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Warming enhanced the interaction effects of fungi and fungivores and soil potassium mineralization in tropical forest

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Abstract

Potassium (K) cycling in forest systems has received less attention than nitrogen (N) and phosphorus (P) cycles, despite its critical role in maintaining primary production and regulating water economy and use under climate warming. This study conducted a 10-year study in which we translocated dominant tropical forest tree seedlings and underlying soil (i.e., in situ soil) from high-altitude sites (600 m a.s.l.) to lower altitude sites at 300 m a.s.l. (+1.0 °C) and 30 m a.s.l.

(+2.1 °C) to simulate climate warming in southern China. We investigated soil microbial and nematode communities, soil and foliar K concentrations at the aggregate level, and tree growth under different altitude sites. Microbial community was characterized by high-throughput sequencing, nematodes were identified to the genus level using microscope. The findings revealed that warming treatments significantly ($p < 0.01$) increased soil fungal gene abundance (+78 % at 300 m and +62 % at 30 m), fungal/bacterial abundance ratio (+121 % at 300 m and +101 % at 30 m), and soil fungivore abundance (+274 % at 300 m and +233 % at 30 m). These results indicate a shift in the soil decomposition pathway from bacterial to fungal-based channels.

In addition, warming amplifies the interactions between fungi and fungivores. Aggregates had few effects on microbial biomass, but had significant effect on nematode abundance. Soil microcosm experiments consistently demonstrated that addition of the dominant fungivore *Aphelenchoides* significantly ($p < 0.05$) enhanced soil exchangeable K by stimulating fungal gene abundance and activity. Furthermore, warming-induced changes in forest communities were observed. At the species-specific tree level, *Syzygium rehderianum* demonstrated the ability to take advantage of this scenario, exhibiting increased K uptake (− 4% at 300 m and +32 % at 30 m). This may be attributed to the species being ectomycorrhizal-forming, where colonizing root surfaces can mobilize interlayer and structural K from the minerals. In contrast, *Machilus breviflora* exhibited lower foliar K concentrations (− 42 % at 300 m and − 41 % at 30 m) and reduced growth. However, warming had little effect on *Shima superba*, *Myrsine seguinii*, *Itea chinensis*, and *Ardisia lindleyana* growth. Warming-induced changes in the plant–soil system K cycle highlight the emergence of a new ecosystem structure with different soil web structures and distinct plant community species composition. Our results prompt further research to understand the microbiome-mediated complexities of understudied nutrient cycles, which are likely to be further altered in the future owing to climate change.

Keywords: Tropical forests, Warming, Potassium mineralization, Microbial and nematode community, Microbial-nematode interactions

Introduction

Over the next two decades, global models predict a significant and unprecedented warming trend in tropical forests (Reed et al., 2012). These forests are crucial components of the Earth's terrestrial gross primary production, accounting for approximately one-third, and store nearly half of the Earth's carbon in vegetation (Hubau et al., 2020). Therefore, even minor changes in tree growth in tropical forests under climate warming can have substantial impacts on global gross primary production. In the subtropical region of China, the mean annual temperature is projected to rise by 0.9°C over the next 45 years and by 1.5°C over the next 70 years (Wu et al., 2020). As a key factor affecting tropical forest ecosystems, warming can lead to changes such as shifts from fewer larger trees to more smaller woody individuals under future global warming and drought scenarios (Zhou et al., 2013). Despite the importance of tropical ecosystems, they have been relatively less studied compared to temperate forests in previous warming experiments (Soto-Correa et al., 2013; DeAngelis et al., 2015).

Soil nutrient availability is essential for plant growth, and recent studies suggest that warming could increase soil nitrogen (N) and phosphorus (P) cycling in sub/tropical ecosystems (Lie et al., 2019; Wang et al., 2019). With warming leading to decreased soil moisture (Lie et al., 2021), the demand for soil potassium (K) uptake by plants and microorganisms may increase to regulate water fluxes and use efficiency under more drought conditions. However, there is limited knowledge about the role of K and its changes under global change (Sardans et al., 2015). Particularly, the effects of warming on K cycling and its underlying mechanisms remain poorly understood, especially in humid K-deficient tropical forests. K is vital in fundamental metabolic processes and plays a crucial role in plants' resistance to drought induced by climate warming (Sardans et al., 2015; Sardans et al., 2021). Although K accounts for 2.6% of the Earth's crust, its uptake by plants is restricted since directly available K (i.e., in soil solution) typically constitutes only a small proportion (0.1–0.2%) of the total soil K (Sardans et al., 2015). Soil K availability is classified based on its accessibility to plant roots: soluble and exchangeable forms are considered rapidly available (available K) and can be replenished by non-exchangeable K when depleted due to plant removal and/or leaching, potentially with significant contributions from increased

microbial activity (Li et al., 2021). Some studies have suggested that K significantly limits tree growth and ecosystem productivity in forest ecosystems (Tripler et al., 2006). In tropical forests, available K is often scarce due to intense soil mineral weathering and leaching through runoff and deep drainage (Sattar et al., 2019). In more productive tropical areas, plants need to uptake more K compared to temperate regions (Sardans et al., 2015). For instance, long-term fertilization experiments conducted in the Panama rainforest have observed some degree of K limitation on net primary production (Wright et al., 2018).

Microbes play a crucial role in the natural K-cycle by solubilizing K-bearing minerals (Diep and Hieu, 2013; Sun et al., 2019). Bacterial and fungal species are known to convert K minerals into soluble forms through the release of organic acids, exchange reactions, chelation, and complexation (Meena et al., 2015; Sattar et al., 2019). Under climate warming, fungi are more resilient to water stress compared to bacteria, potentially leading to an increase in their relative contribution to the soil microbial community (Zhang et al., 2005). This shift towards a higher fungal contribution may alter the soil K mineralization process, favoring fungal-based channels over bacterial-based ones, and could have long-term implications for the complex K cycles mediated by the microbiome.

Soil fauna, particularly nematodes, also play a significant role in soil ecological processes. Nematodes are abundant and diverse soil animals that occupy various trophic consumer levels and exhibit different feeding strategies (Bardgett and van der Putten et al., 2014). Considered key components of the soil food web, microbial-feeding nematodes can indirectly stimulate soil microbial activity, regulate microbial communities, and influence soil nutrient cycling (Yeates et al., 2003). Their interactions have been shown to increase soil C, N, and P mineralization and improve nutrient availability for plants (Holtkamp et al., 2011; Sauvadet et al., 2016; Jiang et al., 2017). Warming may directly increase nematode abundance by stimulating reproduction or indirectly through a bottom-up effect, such as increased root carbon input and microbial biomass (Guo et al., 2021). High fecundity nematode species are likely to respond more to warming as they can quickly reproduce in enriched habitats. However, the response of soil microbes and invertebrate detritivores, including nematodes, to warming may not be synchronous (Thakur et al.,

2018). Invertebrate soil detritivores' feeding activity may be more sensitive to warming compared to microbial activity (Sünnemann et al., 2021). For instance, a recent study has demonstrated that climate warming profoundly stimulates faunal (but not microbial) decomposition during the warm season in an alpine meadow (Yin et al., 2022). Presumably, changes in the nematode population under warming will eventually affect the plant-soil K cycle by altering the microbial population. However, this aspect has not been adequately studied, creating a knowledge gap that our study aims to address.

We conducted a 10-year plant-soil ecosystem transplantation experiment in a tropical forest at various elevations to leverage natural temperature differences. Our study aimed to assess the effects of warming on soil microbe and nematode communities, K mineralization, foliar K concentrations, and growth of the dominant tree species. Our hypotheses were as follows: (1) Warming might increase the relative contribution of fungi to the soil microbial community, leading to enhanced K mineralization in initially K-deficient tropical forest soil. (2) The higher presence of fungi could stimulate fungivore populations due to increased food sources, resulting in heightened interactive effects between fungi and fungivores and, consequently, an amplification of fungal-mediated K mineralization. (3) Changes in soil available K could affect plant K uptake and growth, potentially influenced by the dominant plant species, including arbuscular mycorrhizal-forming and ectomycorrhizal-forming species, which exhibit different drought tolerance.

Our findings significantly contribute to advancing the understanding of microbiome-mediated, complex, and understudied nutrient cycles, which are expected to continue experiencing alterations in the future under the influence of climate change.

2. Materials and methods

2.1 Study site

We conducted the warming experiment at Dinghushan Biosphere Reserve in South China (112°10'E, 23°10'N), which lies in a region with a typical tropical monsoon climate. The mean annual temperature is approximately 21°C. The mean annual precipitation is about 1900 mm.

Soils (pH 4.0–4.9) are highly weathered Ultisols developed on sandstone and shale, and are generally rich in Fe minerals (Lie et al., 2022). In this area, mountain evergreen broad-leaved, coniferous mixed broadleaf, and monsoon evergreen broadleaf are the major forest types that dominate at altitudes of 600 m a.s.l., 300 m a.s.l., and 30 m a.s.l., respectively. *Schima superba*, *Machilus breviflora*, and *Syzygium rehderianum* dominate forest growth and cover at these three altitudes.

2.2 Translocation experiment design

We used the natural temperature differences between the sites at different elevations to simulate climate warming. All sites were located on a south-facing slope with similar gradients, amount of sunlight, and precipitation; temperature differences were the main environmental factor changing among the three sites (Liu et al., 2017). In March 2012, three similar growth chambers (3×3×0.8 m, Length, width, and height) were placed at each of the elevations (600, 300, and 30 m) (Fig. 1). Each temperature treatment had three replicates. The below-ground section of each growth chamber was surrounded by a concrete brick wall sealed with ceramic tiles to prevent the lateral or vertical movement of rainfall. Two holes (inner diameter 2 cm), one at the top and one at the bottom of the wall, were connected to stainless steel buckets to collect surface runoff and underground water, respectively (Fig. 1).

In April 2012, soils from three depths (0–20, 20–40, and 40–70 cm) were collected from the evergreen broad-leaved forests at an elevation of about 600 m. They were homogenized separately and then transferred in individual layers into all chambers at all three elevations. One-year-old seedlings (basal stem diameter about 4 mm; height about 30 cm) of the six dominant plant species (*Schima superba*, *Itea chinensis*, *Machilus breviflora*, *Myrsine seguinii*, *Ardisia lindleyana*, and *Syzygium rehderianum*) were collected from the control site located at 600 m. *S. superba* and *I. chinensis* are mid-succession species, while *M. breviflora* and *S. rehderianum* are late-succession species. Specimens of *M. seguinii* and *A. lindleyana* were very small and constituted less than 1.1% of the total biomass.

Six replicates per species were randomly transplanted into each chamber. Then, the whole plant-soil system (consisting of the *in situ* soil and dominant plant species) was then translocated from 600 m to 300 and 30 m (from cooler to warmer sites). Campbell 109 constantan-copper

thermocouples were used to record soil temperatures (at 5 cm) in each chamber. The average monthly soil temperatures at a depth of 5 cm significantly increased by 1.0°C and 2.1°C at elevations of 300 and 30 m, respectively (Lie et al., 2021). Compared to the moisture at 600 m, the average monthly soil volumetric water content at a depth of 5 cm significantly decreased at an elevation of 30 m but was not significantly affected at 300 m (Lie et al., 2022).

2.3 Soil sample collection and aggregate fractionation

In December 2021, we took five soil cores (each 5 cm in diameter and 10 cm in depth) from each chamber and homogenized them thoroughly to form a composite sample. Soil samples were first sieved through a 4-mm mesh, and sterilized tweezers were used to remove visible roots and stones. Then, soil samples were sieved through a 250-μm mesh into two aggregate sizes: the > 250-μm-size fractions were defined as the macroaggregate fraction and the < 250-μm-size fractions as the microaggregate fraction (Su et al., 2021); each aggregate fraction was homogenized for chemical and biological analyses. A fresh subsample of the homogenized macroaggregate/microaggregate soil fraction was used for nematode extraction, and another subsample of each fraction was stored at -80 °C to analyze the soil microbial community. The remaining fresh soil was then air-dried to be used for the soil K-concentration analysis.

2.4 Soil K analysis

Soil exchangeable K was extracted using 1 M ammonium acetate, non-exchangeable K was extracted with 1.0 mol L⁻¹ HNO₃, and soil was digested with HNO₃-HClO₄-HF following the method (Bao, 2000). Soil exchangeable K, non-exchangeable K, and plant and soil total K were determined by flame atomic absorption spectrometry (Z-5300, Polarized Zeeman Atomic Absorption Spectrophotometer) using the extracted and digested liquid mentioned above.

2.5 Soil microbial and nematode communities' analysis

Power Soil DNA Isolation Kit (MoBio, California, USA) was used to extract DNA from 0.5 g of frozen soil as the manufacturer's protocol. The V3-V4 region of the 16S rRNA gene and the ITS region of the 18S rDNA gene were amplified for the bacterial and fungal communities analysis (Adams et al., 2013; Bates et al., 2011). The high-throughput sequencing of the 16S and 18S genes were conducted by the Majorbio Company (Shanghai, China) using the Illumina NovaSeq6000 platform. The 16S rRNA and 18S rDNA sequences data are deposited in the NCBI Sequence Read

Archive under accession numbers PRJNA (910957). The ABI 3700 Real-Time PCR System was employed to quantify the abundance of bacterial and fungal gene.

We extracted nematodes from 50 g of fresh soil using the cotton-wool filter method (Townshend et al., 1963). At least 100 nematodes within each sample were identified to genus level following standard identification keys (Bongers, 1988). Then, these nematodes were classified into four trophic groups: bacterivores, fungivores, omnivores-predators, or herbivores. We calculated the nematode channel ratio (NCR) index, which explains the relative contributions of the bacterial-based energy channel or the slower fungal-based channel and is calculated as $NCR = B/(B + F)$, where B and F are the relative contributions of bacterivores and fungivores to the total nematode abundance, respectively (Yeates et al., 2003).

2.6 Evaluate the interaction effects of fungi and fungivores in microcosm experiments

We added the natural microbial community with and without fungivores to autoclaved soils to evaluate the interactive effects of soil nematode and microbes on soil K mineralization (Sun et al., 2019). 72 tissue culture bottles (240 mL) were filled with 30 g of air-dried soils from each aggregate fractionation in each chamber (collect four culture bottles for each aggregate fraction) of the field experiment (9 chambers $\times$ 2 fractions $\times$ 4 bottles/each aggregate fraction = 72). Before filling the microcosms, these soils were autoclaved (120 °C, 70 min) for two successive days. Then, within each of the 72 microcosms, 2 mL of microbial suspension was added. The microbial suspension was prepared by stirring 10 g of dry-weight-equivalent fresh soil from plots of this experiment with 40 mL of sterile distilled water for 1 hour. The solution was then filtered through millipore filters (30 μ m pore-size) to remove nematodes and obtain a microbial suspension.

In parallel, we isolated the dominant fungivores *Aphelenchoides* sp. from the field experiment, mixing different populations from all the nine chambers and used this species as a model. First, these nematodes were surface sterilized with 0.1% malachite green over 5 min. Malachite green is an organic dye used extensively as a fungicide. Then these nematodes were washed with sterile distilled water. We then created a density-gradient of nematode (*Aphelenchoides* sp.) into the microcosms, by adding either 0, 27, 81 or 135 individuals into the four microcosms coming from tissue culture bottle of macroaggregate and microaggregate fraction as the nematode density in the field experiment.

Sterile water was used to adjust soil moisture (17%). We put these culture bottles into a thermostatic incubator (20 °C) and incubated them in a dark environment for 14 days. A previous study showed an adult to adult cycle of *Aphelenchoides rutgersi* was 13-14 days at 20 °C (Ruess et al., 2000). After the incubation period, we mixed the soils uniformly in all the culture bottles to analyze fungi gene abundance, *Aphelenchoides* sp. density, and the available K.

2.7 Determination of plant foliar K and growth

Mature leaves were randomly collected from six tree species in December 2021. The total plant foliar K was digested with H₂SO₄-H₂O₂ according to the method (Bao, 2000). Plant height (H) was measured as the distance between the soil surface and the top of the tree; the basal diameter (D) was measured at the soil surface. A proxy of the tree volume of each species was calculated using the formula of D²H (Lie et al., 2021).

2.8 Statistical analysis

Statistical analyses were performed using SPSS v. 17.0 (SPSS Inc., Chicago, IL). The main effects of warming and aggregate fraction, and their interaction effects on soil microbial gene abundance, nematode density, and plant nutrients were tested using two-way factorial ANOVA. The treatment effects of warming on the relative abundance of bacterial and fungal communities were tested using a one-way analysis of variance, along with Tukey's multiple comparison tests to control for falsely significant results ($P < 0.05$). Differences in microbial community composition (Bray-Curtis dissimilarity matrix) in the three treatments were assessed by permutational multivariate ANOVA (PERMANOVA) and visualized using principal coordinate analysis (PCoA). Interaction network analysis was used to visualize the associations between fungivores and fungal communities, we constructed the interaction networks by calculating the possible pairwise Spearman's rank correlations. We considered the dominant fungal communities with an average abundance of more than 0.1% to reduce network complexity. A valid cooccurrence was considered a statistically robust correlation between species with a P -value < 0.05 . Correlation analyses were performed using the psych packages in R software. The correction test function was used to correct for multiple comparisons with the psych package. Correlation networks were conducted using Gephi software.

In the microcosm experiment, the main effects of soil from different elevations and nematode

addition, and their interaction on fungi abundance and availability K were tested using two-way ANOVA. The different nematode addition on fungal gene abundance and availability K were tested using a one-way variance analysis and Tukey's multiple comparison tests to control for falsely significant results.

3. Results

3.1 Soil K supply

The warming treatment resulted in a significant increase in soil non-exchangeable K. However, the effects of aggregate fraction and the interactive effects of aggregate fraction and warming did not impact soil exchangeable K, non-exchangeable K, or total K (Table 1).

3.2 Soil microbial community

Comparing with the 600 m site, the warming treatment at 300 m did not alter the bacterial community structure, while the warming treatment at 30 m had a noticeable impact on the bacterial community structure (Fig. S1). Specifically, the warming treatment at 30 m led to a decrease in the relative abundance of Proteobacteria and an increase in the relative abundance of Chloroflexi in the macroaggregate fraction (Fig. 2a). Furthermore, comparing with the 600 m site, the warming treatment at 300 m did not modify the fungal community structure, whereas the warming treatment at 30 m resulted in changes in the fungal community structure (Fig. S2). In particular, the warming treatment at 30 m increased the relative abundance of Ascomycota and decreased the relative abundance of Basidiomycota compared to the 600 m site (Fig. 2b).

The effect of aggregate fraction did not influence the relative abundance of bacterial phyla. However, the effect of warming increased the relative abundance of Chloroflexi ($P = 0.003$) but decreased the relative abundance of Myxococcota ($P = 0.020$). Nevertheless, the interactive effects of aggregate fraction and warming did not have an impact on the relative abundance of bacterial phyla (Fig. 2a). On the other hand, the effect of aggregate fraction significantly affected the relative abundance of Mortierellomycota in fungal phyla. Additionally, the effect of warming

increased the relative abundance of Ascomycota ($P = 0.000$) and Mucoromycota ($P = 0.027$) but decreased the relative abundance of Basidiomycota ($P = 0.002$) and Mortierellomycota ($P = 0.026$). However, the interactive effects of aggregate fraction and warming did not influence the relative abundance of fungal phyla (Fig. 2b). Moreover, the effect of warming did not alter bacterial gene abundance but significantly increased fungal gene abundance and the fungal-to-bacterial ratio (Fig. 3).

3.3 Soil nematode community

The effect of aggregate fraction significantly increased the densities of total nematodes, herbivores, bacterivores, fungivores, and omnivore-predators. Specifically, the soil in the macroaggregate fraction had more nematodes than the soil in the microaggregate fraction (Fig. 4). Furthermore, warming had a significant impact by increasing the densities of total nematodes, herbivores, and fungivores. The interactive effects of aggregate fraction and warming showed a highly significant impact on total nematodes, herbivores, and fungivores. Additionally, warming significantly increased the nematode channel ratio.

3.4 The interaction effects of fungi and fungivores on K mineralization

In the 30 m soil food web, there were more positive correlations compared to the 600 m soil (Fig. 5). Notably, the dominant fungivore *Aphelenchoides* (Fig. S3) showed strong positive correlations with the relative abundance of Ascomycota in the 30 m soil (Fig. 5). With the enhanced connectivity and biotic interactions between fungivores and the fungal community under warming, we proceeded to explore the ecological functions of fungivores on K mineralization. To do this, we introduced the natural microbial community with and without fungivores to autoclaved soils. After a 14-day incubation, the addition of *Aphelenchoides* sp. resulted in increased soil fungal gene abundance and exchangeable K (Fig. 6).

3.6 Plant foliar K and growth

The warming treatments had a significant impact on plant growth, increasing it in *S. rehderianum* but decreasing it in *M. breviflora* (Fig. 7). However, the warming treatments had little effect on the plant growth of *S. superba*, *M. seguinii*, *I. chinensis*, and *A. lindleyana* (Fig. 7). Regarding foliar K concentrations, the warming treatment at 300 m and 30 m decreased the levels in *M. breviflora*, *M. seguinii*, and *I. chinensis* (Fig. S4). Conversely, the warming treatment at 30 m increased foliar K concentrations in *S. rehderianum*. For other species, the warming treatments did not have a significant effect on foliar K concentrations (Fig. S4).

4. Discussion

4.1 Effects of warming on soil microbial communities and soil K mineralization

Our findings revealed distinct differences in bacterial communities at 30 m compared to 600 and 300 m, as the warming treatment at 30 m significantly decreased the relative abundance of Proteobacteria compared to the treatment at 600 m. This reduction may be attributed to decreased organic carbon in soils under warming (Fang et al., 2020), as copiotrophic bacteria (e.g. Proteobacteria) tend to respond negatively to oligotrophic environments. It is worth noting that Proteobacteria include many bacteria with significant K-solubilizing ability (Zhang and Kong, 2014), suggesting that the K mineralization process mediated by these bacterial taxa was weakened under warming. Additionally, the warming treatment at 30 m increased the relative abundance of Chloroflexi compared to the treatments at 300 and 600 m, as these oligotrophic Chloroflexi are well adapted to survive under dry, low nutrition conditions (Yang et al., 2021).

Furthermore, warming led to a decrease in the abundance of Basidiomycota but an increase in the relative abundance of Ascomycota, indicating a potential competition between these two groups of microbial taxa. Basidiomycota tends to thrive in humid environments, while Ascomycota are better equipped to withstand thermotolerant stresses and exhibit drier environmental preferences, demonstrating higher competitive abilities (Nottingham et al., 2022). The increase in the relative abundance of the dominant thermophilic fungus *Talaromyces* (Ascomycota) under the warming

treatment (Fig. S5) (Mallek-Fakhfakh and Belghith, 2016) aligns with these findings. Previous studies have suggested that the ascomycetous *Talaromyces* can solubilize otherwise unavailable forms of K-bearing minerals such as micas, illite, and orthoclase through the release of organic acids, contributing to K release and availability (Song et al., 2015; Goh et al., 2020).

Moreover, our results indicate that warming increased fungi gene abundance, likely due to the decrease in carbon quality (Fang et al., 2020) and nitrogen availability (Lie et al., 2021) induced by experimental warming, favoring soil fungal growth over bacterial growth and resulting in an overall increase in fungal contribution to the total soil microbial community and enhanced K mineralization. This finding supports our initial hypothesis that the relative contribution of fungi to soil K mineralization is heightened in tropical forests under climate warming. These results align with studies conducted in alpine regions, where climate warming and associated vegetation shifts have been linked to an increased molar proportion of available-K in soils (Mavris et al., 2015).

4.2 Effects of warming on the soil nematode community and soil K mineralization

Warming had a significant positive effect on the density of fungivores, mainly attributed to the increase in the *Aphelenchoides* genus (Fig. S3), a group of species known for their adaptability to a wide range of soil conditions and their ability to maintain a high population density at temperatures between 10–35 °C (Kitagami et al., 2020). The direct impact of warming on fungivore abundance can be explained by its stimulation of their development and reproduction, especially for high-fecundity nematode species, which can rapidly thrive in warmer habitats (Guo et al., 2021). Additionally, warming indirectly influences fungivore density through its effects on soil fungal biomass, which can exert bottom-up control on higher trophic-level fungivores through the soil food web (Sauvadet et al., 2016). At our study site, soil warming led to an increase in saprotrophic fungi, a food resource for *Aphelenchoides* (Ruess et al., 2000), further supporting the dominance of *Aphelenchoides* under high-temperature treatments, as reported by Kitagami and Matsuda (Kitagami et al., 2020).

The marginally negative effect of warming on Nematode Channel Ratio (NCR) provides

additional evidence that the main decomposition pathway in the soil may shift towards a fungal-dominated soil system. This highlights the importance of investigating the ecological functions of soil fauna in the soil food web to better understand soil decomposition under climate warming.

In line with the metabolic theory of ecology, warming is expected to enhance individual metabolic processes and growth, leading to increased biotic interactions, such as predation, between different trophic levels at higher temperatures (Vergutz et al., 2004). However, despite being vital drivers of nutrient release, trophic interactions, and plant nutrient acquisition, soil fauna remains relatively understudied compared to soil bacteria and fungi (Crowther et al., 2015). Our study sheds light on the significant role of soil fauna in enhancing soil microbial-mediated K-mineral mineralization. The presence of the dominant fungivore *Aphelenchoides* notably increased soil exchangeable K (Fig. 6), mainly due to the warming-enhanced taxon connectedness and potential biotic interactions between fungi and the fungivore *Aphelenchoides*. In accordance with our second hypothesis, our findings suggest that warming increases fungivore abundance and enhances interactions with fungi, thereby augmenting the indirect effects of microbial-mediated K mineralization.

4.3 Warming effects on plant community and plant-soil system functioning

S. rehderianum exhibited greater biomass and foliar K concentrations following the warming treatment, likely due to its ectomycorrhizal-forming nature, which enables it to mobilize interlayer K and structural K from minerals (Yuan et al., 2004). Additionally, ectomycorrhizal-forming species generally have higher drought tolerance compared to arbuscular mycorrhizal-forming species in tropical forests (Zhao et al., 2021). Conversely, *M. breviflora* showed lower foliar K concentrations and reduced growth, possibly negatively impacted by warming-induced decreases in stomatal density (Wu et al., 2020). Our findings underscore the species-specific responses to warming, with *S. rehderianum* exhibiting greater competitive ability under more stress conditions linked to water and nutrient limitation. Both *S. rehderianum* and *M. breviflora* are late-succession species (Zheng et al., 2020), and climate warming may lead to changes in the plant community composition of these late-succession species. Consistent with our third hypothesis, our results

suggest that warming, at least in part, affects the K cycle in the plant-soil system, leading to novel ecosystem structures with different soil web structures, distinct plant community species composition, and even different total biomass. These findings align with previous studies, such as a fertilization experiment in Panama, which observed a limiting role of K in the growth of certain species (Wright et al., 2018). Further studies are urgently needed to understand how these distinct plant community compositions may affect functions such as the carbon cycle in tropical forests in a warmer world.

Conclusion

Our 10-year warming study indicates that warming can shift microbial community compositions, potentially affecting K uptake/cycling and plant productivity. Additionally, warming enhances the interaction effects of fungi and fungivores, as well as K mineralization. As warming and drought increase, the community structure of tree seedlings may be altered, with an increase in ectomycorrhizal-forming species and a decrease in arbuscular mycorrhizal-forming species. The elevated water demand under warming likely contributes to the increased need for K uptake, prompting the tropical forest system to adapt to changing circumstances. Given the significance of K as a sub-limiting or limiting factor in tropical forests, considering the substantial leaching and limited available K, our results further highlight the importance of understanding the microbiome-mediation of complex, understudied nutrient cycles, which will continue to be impacted by climate change in the future.

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Conflict of interests

The authors declare no conflict of interests.

Data availability

The data will be made available on request.

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