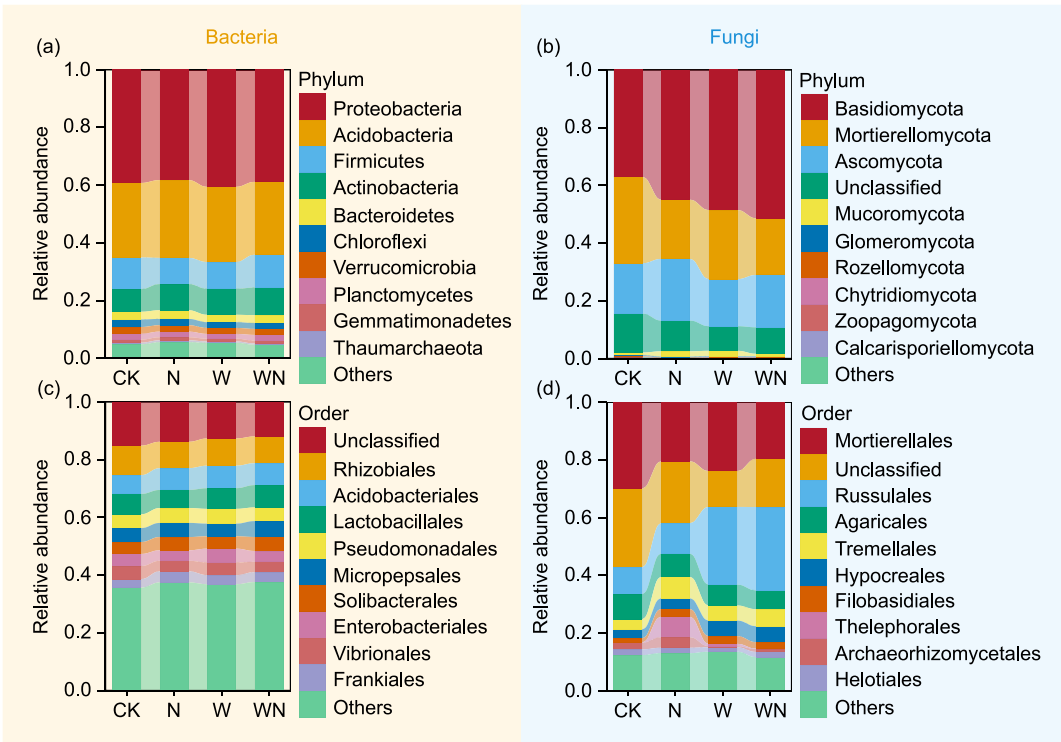
Fig. 2. The relative abundances of dominant soil microbial communities among different treatments. The relative abundances of top10 bacterial (a) and fungal (b) communities at phyla level. The relative abundances of top10 bacterial (c) and fungal (d) communities at order level. The treatments include the control (CK), nitrogen addition (N), warming (W), and warming plus nitrogen addition (WN).

Table 1
Results of permutational multivariate analysis of variance of the effects of warming (W), nitrogen addition (N), and their interaction on microbial beta diversity. The × sign indicates interaction effect.

Effect	Bacteria						Fungi					
	BC		WU		βMNTD		BC		WU		βMNTD	
	F	P	F	P	F	P	F	P	F	P	F	P
W	0.465	0.566	0.919	0.383	0.766	0.492	5.070	0.056	1.755	0.189	0.114	0.897
N	2.269	0.117	1.163	0.304	0.339	0.774	0.573	0.452	0.543	0.461	2.329	0.122
W × N	0.772	0.417	0.583	0.549	1.219	0.293	0.140	0.740	0.028	0.949	0.974	0.354

BC stands for Bray-Curtis dissimilarity, βMNTD is the beta mean nearest taxon distance, and WU is the Weighted UniFrac dissimilarity.

4. Discussion

In the field of climate change and microbiology research, a crucial question is how microbes are impacted by climate change and the mechanisms involved (Tiedje et al., 2022). By investigating the change in soil microbial community in a global change experiment in an old-growth subtropical forest, this study revealed how warming, nitrogen, and their interactions affect microbial diversity, community composition, and community assembly.

4.1. Differential responses of microbial alpha diversity to warming and nitrogen addition

We found that soil microbial alpha diversity is impacted more by warming than by nitrogen addition (Fig. 1; Fig. S2). This response to a decrease in microbial alpha diversity due to warming is consistent with study in tropical forest (Nottingham et al., 2022b), but opposite to observations in temperate forest (DeAngelis et al., 2015). The possible explanations were, first, owing to the high average annual soil temperatures in tropical and subtropical regions, these temperatures could serve as a thermal maximum for the survival of numerous species (Nottingham et al., 2022b). Second, warming is accompanied by a decrease in soil moisture, which leads to decreased microbial and soluble substrate mobility and cellular water potential, therefore negatively impacting microbial alpha diversity (Gupta et al., 2022).

We found a negligible influence of nitrogen addition on microbial alpha diversity (Fig. 1; Fig. S2). Theoretically, inorganic nitrogen typically exerts both direct and indirect influences on microbial alpha diversity (Yang et al., 2022). Several recent *meta*-analyses and field experiments have demonstrated that nitrogen addition has been associated with decreases in soil microbial alpha diversity in various ecosystems (Philippot et al., 2013; Yang et al., 2022). There could be several possible explanations for the unexpected findings of this study. First, high soil nitrogen levels in nitrogen-rich subtropical forest do not limit the reproduction and metabolism of soil microbes. In this study, inorganic nitrogen was supplemented to the soil to simulate the present state of atmospheric nitrogen deposition. However, the quantity of nitrogen could not have been sufficient to significantly alter the utilization of nitrogen by soil microbes. Similar findings have been found in a secondary forest (Feng et al., 2023). Second, initial soil condition is an important factor influencing alterations to microbial alpha diversity with nitrogen addition. For instance, if the carbon-to-nitrogen ratio in the soil is greater than 10, nitrogen addition may mitigate the effects on microbes (Yang et al., 2022). Old-growth subtropical forests have been
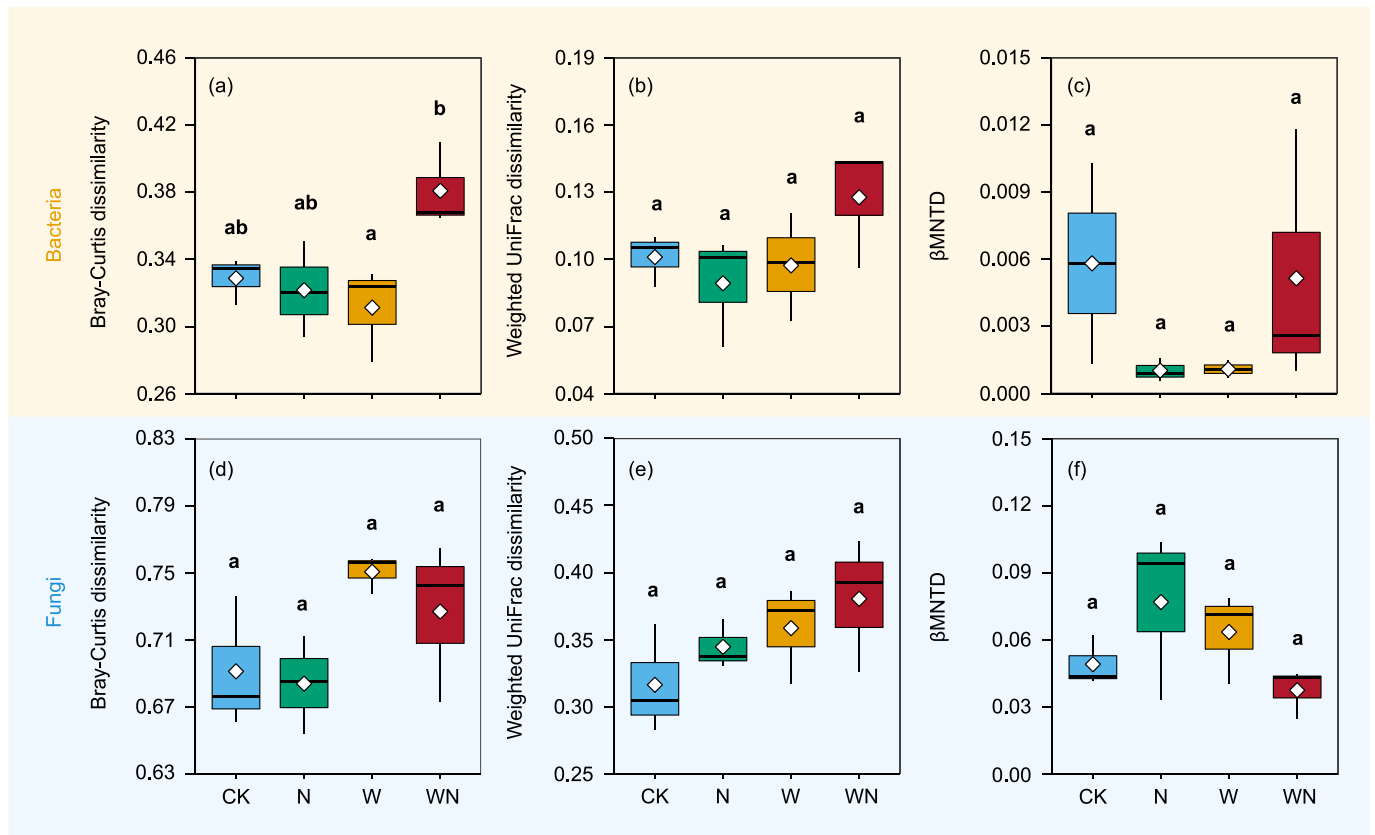
Fig. 3. Effects of nitrogen addition (N), warming (W), and warming plus nitrogen addition (WN) on bacterial Bray-Curtis dissimilarity (a), bacterial Weighted UniFrac dissimilarity (b), bacterial βMNTD (c), fungal Bray-Curtis dissimilarity (d), fungal Weighted UniFrac dissimilarity (e), and fungal βMNTD (f). Distinct lowercase letters mean significant differences at $P < 0.05$ level among treatments. CK denotes the control, while βMNTD is the beta mean nearest taxon distance.

observed to possess significant carbon stocks (Xiong et al., 2020; Zhou et al., 2006), resulting in a higher enzyme activities and content of labile carbon in soil compared to other ecosystems. Furthermore, we did not find obvious differences in microbial alpha diversity as a result of the interaction between warming and nitrogen addition (Fig. 1), which indicates that soil microbial alpha diversity was more vulnerable to warming than nitrogen addition in the old-growth subtropical forest.

4.2. Warming and nitrogen addition do not alter soil microbial community composition and beta diversity

Unexpectedly, our study found that warming did not alter microbial community composition and beta diversity in soil (Fig. 2; Fig. 3). Possible mechanisms that could explain this finding include the following. First, in our study, the duration of the warming period was relatively short (<3 years). Short-term (<5 years) warming had no significant effect on microbial community composition and beta diversity in soil, whereas long-term (>7 years) warming significantly altered microbial community composition and beta diversity in soils of temperate forest and subtropical planted forest (DeAngelis et al., 2015; Wang et al., 2019; Zhao et al., 2023). Second, generally, warming is believed to have the potential to enhance soil nitrogen transformation rates, thus resulting in elevated soil nutrients availability (Niu et al., 2023). Nevertheless, in our study, no significant difference in soil inorganic nitrogen and soil pH was observed between the warming and control. It seems that the modest changes in soil nitrogen pools by warming may be the consequence of lower nitrogen turnover rates linked to soil moisture reduction and old-growth subtropical forests are nitrogen-rich forests (Niu et al., 2023; Wang et al., 2018). Such soil conditions did not change under warming, which may also partly indicate that warming did not significantly influence microbial community composition and beta diversity.

The negligible response of microbial community composition and beta diversity in soil to nitrogen addition found in our study is inconsistent with the results of previous research, which had revealed that nitrogen addition alters microbial community composition and beta diversity in soils of tropical and temperate forests (Ma et al., 2018; Wang et al., 2018). This can be explained in several ways. On the one hand, in our study, the quantity of nitrogen addition did not attain the critical threshold for changes in microbial community. Previous investigations have revealed that low nitrogen deposition has small influences on microbial community composition and beta diversity in soil, while high nitrogen deposition significantly alter microbial community composition and beta diversity (Mu et al., 2021). On the other hand, nitrogen deposition has not lead to a significant reduction in soil pH. Several previous investigations have indicated that soil pH reduction due to nitrogen addition is the good predictor of both microbial community composition and beta diversity in forests (Wang et al., 2018; Xing et al., 2022). Furthermore, nitrogen addition usually has not significant effects on plant productivity (Feng et al., 2023), which might have neutral effects on microbial community composition and beta diversity in forest ecosystems.

4.3. Stochastic processes were dominant under warming and nitrogen addition

Since stochastic and deterministic are two major topics in the research of microbial community dynamics (Stegen et al., 2013). Here, we discovered that stochastic processes possess a larger role than deterministic processes in all treatments (Fig. 4). This finding is similar to previous research in tropical forests (Chen et al., 2023; He et al., 2021). It exhibited that variable selection and dispersal limitation were
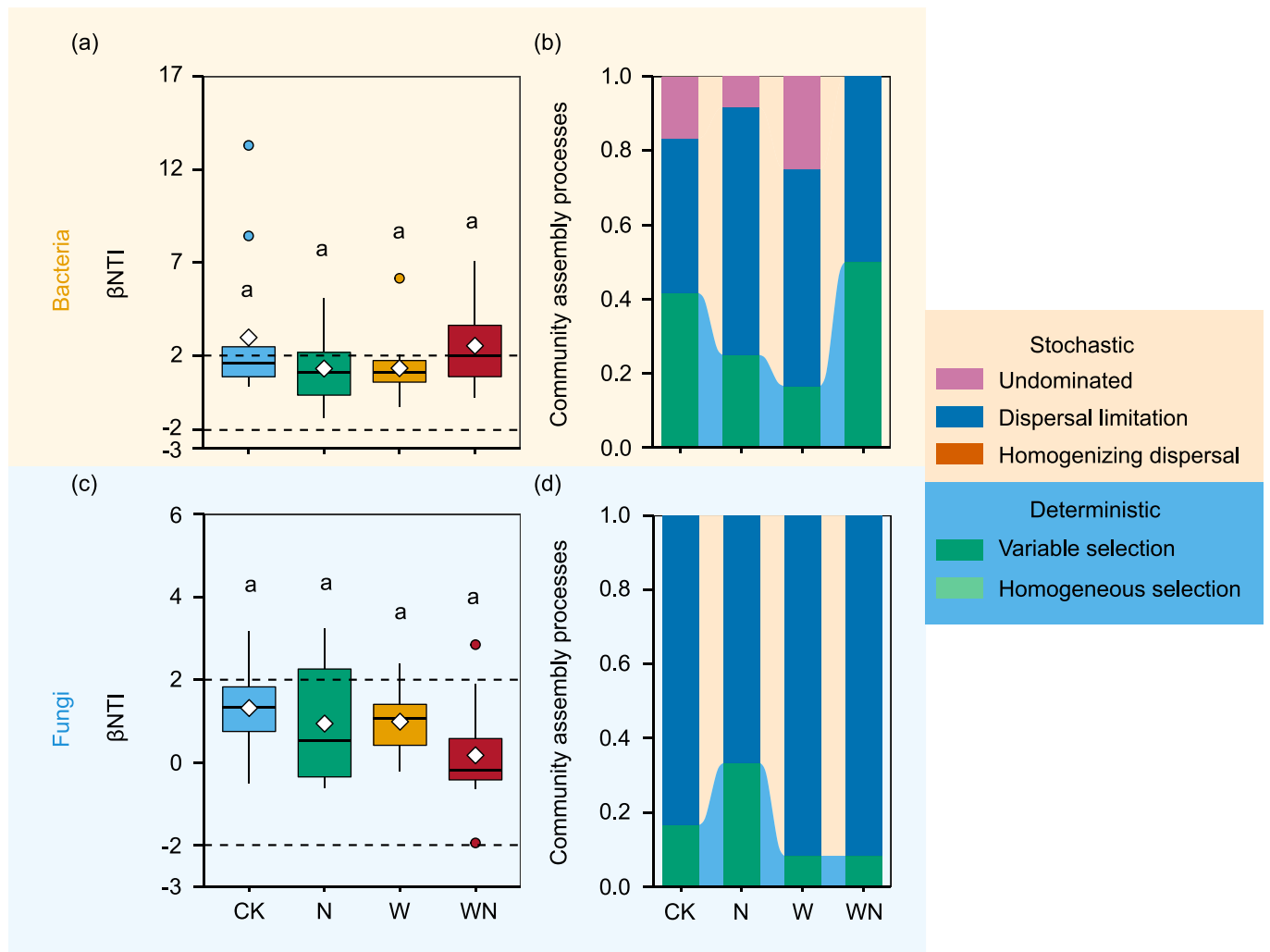
Fig. 4. Distribution of βNTI of bacterial (a) and fungal (c) among treatments. The percentages of turnover in bacterial (b) and fungal (d) community assembly dominated mainly by different stochastic processes (dispersal limitation and homogenizing dispersal) and deterministic processes (variable and homogeneous selection), and the percentages that was not governed by any single process (Undominated) among treatments. The significance thresholds at βNTI = −2 and +2 are denoted by the horizontal dashed black lines. The treatments include the control (CK), warming (W), nitrogen addition (N), and warming plus nitrogen addition (WN).

the most significant ecological processes in the community assembly of bacteria and fungi (Fig. 4). Due to their stronger dispersal ability compared to larger organisms, soil microbes with smaller body sizes such as bacteria are anticipated to be less impacted by dispersal limitations (Xu et al., 2020). One possible explanation is that higher precipitation and temperature in this study site can serve as environmental constraints that promote larger dispersal limitation, possibly due to greater environmental heterogeneity brought about by wetter substrates; therefore, bacterial community is more likely to lead to greater dispersal limitations (Zhang et al., 2023). Unlike bacteria, fungi have large body size and low dispersal capacity, dispersal limitations control fungal community assembly even over short distances (He et al., 2021). Old-growth subtropical forests have high plant diversity and the habitat generally exhibits strong space diversity (Dini-Andreote et al., 2015). Variable selection was one of the important ecological processes in the assembly of bacterial and fungal community (Fig. 4). Studies have discovered that soil microbes are linked to plant composition (Chen et al., 2023; Liu et al., 2023). For example, *Patescibacteria* are symbiotic or parasitic with hosts because of the absence of several metabolic enzymes (Liu et al., 2023).

Our findings also did not confirm the hypothesis proposed by Zhou et al., (2014) that non-nutrient disturbances decrease stochastic

processes. It was found that experimental warming increased soil temperature, thereby gradually decreasing stochasticity through selective pressure, and soil temperature, drought, and plant biomass were correlated with increased homogeneous selection (Ning et al., 2020). Old-growth subtropical forests possess unique characteristics that set them apart from other ecosystems, such as remarkably high biodiversity in both above- and below-ground, as well as a substantial soil carbon stock (Xiong et al., 2020; Zhou et al., 2006). These traits could weaken the effects of selective pressure from temperature and drying under warming. It is therefore not surprising that stochastic processes govern the community assembly in the old-growth forests. Warming slightly increased stochastic processes in the community assembly of bacteria and fungi (Fig. 4b). It may be that warming promotes the activity of metabolic enzymes, making more resources available to soil microbes. As our findings indicated, both bacterial and fungal βNTI were significantly associated with most metabolic enzymes (Fig. S8). Studies have reported that stochastic processes would be linked to soil nutrient status and larger availability of resource (Zhou et al., 2014).

Nitrogen addition increased the stochastic process of bacterial community assembly (Fig. 4b), which supported the hypothesis 3 that stochasticity will increase in ecosystems following nutrient input (Zhou et al., 2014). Finding no significant correlation between bacterial βNTI

(a)

(b)
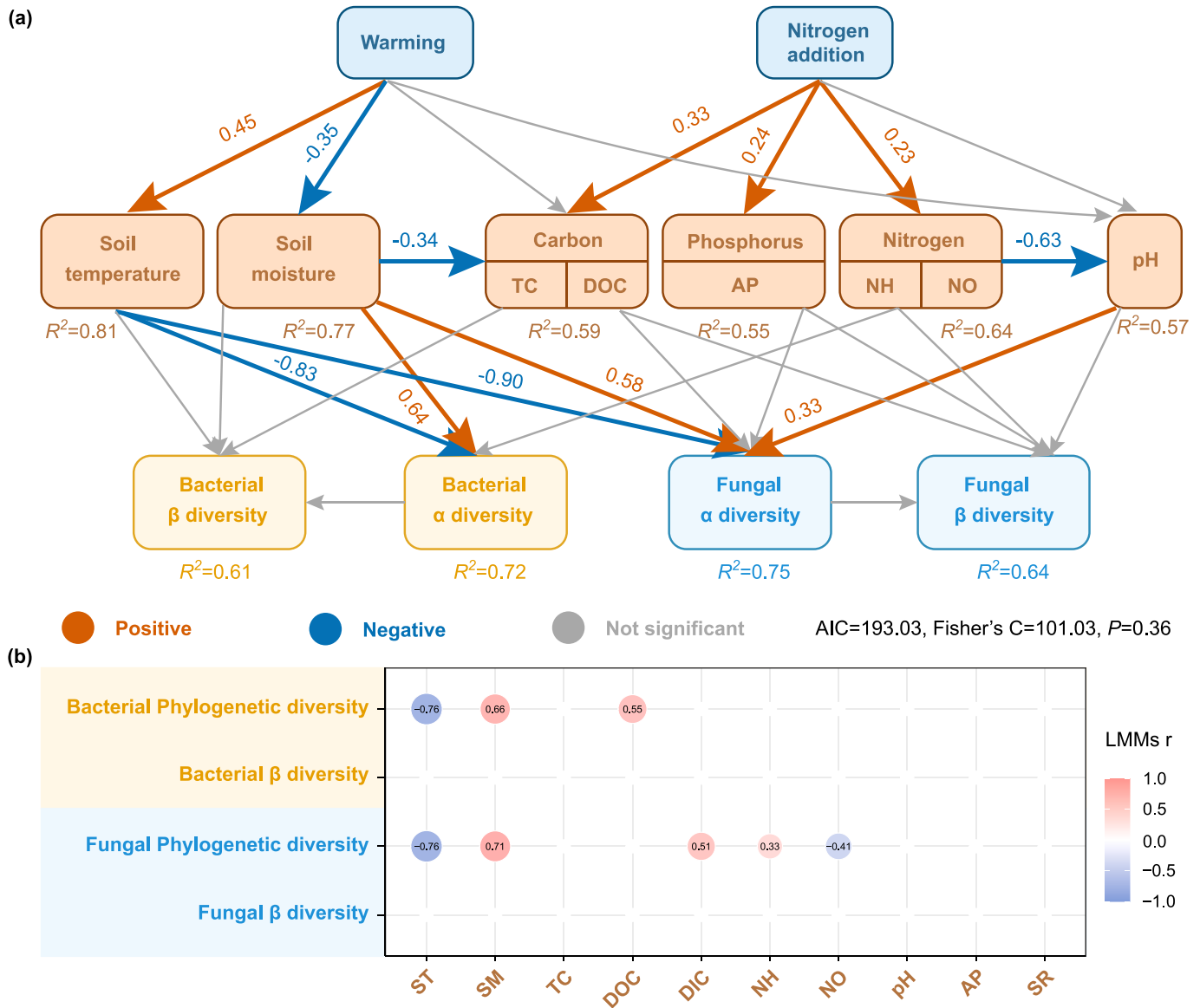
Fig. 5. Environmental drivers of microbial diversity. Structural equation models illustrating the associations among treatments, soil parameters, and bacterial and fungal diversity (a). Negative and positive relationships were expressed by blue and red arrows, respectively. Significant ($P < 0.05$) or non-significant associations are shown as solid and dashed lines, respectively. The standard path coefficients were indicated by numbers near the pathway arrows. Each dependent variable's R^2 expresses the proportion of variance explained. Correlations between microbial diversity and soil variables (b). The color represents the correlation coefficient derived from the linear mixed-effects models. Wald type II χ^2 tests determine statistical significance. False discovery rate was used to adjust the P values. Only significant correlations at $P < 0.05$ are colored. Numbers inside cells are corresponding correlation coefficients. Soil variables included soil moisture (SM), temperature (ST), total carbon (TC), dissolved inorganic carbon (DIC), available phosphorus (AP), NO$_3$-N (NO), dissolved organic carbon (DOC), NH$_4^+$-N (NH), pH (pH), and soil respiration (SR). β diversity is the Bray-Curtis dissimilarity and α diversity is the phylogenetic diversity.

and any soil nutrients in the partial mantel test results (Fig. 6a) suggests that nitrogen addition had small effects on soil properties and may have resulted in fewer habitats heterogeneity. Accordingly, stochastic events may play a greater role in regulating the bacterial community assembly. Conversely, in fungal community assembly, nitrogen addition enhanced the significance of deterministic process (Fig. 4d). Fungal βNTI exhibited a significant correlation with soil available phosphorus (Fig. 6b). This may be due to nitrogen addition affecting the utilization of phosphorus by fungi, thereby causing potential deterministic environmental filtering.

Notably, in bacterial community assembly, the deterministic processes were stronger in warming plus nitrogen addition than in the control, and variable selection emerged as the dominant deterministic process (Fig. 4b). In most cases, variable selection results in dissimilar biotic communities due to variations in biotic and abiotic conditions

(Feng et al., 2018). However, for fungal community assembly, the deterministic processes were weaker in the warming plus nitrogen addition than in the control (Fig. 4d). This result suggested that interactive global change factors may enhance the variation in both abiotic and biotic factors, resulting in alterations in microbial community assembly. It is vital to concern the interactive effects of global change factors on microbial community, as these factors do not occur in isolation (Zheng et al., 2022). Therefore, it is likely that microbial communities are shaped by a more complicated mechanism than simply the influences of warming and nitrogen addition on soil traits.

5. Conclusion

Our research demonstrated that the decline in soil microbial alpha diversity is primarily attributed to the warming effect, which leads to
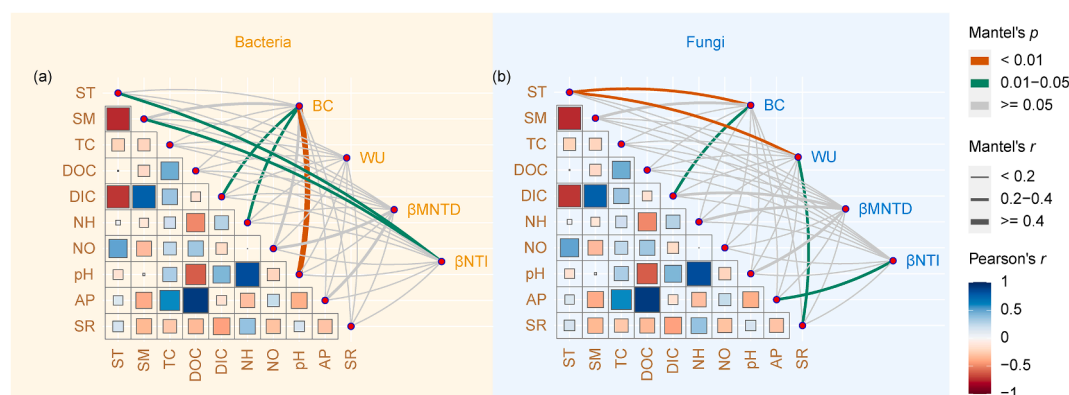
Fig. 6. Pairwise comparisons of soil variables are displayed, and the Pearson correlation coefficient is indicated by a color gradient. Bacterial (a) and fungal (b) Bray-Curtis dissimilarity, Weighted UniFrac dissimilarity, βMNTD, and βNTI were correlated with each soil variable using partial mantel tests. The width of the edges represents the mantel's *r* statistic for the respective correlations, while the color of the edges indicates the statistical significance determined through 9999 permutations. BC stands for Bray-Curtis dissimilarity, WU is the Weighted UniFrac dissimilarity, βNTI is the beta nearest taxon index, and βMNTD is the beta mean nearest taxon distance. Soil variables included soil moisture (SM), temperature (ST), total carbon (TC), dissolved inorganic carbon (DIC), available phosphorus (AP), NO_3^--N (NO), dissolved organic carbon (DOC), NH_4^+-N (NH), pH (pH), and soil respiration (SR).

alterations in the soil microclimate, particularly soil moisture and temperature. Our findings indicate that in the primary subtropical forest, microbial alpha diversity is more resistant to nitrogen addition than warming. The microbial community composition and beta diversity in soil had not significantly difference between experimental and control treatments in our study. Although the experimental treatments altered, to varying degrees, the relative significance of the processes of microbial community assembly, stochastic processes were dominated for the microbial community assembly in the primary subtropical forest. Our findings highlight that microbial community composition and assembly may be able to withstand short term global changes in the primary forest, especially stochastic processes of soil microbial community play a vital role in acclimation to future global change.

CRediT authorship contribution statement

Debao Li: Writing – original draft, Visualization, Software, Investigation, Data curation. **Chuansheng Wu:** Investigation, Conceptualization. **Jianping Wu:** Writing – review & editing, Supervision, Conceptualization.

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.

Data availability

Data will be made available on request.

Acknowledgement

Author contributions

CW and JW designed the experiment. DL took samples and performed data analysis. DL and JW wrote the paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecolind.2024.111618.

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