Plant Soil (2024) 501:139–153
https://doi.org/10.1007/s11104-023-06175-4

RESEARCH ARTICLE

# Plant managements but not fertilization mediate soil carbon emission and microbial community composition in two Eucalyptus plantations

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Received: 22 February 2023 / Accepted: 13 July 2023 / Published online: 21 July 2023

## Abstract

*Background and aims* Forest management practices affect soil carbon dynamics, particularly by changing the diversity of aboveground plant functional groups. However, we have a limited understanding of the underlying mechanisms for how plant management affects soil respiration in planted forest ecosystems.

*Methods* We conducted a 3-year manipulation experiment of plant functional groups that included understory removal, tree root trenching, and fertilization treatments in 2-year-old and 6-year-old Eucalyptus plantations in the subtropical region, to explore the responses of soil carbon emission and microbial community composition.

*Results* Soil respiration was significantly suppressed by understory removal (-38%), tree root trenching (-41%), and their interactions (-54%), but fertilization alone and in interactions had no significant effect. Soil bacterial and fungal diversity was negatively affected by understory removal and tree root trenching, respectively. Soil respiration and microbial diversity were lower in younger plantations. Reductions in soil carbon emissions were associated with losses of plant functional groups and soil microbial diversity, while increases in soil respiration were associated with soil physicochemical factors, soil temperature, and plantation age.

*Conclusions* The results indicated that understory removal and tree root trenching strongly affected soil

Responsible Editor: Manuel Esteban Lucas-Borja.

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1007/s11104-023-06175-4.

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respiration, while the power effects were regulated by soil microbial community and soil properties in contrast plantation ages. Our findings highlight that plant management is of great significance to the soil carbon emission processes in afforested plantations.

**Keywords** Soil respiration · Afforestation · Understory removal · Plant management · Soil microbial community · Eucalyptus plantation

## Introduction

Biodiversity, species identity, and functional traits on the aboveground plant communities affect the function and structure of the belowground cycling of carbon (C) (Bardgett and van der Putten 2014; Bastida et al. 2021; McClelland et al. 2021), which in turn affects C emissions and global climate change (Hooper et al. 2005; Tilman et al. 2014; Chen et al. 2019a). The growth of large-scale forest plantations usually increases the ecosystem's C pool, which through C sequestration may reduce atmospheric $CO_2$ concentration and mitigate climate warming (Piao et al. 2009; Grassi et al. 2017; Ahirwal et al. 2021). Soil carbon emission or soil respiration is an important component of the forest C cycle, i.e., it is one of the main pathways by which C fixed in the biosphere returns to the atmosphere (Jobbágy and Jackson 2000; Olsson et al. 2005; Sayer and Tanner 2010). Differences in plantation biodiversity and management can directly influence forest soil properties (including water content, temperature, nutrient input, and soil microbial communities) and thereby affect soil respiration and C cycling (Raich and Tufekcioglu 2000; Giuggiola et al. 2018; Delgado-Baquerizo et al. 2019). However, there is no comprehensive understanding of how plant management over time could affect the terrestrial C budget through plantation establishment and growth.

Eucalyptus trees grow rapidly and produce high yields of wood for the paper-making industry (Wan et al. 2015; Wu et al. 2015; Nadal-Sala et al. 2021). Studies have shown that Eucalyptus plantations cover approximately 1.7 million hectares in China, which young Eucalyptus plantations sequester large quantities of C compared with native plantations (Chen et al. 2011; Wan et al. 2015; Ferreira et al. 2018). Many studies have assessed the effects of plantation management on soil C dynamics, e.g., plantation tree species selection (Binkley et al. 2006), tree root trenching (Phillips and Fahey 2007), removal of understory plants (Wu et al. 2011b), grazing (Mueller et al. 2017), soil biotic interactions (Wang et al. 2021), and fertilizer addition (Yu et al. 2019), but there is uncertainty regarding the relationship between plantation management and soil respiration that is the second largest C efflux in terrestrial ecosystems (Machmuller et al. 2018).

In the Eucalyptus plantations, plant functional groups (PFGs) can be separated into a canopy functional group and an understory functional group due to their simple plant community composition (Wu et al. 2011b). Accordingly, the role of canopy functional group was indicated by tree root trenching, while the role of understory functional group was shown with removal in forest ecosystems (Wu et al. 2011a; Fanin et al. 2019). Managements of both groups can affect the soil C dynamics (Docherty and Gutknecht 2019; Grau-Andrés et al. 2020) by changing the microclimate (Wan et al. 2014), soil physicochemical properties (Yahdjian et al. 2017; Fanin et al. 2019), and soil microorganism community (Urcelay et al. 2009; Liu et al. 2021). Soil microorganisms play a crucial role in ecosystem functions and services, such as the decomposition of litter (Delgado-Baquerizo et al. 2016a), nutrient mineralization (Bahram et al. 2018), and the maintenance of edaphic conditions (Jing et al. 2020; Zhou et al. 2023). The role of soil microbial communities in soil C emission after changes in PFGs is important (Marshall et al. 2011; De Long et al. 2016; Bastida et al. 2021). However, the mechanisms by which management of plant functional groups (PFGs) affect soil C processes are poorly understood (Nilsson and Wardle. 2005; Wang et al. 2014; Ferreira et al. 2018; Zhang et al. 2021). The lack of information on the impact of the management of PFGs and soil microorganisms also leads to increased uncertainty in the evaluation of an ecosystem C pool (Zhao et al. 2013; Winsome et al. 2017; Crowther et al. 2019; Grau-Andrés et al. 2020).

In the present study, we investigated how soil respiration and the soil microbial community composition were affected by managements in PFGs, i.e., understory plant removal and tree root trenching. The effects of fertilization and all treatment interactions after management in PFGs on below-ground properties were also investigated. The Eucalyptus plantations are usually harvested around 6 years growth in south China, so the two plantation ages such as 2- and 6-year-old Eucalyptus plantations were selected in this study. In addition, previous studies had found that carbon input from plants strongly affects soil respiration in forest ecosystems (Wu et al. 2011a; Fanin et al. 2019). We tested two hypotheses in this study: (1) Understory plant removal and tree root trenching will reduce soil respiration in Eucalyptus plantations of different ages; and (2) The effects of management in PFGs will be regulated by soil physicochemical characteristics and microorganisms in plantations of different ages.

## Materials and methods

### Site description

The research was conducted in two Eucalyptus plantations at the Tianma National Forestry Farm (117°24′ E, 24°18′N) in Zhangzhou City, Fujian Province, China. This region has a subtropical monsoon climate with mean annual precipitation (MAP) of 1503 mm and a mean annual temperature (MAT) of 21 °C. The soil is an acrisol, which is a red soil in the Chinese soil classification system. The two plantations had the same soil type and texture, and a similar history of disturbance. The plantations were planted with 1-year-old *Eucalyptus urophylla*×*grandis* saplings in 2011 for the younger plantation (2-year-old) and 2007 for the older plantation (6-year-old); the distance between saplings was 2 m within a column, and 3 m between rows. The average diameter at breast height (DBH, 1.3 m height) of young and old plantations were 9.47 and 13.68 cm when the experiment began in February 2012 (Fan et al. 2015). Understory species in the plantations were dominated by *Pseudosasa amabilis*, *Rubus swinhoei*, *Miscanthus sinensis*, *Dicranopteris dichotoma*, and *Smilax china* (Fan et al. 2015).

### Experimental design

The same random block design with three replicates was used in each Eucalyptus plantation. On each plantation, three plots (15 m × 15 m) were established > 100 m from each other. Inside each 15 × 15 m plot, we randomly established eight subplots corresponding to eight treatments. These eight treatments were as follows: (1) the control (CK); (2) understory removal (UR); (3) tree root trenching (Tre); (4) fertilization (Fer); (5) understory removal and tree root trenching (UR + Tre); (6) understory removal and fertilization (UR + Fer); (7) tree root trenching and fertilization (Tre + Fer); and (8) understory removal, tree root trenching, and fertilization (UR + Tre + Fer). For understory removal subplots, the area was 5 m × 5 m where understory plants were manually removed monthly with a machete and hoe. Tree root trenching subplots were placed in between the rows of trees where the area was 1 m × 1 m and a 40-cm-deep trench was dug. The trenching subplots were lined with a PVC board to stop new tree roots into the subplot. For fertilization, urea was added at the start of the experiment and broadcasted by hand at 25 kg N $ha^{-1}$ $year^{-1}$. Since the old roots in soil may affect soil respiration during decomposition, all treatments were initiated in February 2012 and soil respiration measurements were started in May 2012.

### Soil sampling and measurement

Soil samples (0 to 20 cm depth after surface litter and rock was removed) were collected from each subplot in December 2014, using a 3-cm-diameter soil corer. The samples were passed through a 2-mm sieve to remove stones and roots and were thoroughly mixed and then divided in half. One half was for physicochemical analyses, and the other half was stored at -20℃ before microbial analysis.

In situ soil respiration was measured between 9 a.m. and 12 a.m. on one day each month from May 2012 to December 2014, with a Li-cor 8100 automated soil flux system (LI-COR Inc., Lincoln, NE, USA); soil respiration was measured in a PVC collar (20 cm diameter and 5 cm high; one collar per subplot). The PVC collar was embedded into the soil surface 2 cm deep after removing living plants and surface leaf litter from the collar area. Soil temperature (ST, ℃) at 5 cm depth and soil water (volume %) were measured monthly with probes attached to the soil flux system.

All soil analysis methods were cited from Liu (1996). In brief, soil water content (SWC, dry weight%) was gravimetrically determined by oven drying fresh soil at 105℃ to a constant weight. Soil pH was measured with a pH meter in a 1: 2.5

mixture of soil: water. Soil organic carbon (SOC, $g \cdot kg^{-1}$) was analyzed by the acid-dichromate $Fe_2SO_4$ titration method with air-dried soil. $NO_3^-$-N ($mg \cdot kg^{-1}$) and $NH_4^+$-N ($mg \cdot kg^{-1}$) in filtered KCl extracts of fresh soil samples were measured using a flow injection autoanalyzer (FIA, Lachat Instrument, USA). Total nitrogen (TN, $g \cdot kg^{-1}$) contents were measured after micro-Kjeldahl using the flow injection autoanalyzer. Total phosphorus (TP, $g \cdot kg^{-1}$) was determined by a colorimetric assay after wet digestion with $H_2SO_4$ and $HClO_4$. Available phosphorus (AP, $mg \cdot kg^{-1}$) was determined with an acid extracting solution (0.025 M HCl and 0.03 M $NH_4F$). Total potassium (TK) was analyzed by an inductively coupled plasma mass spectrometer (ICP-MS, Agilent, Santa Clara, CA, USA).

Soil DNA was extracted from 0.25 g defrosted samples using the PowerSoil DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA), and genomic DNA was detected by 1% agarose gel electrophoresis. To determine the composition and diversity of bacterial and fungal communities, the paired primers of 515 F (5’-GTGCCAGCMGCCGCGG-3’) and 907R (5’-CCGTCAATTCMTTTRAGTTT-3’) with a barcode were used to amplify the bacterial 16 S rRNA gene (Xiong et al. 2012), and the paired primers of SSU0817F (5’- TTAGCATGGAATAATRRAATAGGA-3’) and SSU1196R (5’- TCTGGACCTGGTGAGTTTCC-3’) with a barcode were used to amplify the fungal 18 S rRNA gene (Rousk et al. 2010). The sequences were processed with the QIIME pipeline (Callahan et al. 2016). Paired-end sequencing of PCR amplicons was performed on an Illumina Miseq PE250 sequencer (Illumina, San Diego, CA, USA). Paired-end reads were assembled using FLASH to obtain raw tags. In brief, paired-end reads were merged into single sequences, and the low-quality merged sequences were removed from downstream analysis. After the chimeras were removed, 97% similar sequences were clustered into operational taxonomic units (OTUs) by using the Usearch program. Taxonomic names were assigned using the Ribosomal Database Project (Wang et al. 2007); the community composition of each sample was measured at all levels (domain, kingdom, phylum, class, order, family, genus, and species). If the relative abundance of a fungal or bacterial OTU was $\leq 1\%$, the OTU was classified as Others. According to the meaning of biodiversity indices, the Chao1 and Shannon indices were selected in the present study.

## Statistical analyses

The $Q_{10}$ values (the temperature sensitivity of soil respiration) for all of the treatment plots were derived from soil respiration rate against monthly soil temperature that was fitted with an exponential growth model. The exponential growth model and $Q_{10}$ values were calculated as follows:

$$R_s = ae^{bT} \tag{1}$$

$$Q_{10} = e^{10b} \tag{2}$$

Where *Rs* is the soil respiration rate (μmol $CO_2$ $m^{-2}$ $s^{-1}$); *e* is the base of the natural logarithm function; *T* is the soil temperature (℃); *a* and *b* represent models fitting constant values; $Q_{10}$ is the temperature sensitivity value of soil respiration (Sierra 2012).

One-way analysis of variance (ANOVA) and the least significant difference (LSD) were used to analyze the effects of different treatments in each plantation on soil respiration rate and soil physicochemical properties. Furthermore, three-way analysis of variance (ANOVA) with two covariates (month and plantation age) was used to assess the effects of understory removal, tree root trenching, fertilization, and their interactions on the soil respiration rate. All analyses were performed in R version 4.0.3 (R Core Team 2020). The R packages *vegan*, and *ggpubr* were used to analyze the diversity and community of soil microorganisms. Principal coordinates analysis (PCoA) and permutational multivariate analysis of variance (PERMANOVA) were used to determine the effect of plantation age and PFGs removal treatments on soil microbial communities (Lajoie and Kembel 2021). Redundancy analysis (RDA) was performed to determine the relationships between microbial communities, soil physicochemical properties, and environmental factors (soil temperature and moisture). The most discriminating soil property variables were selected by the “backward selection” procedure with the *vegan* package. Before the RDA analysis was performed, the variance expansion coefficient of all soil environmental factors was calculated. To explore how plantation age and plant functional groups influenced the soil respiration rate, soil physicochemical properties, and microbial community, the R packages vegan, lme4, and MuMin were used in the variance partitioning analyses (VPA). Statistical significance was determined at $P < 0.05$.

## Results

### Soil microclimate and physicochemical properties

Three-way ANOVAs showed that soil temperature, pH, SOC, $NH_4^+$-N, TN, TP, AP, and TK significantly differed between the 2- and 6-year-old plantations ($P < 0.001$; Table 1; Appendix S1: Table S1). Soil temperature was 3℃ higher in the 2-year-old plantation than in the 6-year-old plantation ($P < 0.01$). The contents of SOC, TN, and TP were significantly higher in the 2-year-old plantation than in the 6-year-old plantation. In contrast, the soil pH, NH4+-N, AP, and TK contents were significantly lower in the 2-year-old plantation than in the 6-year-old plantation (Table 1; Appendix S1: Table S1).

Three-way ANOVAs showed that the interaction of understory removal × tree root trenching × fertilization (UR×Tre×Fer) increased SOC ($P < 0.05$; Table 1). The interaction of understory removal and tree root trenching (UR×Tre) increased soil temperature ($P < 0.05$; Table 1). The interaction of understory removal and fertilization (UR×Fer) increased soil pH ($P < 0.05$; Appendix S1: Table S1).

### Respones of soil respiration rate

The soil respiration rate was significantly different in the 2- and 6-year-old plantations ($P < 0.001$; Table 2). The mean soil respiration rates were lower in the 2-year-old plantation (3.20 μmol $CO_2$ $m^{-2}$ $s^{-1}$) than in the 6-year-old plantation (3.39 μmol $CO_2$ $m^{-2}$ $s^{-1}$) in CK treatment. The soil respiration rate significantly differed among months ($P < 0.001$), with the lowest in January (1.31 μmol $CO_2$ $m^{-2}$ $s^{-1}$) and the highest in July (4.08 μmol $CO_2$ $m^{-2}$ $s^{-1}$) for the 2-year-old plantation, with the lowest in January (1.40 μmol $CO_2$ $m^{-2}$ $s^{-1}$) and highest in July (5.05 μmol $CO_2$ $m^{-2}$ $s^{-1}$) for the 6- year-old plantation (Fig. 1a; Table 2). Three-way ANOVAs showed that understory removal (UR), tree root trenching (Tre), and their interaction significantly reduced the soil respiration rate in all years and seasons (Fig. 1b; Table 2; Appendix S1: Table S2). The effect of fertilization on soil respiration rate was minor and fertilization did not have a significant effect on the soil respiration in the second and third years when compared with the first year (Fig. 1b; Table 2).

One-way ANOVA showed that understory removal (UR), tree root trenching (Tre), and understory removal + tree root trenching significantly reduced the soil respiration rate (UR: -38%, Tre: -41%, UR + Tre:

**Table 1** Effects (*P* values) of plantation age, treatments, and their interactions on the soil microclimate and physicochemical properties in the 2- and 6-year-old Eucalyptus plantations in China

| Source | ST | SM | pH | SOC | $NO_3^-$-N | $NH_4^+$-N | TN | AP | TP | TK |
|---|---|---|---|---|---|---|---|---|---|---|
| Age | **< 0.001** | 0.824 | **< 0.001** | **< 0.001** | **0.016** | **0.003** | **< 0.001** | **< 0.001** | **< 0.001** | **< 0.001** |
| UR | 0.994 | 0.564 | 0.423 | 0.578 | 0.072 | 0.087 | 0.057 | 0.834 | 0.160 | 0.226 |
| Tre | 0.405 | 0.101 | 0.468 | 0.395 | 0.340 | 0.337 | 0.569 | 0.133 | 0.079 | 0.609 |
| Fer | 0.963 | 0.357 | 0.469 | 0.972 | 0.287 | 0.612 | 0.751 | 0.168 | 0.118 | 0.783 |
| UR×Tre | **0.046** | 0.211 | 0.354 | **0.035** | 0.854 | 0.350 | 0.115 | 0.451 | 0.646 | 0.673 |
| UR×Fer | 0.635 | 0.327 | **0.011** | 0.858 | 0.620 | 0.565 | 0.601 | 0.581 | 0.118 | 0.188 |
| Tre×Fer | 0.481 | 0.168 | 0.769 | 0.399 | 0.125 | 0.766 | 0.245 | 0.785 | 0.200 | 0.858 |
| UR×Tre×Fer | 0.710 | 0.377 | 0.148 | 0.006 | 0.411 | 0.476 | 0.163 | 0.949 | 0.339 | 0.691 |

Abbreviations: ST: soil temperature; SM: soil moisture (%); Age: plantation age; UR: understory removal; Tre: tree root trenching; Fer: fertilization; UR×Tre×Fer: interactions among understory removal, tree root trenching, and fertilization. OC: soil organic carbon; $NO_3^-$-N: nitrate nitrogen; $NH_4^+$-N: ammonium nitrogen; TN: total nitrogen; AP: available phosphorus; TP: total phosphorus; TK: total potassium. Significance was set at $P < 0.05$. The actual values can be found in supplementary Table 1

Significant effects are indicated in bold font

**Table 2** Effects (*F* and *P* values) of the month, plantation age, treatments, and their interactions on soil respiration in the 2- and 6-year-old Eucalyptus plantations in China

| Source | 2-year-old | | 6-year-old | | Both plantations | |
|---|---|---|---|---|---|---|
| | *F* | *P* | *F* | *P* | *F* | *P* |
| Month | 7.931 | **< 0.01** | 21.943 | **< 0.001** | 30.342 | **< 0.001** |
| Age | / | / | / | / | 38.004 | **< 0.001** |
| UR | 55.843 | **< 0.001** | 44.289 | **< 0.001** | 96.154 | **< 0.001** |
| Tre | 153.366 | **< 0.001** | 59.951 | **< 0.001** | 186.313 | **< 0.001** |
| Fer | 0.533 | 0.465 | 0.134 | 0.714 | 0.024 | 0.878 |
| UR×Tre | 11.165 | **< 0.001** | 7.831 | **< 0.01** | 18.014 | **< 0.001** |
| UR×Fer | 7.367 | **< 0.01** | 1.094 | 0.296 | 6.131 | **0.013** |
| Tre×Fer | 4.223 | **0.040** | 1.454 | 0.228 | 0.086 | 0.769 |
| UR×Tre×Fer | 7.189 | **< 0.01** | 0.194 | 0.660 | 3.908 | **0.048** |

Abbreviations: Age: plantation age; UR: understory removal; Tre: tree root trenching; Fer: fertilization; UR×Tre×Fer: interactions between understory removal, tree root trenching, and fertilization. Significance was set at $P < 0.05$

Significant effects are indicated in bold font

-54%; $P < 0.001$) (Fig. 1e; Table 2; Appendix S1: Table S2). Fertilization (Fer) alone did not significantly affect the soil respiration rate ($P = 0.88$), but understory removal + fertilization (UR + Fer) did significantly reduce soil respiration (-29%, $P < 0.05$). The three factors understory removal + tree root trenching + fertilization (UR + Tre + Fer) also reduced soil respiration rates (-52%, $P < 0.05$; Fig. 2e; Table 2; Appendix S1: Table S2).

The $Q_{10}$ value for the 2-year-old plantation ($Q_{10} = 1.81$) was lower than for the 6-year-old plantation ($Q_{10} = 2.04$). The soil respiration rate increased with temperature increases ($R^2$: 33-49%), and $Q_{10}$ values were higher with understory removal (UR), tree root trenching (Tre), fertilization (Fer), and their combinations than with CK (Fig. 2; Appendix S1: Fig. S1). The loss of functional groups had positive effects on the temperature sensitivity of soil respiration, but Fer attenuated this effect (Fig. 2; Appendix S1: Fig. S1).

## Soil microbial diversity and community composition as affected by plantation age and treatments

The bacterial Chao1 and Shannon indices indicated higher diversity in the 6-year-old plantation than in the 2-year-old plantation ($P < 0.001$) (Fig. 3a, b; Appendix S1: Table S3). The fungal Chao1 index was higher in the 6-year-old plantation than in the 2-year-old plantation ($P < 0.001$), but there was no significant difference in fungal diversity between plantation ages as measured by the Shannon index ($P = 0.55$) (Fig. 3c, d; Appendix S1: Table S3).

Understory removal (UR) significantly reduced bacterial diversity (Chao1 index $P < 0.05$) (Fig. 3; Appendix S1: Table S3). Fungal Chao1 index was significantly reduced by tree root trenching (Tre) or by interactions of tree root trenching × fertilization (Tre ×Fer) (Fig. 3; Appendix S1: Table S3). The bacterial and fungal communities significantly differed between the two plantation ages according to the PCoA and PERMANOVA analysis ($P < 0.001$, PERMANOVA by Adonis) (Fig. 4). Understory removal did not significantly change the microbial communities of bacteria ($P = 0.99$) or fungi ($P = 0.14$); PERMANOVA by Adonis) (Fig. 4; Appendix S1: Fig. S2) on either plantation.

## Relationships between the microbial communities and environmental factors

The dominant soil bacteria in both plantations were Acidobacteria (relative abundance = 42%) and Proteobacteria (relative abundance = 31%) (Appendix S1: Fig. S3a, b). The relative abundances of Acidobacteria were higher in the 2-year-old plantation (46%) than in the 6-year-old plantation (38%), in contrast, the Proteobacteria were lower in the 2-year-old plantation (26%) than in the 6-year-old plantation (35%) (Appendix S1: Fig. S3a, b). The relative abundances of both Acidobacteria and

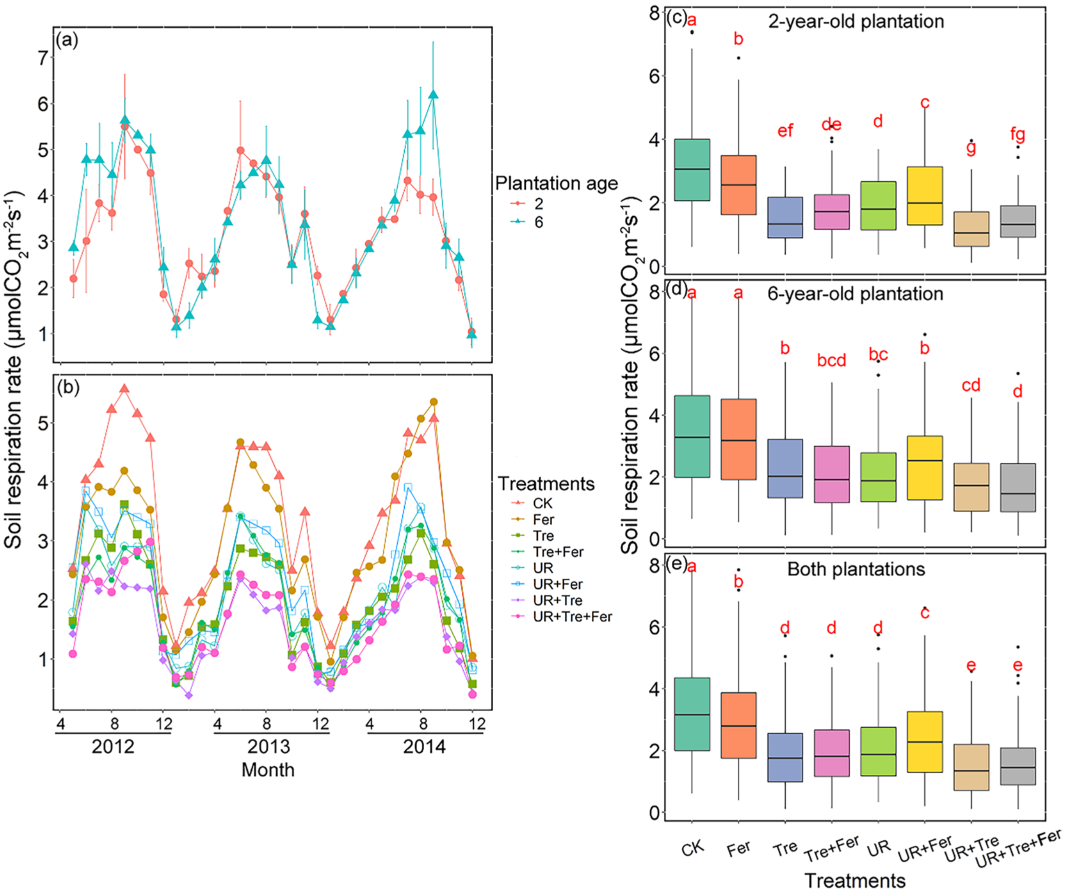

**Fig. 1** Soil respiration dynamics as affected by plantation age (**a**) and treatments (**b**). And effects of different treatments on soil respiration rate in the 2-year-old plantation (**c**), the 6-year-old plantation (**d**), and averaged for both plantations (**e**). Values are means + SE ($n = 3$). For c, d, and e, boxplots indicates the soil respiration rate variation in different treatments (averaged across time). Means in boxes with different lowercase letters are significantly different ($P < 0.05$) between different treatments in the same plantation. CK: the control; Fer: fertilization; Tre: tree root trenching; UR: understory removal; UR + Fer + Tre: combination between understory removal, tree root trenching, and fertilization

Proteobacteria were significantly affected by plantation age ($P < 0.001$), but not by understory removal and tree root trenching ($P = 0.62$ and $P = 0.98$, respectively). The dominant soil fungi in both plantations were Ascomycota (relative abundance = 41%) and Basidiomycota (relative abundance = 46%), and these relative abundances were not significantly affected by plantation age ($P = 0.53$ and $P = 0.64$, respectively), or understory removal and tree root trenching ($P = 0.07$ and $P = 0.05$, respectively) (Appendix S1: Fig. S3c, d).

The relative abundance of Acidobacteria as measured by redundancy analysis (RDA) was positively correlated with SOC, $NO_3^-$-N, TN, and TP, while the relative abundance of Proteobacteria was negatively correlated with soil physicochemical factors (Appendix S1: Fig. S4a). For the Ascomycota, the relative abundance was positively correlated with SM but negatively correlated with $NH_4^+$-N, AP, $NO_3^-$-N, and TN. The relative abundance of Basidiomycota had positive relationships with these factors (Appendix S1: Fig. S4b). On the whole, the composition of the soil microbial community was mainly affected by SOC, $NO_3^-$-N, and TN.

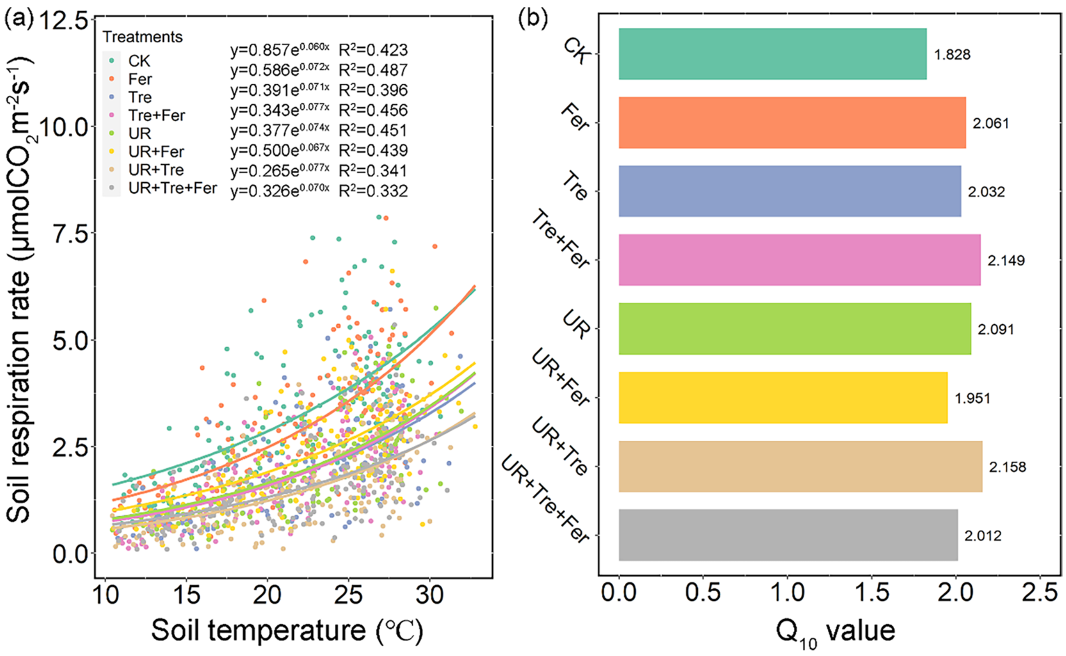

**Fig. 2** Effects of treatments on exponential relationships between soil respiration and soil temperature (**a**), and temperature sensitivity ($Q_{10}$) values (**b**). The linear equation, $R^2$, and $Q_{10}$ values are shown in the figure. CK: control; Fer: fertilization; Tre: tree root trenching; UR: understory removal; UR + Fer + Tre: combination between understory removal, tree root trenching, and fertilization

### Relationships between soil respiration and environmental factors and soil microbial diversity

Variance partitioning analysis (VPA) was used to explore the power of environmental factors on soil respiration, and showed that soil respiration was affected by Eucalyptus plantation age (0.32), understory removal (-0.15), tree root trenching (-0.50), soil temperature (0.13), and microbial diversity (-0.14), SOC (0.17), $NO_3^-$ -N (-0.17), TP (0.50) and AP (0.19) (Fig. 5). Among these factors, plantation age, soil microclimate, and soil physicochemical properties had positive effects on soil respiration, while understory removal, tree root trenching, and bacterial diversity had negative effects on soil respiration. The adjusted $R^2$ of the model was 0.50 (Fig. 5).

## Discussion

In this study, we divided the Eucalyptus plantations into understory and canopy plant functional groups by understory removal and tree root trenching. The effects and potential mechanisms of plant management on soil respiration were explored. We found that both understory removal and tree root trenching reduced soil respiration. Soil environmental factors and microbial communities also regulated soil respiration in both young and old plantations. Our study provides a comprehensive understanding of how the changes in plant functional groups influence soil respiration in forests through both biotic and abiotic factors.

### Effects of understory removal and tree root trenching on soil respiration

Researchers have found that the functional groups of canopy trees and understory plants strongly affect the turnover of soil C in forest ecosystems (Wardle et al. 1999; Binkley et al. 2006; De Deyn et al. 2008; Clemmensen et al. 2013; Chen et al. 2016). In this study, we found that the removal of the understory plants and tree root trenching both significantly, and independently, reduced the soil respiration rate in the Eucalyptus plantations. This negative effect was

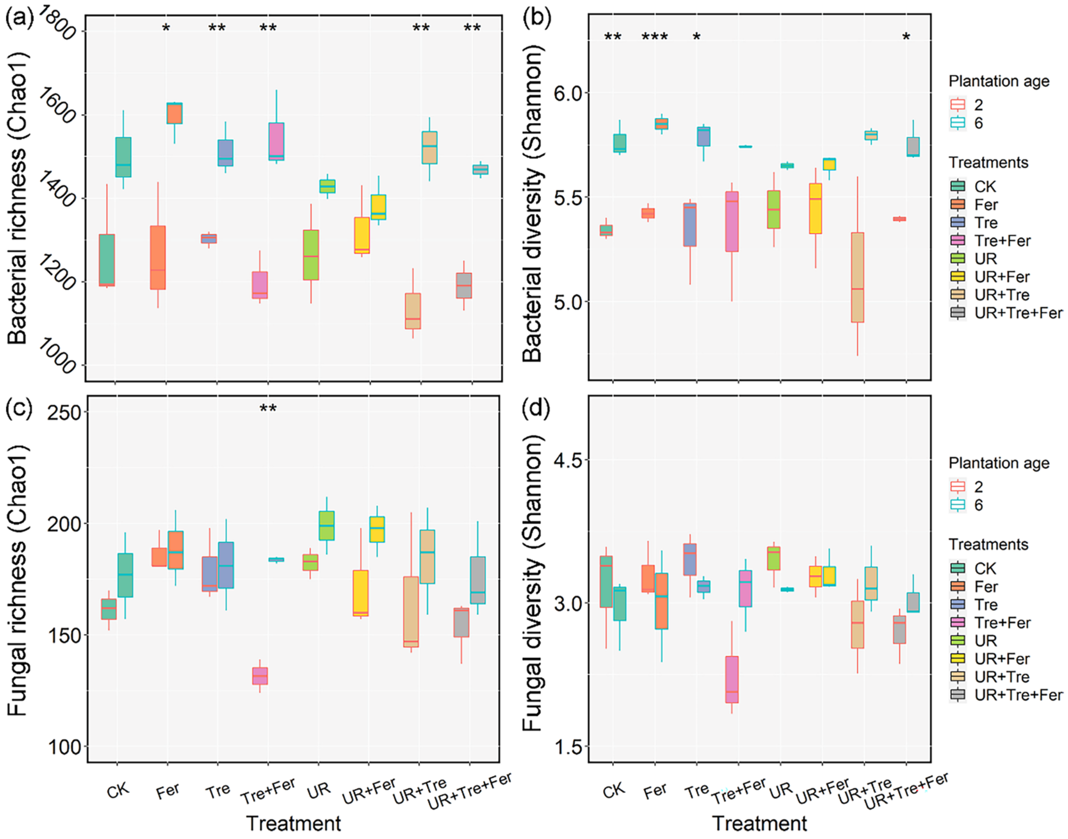

**Fig. 3** Soil microbial diversity of bacteria (**a**, **b**) and fungi (**c**, **d**) at the end of the experiment as affected by plantation ages and treatments. CK: control; Fer: fertilization; Tre: tree root trenching; UR: understory removal; UR + Fer + Tre: combination between understory removal, tree root trenching, and fertilization. Boxplots are explained in Fig. 1. Within each treatment, *, **, and *** indicate significant differences between the 2- vs. 6-year-old plantations at $P < 0.05$, $< 0.01$, and $< 0.001$, respectively

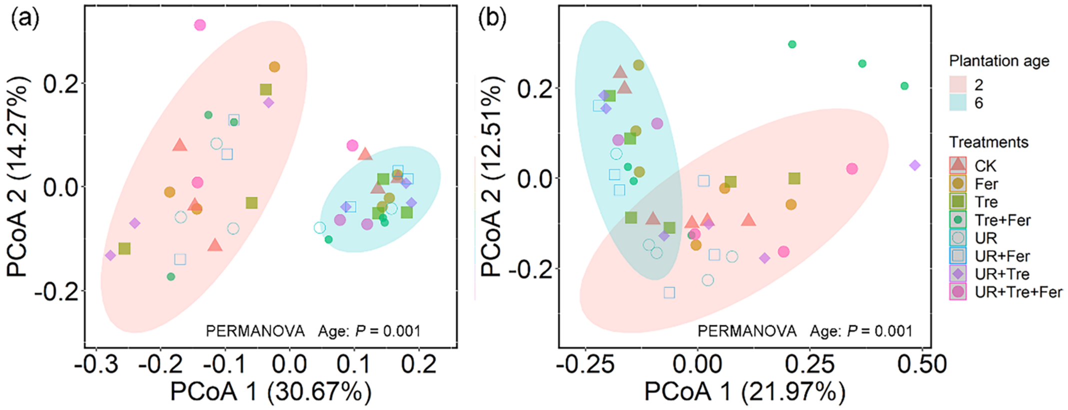

**Fig. 4** Community composition of soil bacterial (**a**) and fungi (**b**) as affected by plantation ages and treatments as indicated by PCoA analysis and PERMANOVA analysis. CK: control; Fer: fertilization; Tre: tree root trenching; UR: understory removal; UR + Fer + Tre: combination of understory removal, tree root trenching, and fertilization

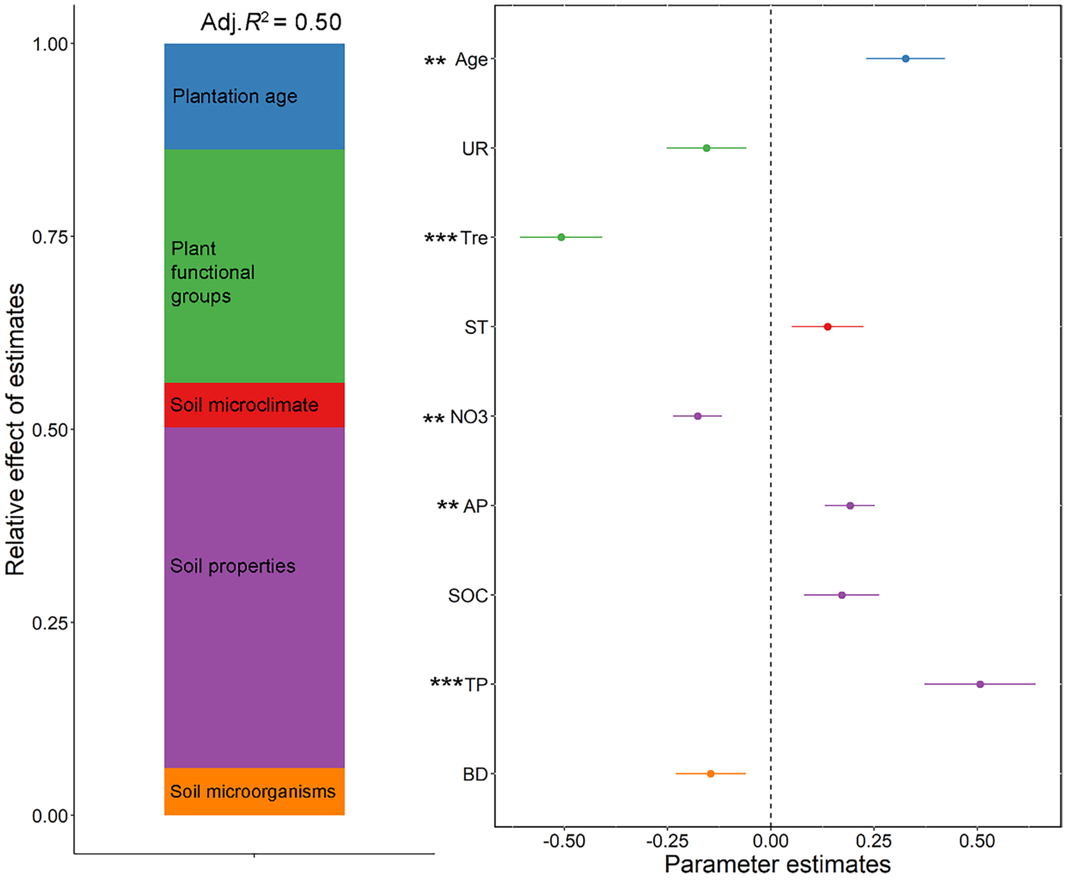

**Fig. 5** Variance partitioning analyses of the relationships among soil respiration, treatments, and other soil factors. Age: plantations age; UR: understory removal; Tre: tree root trenching; ST: soil temperature; SOC: soil organic carbon; $NO_3^-$-N: nitrate nitrogen; AP: available phosphorus; TP: total phosphorus; BD: bacterial diversity. ** and *** indicate significant effects at $P < 0.01$ and $< 0.001$, respectively

amplified when both tree roots and understory plants were removed in the same subplot and was consistent with the results obtained in a mixed subtropical plantation (Wang et al. 2011), a Eucalyptus plantation (Wu et al. 2011a) and a Tibetan subalpine ecosystem (Li et al. 2018). Recent studies have also indicated the profound effects of above-ground PFGs diversity on the carbon exchange of under-ground soil ecosystems, since plant C inputs, soil microbial diversity and community composition, and microclimates are changed after the loss of PFGs (Fanin et al. 2019; Delgado-Baquerizo et al. 2020; Gonzalez et al. 2020; Prager et al. 2021).

Soil fertilization with urea did not significantly affect soil respiration in our experiment. Other experiments have shown that soil respiration had hysteresis and threshold effects in response to N enrichment (Contosta et al. 2011; Du et al. 2018; Zhang et al. 2021), therefore the absence of a significant effect of fertilization indicated that long-term investigation would be needed in the field experiments. Our variance partitioning analysis also confirmed that microclimate, soil microorganisms, and soil physicochemical factors interactively affect soil respiration.

We noted that there was a decrease in soil microbial diversity after the removal of aboveground plant biodiversity and suggested this explained the soil respiration differences (Wardle et al. 2008; Strecker et al. 2016; Chen et al. 2019a; Bastida et al. 2021). The explanation was that the PFGs removal leads to reduce the inputs of litter and root exudates from plants, resulting in the reduction of SOC and consequently decreased soil respiration (Wu et al. 2011b; Winsome et al. 2017; Fanin et al. 2019). In our experiment, the SOC content was reduced under the combined effects of understory removal and tree root trenching, which supported our deduction. Soil respiration with understory removal and tree root trenching treatment, which was similar to the heterotrophic respiration, had lowest mean values in both plantations also indicated that soil microorganisms prefer to use fresh carbon from photosynthesis (Chen et al. 2016; Machmuller et al. 2018). This indicated the tight link between above- and below-ground organisms (Clemmensen et al. 2013; Chen et al. 2019b; Yang et al. 2020; Bastida et al. 2021). Furthermore, our experimental results showed that the difference in the microbial diversity was dependent on the plantation age, with the 2-year-old plantation having lower diversity than the 6-year-old plantation. This could explain why the reduction in soil respiration after the loss of PFGs was greater in the young plantation than in the old one. Since the decreases of plant carbon inputs would limit the activities of soil microorganisms (Wu et al. 2013).

## Plantation age affects soil respiration

Our results indicated that the variation in soil respiration over time in Eucalyptus plantations of different ages was mainly related to seasonal microclimatic factors and especially soil temperature, with higher respiration rates in the summer. Other studies such as in subtropical pine plantations (Yu et al. 2019) and tropical forests (Machmuller et al. 2018; Waring et al. 2021) have also found that soil respiration was highest in the summer and was lowest in the winter. In addition, soil respiration was greater in the older than in the younger plantation, which is similar to previous results found in loblolly pine plantations (Wiseman and Seiler 2004) and Massoniana plantations (Yu et al. 2019). The average soil respiration in the 6-year-old plantation was more than three times higher than the soil respiration in the 2-year-old plantation. The first reason would be higher soil C metabolic activities in the older Eucalyptus plantation than in younger, which was supported by another study in a Eucalyptus plantation in a subtropical region (Chen et al. 2013). Second, the forest microclimate had a significant impact on soil respiration (Ma et al. 2014; Giuggiola et al. 2018; Bertrand et al. 2020; Zellweger et al. 2020). For example, we found that the higher plant coverage in the 6-year-old plantation than in the 2-year-old plantation (Fan et al. 2015), would input more plant-induced C from aboveground plants and contribute to the higher soil respiration. The higher soil respiration in the old plantation would lead to a negative effect on soil C storage. Our previous study also indicated that soil organic C storage decreased by 6.7% per year following the establishment of Eucalyptus plantations (Wu et al. 2013).

Studies in both natural forests and plantations have shown that forest type and plantation age greatly affect soil microbial communities (Waldrop et al. 2006; Peerawat et al. 2018; Liu et al. 2019; Wan et al. 2021). In our study, we found that both soils bacterial and fungal diversity was lower in the 2-year-old plantation than in the 6-year-old plantation. Previous reports indicate that soil respiration increases with increasing SOC contents (Wiseman and Seiler 2004). In contrast, we found that SOC content was lower but soil respiration was higher in the 6-year-old plantation, compared to in the 2-year-old plantation. The potential reason could be that soil C content was correlated to the diversity of soil microorganisms, which was higher in the 6-year-old plantation. Clemmensen et al. (2015) also found that lower soil C sequestration was linked to a higher abundance of the mycorrhizal fungi in early successional-stage boreal forests. Our finding is consistent with research on global patterns of soil bacterial diversity (Delgado-Baquerizo et al. 2016b), who found higher soil microbial diversity can respire more soil carbon. Taken together, our finding indicated that SOC content was lower and soil microbial diversity was higher in the older plantation when compared with the younger plantation. These findings were supported by the view that soil respiration increased with the diversity of soil microorganisms (Malik et al. 2018; Waring et al. 2021).

## Conclusions

Through 3-year field experiments, our study had three main findings. First, the management of different plant functional groups, i.e., understory removal and tree root trenching caused changes in soil microorganisms that reduced the soil carbon emission. Both soil nutrients and temperature after plant management contributed to the outputs of soil carbon emission. Second, fertilization had no obvious effect on soil carbon emission in either of the Eucalyptus plantations, indicating that a longer duration for field experiments is needed in the future. Third, the soil respiration rate was higher in the older Eucalyptus plantation than in the younger Eucalyptus plantation, mainly because of higher soil microbial diversity and differences in their community composition. The implication of our findings is that PFGs removal or biodiversity reduction would decrease soil respiration in afforested plantations, but we should take into account the cascade effects from above- to below-ground in the context of land-use change when conducting plant management.

**Acknowledgements** This work was supported by the National Natural Science Foundation of China (Grant No. 31971497;31160153), the Xingdian Scholar Fund of Yunnan Province, the Scientific Research Fund Project of Yunnan Education Department (Grant No. 2023Y0195), the Double Top University Plan Fund of Yunnan University, and the Yunnan University's Research Innovation Fund for Graduate Students (Grant No. 2021Y040).

**Author contribution** Jianping Wu and Wenfei Liu acquired funding and designed the experiment. Bin Wu and Jianping Wu analyzed the data and led the writing of the manuscript. Wenfei Liu, Ying Wu, and Jill Thompson contributed critically to the reviewed and edited manuscript. All authors jointly contributed to the final version.

**Data availability** The data and code (Wu et al. 2022) will be available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w6m905qq4.

**Declarations**

**Conflict of interest** The authors have no conflict of interest to declare.

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