

Stronger effects of termites than microbes on wood decomposition in a subtropical forest

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ABSTRACT

Deadwood contains a sizeable proportion of total forest C, and its decomposition transfers organic C to the atmosphere, other organisms and soils. Microbes have traditionally been thought to be the primary drivers of wood decomposition worldwide, but few studies have tested the relative importance of termites to this process. The aim of this study was to compare the relative contributions of microbes and termites to wood (*Cinnamomum camphora*) decomposition by conducting a field experiment of termite access (with and without termite exclusion) and soil contact (with and without soil contact) treatments in subtropical China. After a two-year period, termites were responsible for an estimated 55.7% and 48.9% of observed wood loss from wood blocks with and without soil contact, respectively. Wood in direct contact with the soil decomposed 1.4 times as fast as wood separated from the soil. Our results show that termites can exceed microbes in importance to wood decomposition in subtropical forests and highlight the importance of soil contact in determining decay rates.

1. Introduction

Forests around the world store a large amount of carbon (C) in soils and dead and living above-ground biomass (including deadwood), which is regarded as a significant C sink (Pan et al., 2011). Deadwood contains about 73 ± 6 Pg of carbon (C) globally (Pan et al., 2011). Understanding the factors that influence rates of C cycling in forests (including wood decomposition) is necessary to quantify the role of forests in the global C cycle (Pan et al., 2011; Intergovernmental Panel on Climate Change, 2014; Tang et al., 2018).

The rate by which wood decomposes varies greatly among and within regions depending on numerous abiotic and biotic factors (Bradford et al., 2014). Although climatic conditions and wood traits set limits on how quickly wood decomposition can proceed, the activities of microbes, insects, and other organisms within deadwood are what ultimately drives this process. Fungi produce the enzymatic machinery

necessary to break down lignocellulose and are generally believed to contribute the most to wood decomposition, although insects are also thought to play an important role (Cornwell et al., 2009; Ulyshen, 2016; Andringa et al., 2019; Wu et al., 2020). Mechanisms by which insects may affect wood decomposition include direct consumption and digestion, substrate alteration (e.g., fragmentation and tunneling), and interactions with bacteria, fungi, and other members of the saproxyllic community (Ulyshen, 2016; Andringa et al., 2019). In addition, wood-dwelling insects also have the potential to affect nitrogen (N) dynamics in decomposing wood by accelerating N fixation and by promoting the release of nutrients immobilized in fungal tissues (Ulyshen, 2015).

Among macro-invertebrates that may affect wood decomposition, termites probably contribute more to wood loss globally than all other insects, although they are primarily limited to relatively warm, moist regions. Recent work suggests that termites may even exceed microbes

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in importance in some regions (Jacobsen et al., 2018; Griffiths et al., 2019; Garrick et al., 2019). However, the relative importance of microbes and insects to wood decomposition remains unknown for much of the world (Dossa et al., 2020). We are far from fully understanding how interactions between these organisms, as well as with wood properties and soils, affect decay rates (Mäkipää et al., 2017; Stutz et al., 2019; Čuchta et al., 2019; Purahong et al., 2019).

Soil contact is known to promote wood decomposition (Gora et al., 2019), but few experiments have explored this question as it relates to both insect and microbial activity (Dossa et al., 2020). As separation from the soil is likely to reduce wood moisture content, both insects and microbes are likely to benefit from direct soil contact (Mäkipää et al., 2017; Law et al., 2019). Many termite species do not nest within their feeding substrate and colonize wood through the soil (Wood, 1978; Wood and Sands, 1978; Takamura, 2001; Dossa et al., 2020) and soil contact will likely favor these organisms. Wood decomposing fungi are also often closely linked to the soil, with some species forming thick cords of hyphae that connect wood to external sources of nutrients through the soil (Boddy, 1999).

In this study, we designed a field experiment to test the relative contributions of macro-invertebrates (termites) and microbes to the decay of wood with soil contact (WSC) and without soil contact (NSC) in a subtropical forest. The specific hypotheses we tested were: 1) termites significantly accelerate wood decomposition; 2) direct soil contact promotes decomposition and is particularly important for termite colonization; 3) termites can contribute more to wood decomposition than microbes.

2. Materials and methods

2.1. Study area

This field study was conducted in a broad-leaved mixed subtropical forest (BLF) at Lushan Mountain in Jiangxi Province of subtropical China (29°31'~29°41' N, 115°51'~116°07' E). The field research area is characterized by a subtropical monsoon climate with four distinct seasons. The mean annual precipitation and temperature range from 1308 to 2068 mm, and from 17.1 to 11.6 °C, respectively (Wu et al., 2018a). The monthly rainfall and air temperature during the decomposition period are given in Appendix 1. According to the FAO soil classification, soil types in Lushan change from ferric to haplic alisols with increasing elevation. Deciduous and evergreen trees grow at the middle altitudes (600–1000 m), including *Platycarya strobilacea*, *Acer davidii*, *Cinnamomum camphora*, *Diospyros kaki* and some deciduous woodland species and shrubs. In addition, some *Cryptomeria japonica* plantations were established about 50 years ago within this elevation zone (Wu et al., 2018b). *Lindera obtusiloba* forests, which include *Cerasus serrulata*, *Castanea seguinii*, *Tilia breviradiata*, and a few shrubs, occur at about 1200 m above sea level (Wu et al., 2019b). The dominant termite communities are *Reticulitermes longicephalus* Tsai et Chen, *Reticulitermes leptomandibularis* Hsia et Fan, *Procapritermes mushae* Oshima et Maki, and *Procapritermes sowerbyi* (Light) (Shi, 1983).

2.2. Experiment design

Our experiment was carried out from January 2017 to December 2018. Within an area of two ha, four 20 × 20 m plots were established and spaced at least 50 m apart. Untreated wood blocks (hereafter 'blocks') of *Cinnamomum camphora* were used to assess decomposition in this study. This species was chosen because it is a common component of subtropical forests in China and the wood needed for the experiment was readily available. The blocks were about 9 cm × 9 cm × 5 cm in size, which is within the diameter range of small coarse woody debris (see Harmon et al., 1986; Palace et al., 2012). Blocks with deformations or knots were discarded. Initial wood mass of all blocks was measured after drying at 60°C for 72 h, and then each block was enclosed with 300-µm

nylon mesh bags. Half the mesh bags had ten holes of 1 cm on both sides and were thus 'open' to the colonization of termites and other fauna (hereafter OMT: open bags) (Cheesman et al., 2018; Griffiths et al., 2019; Law et al., 2019). The remaining bags were completely 'closed' (hereafter CMT: closed bags) to termites but were still accessible to microbes. The mesh bags' edges were sealed with large stainless-steel staples and folded several times to prevent termites and other macro-invertebrates from entering through the ends. We used plastic sheets to separate half of the blocks from the soil within each sample plot to manipulate soil contact. Blocks randomly assigned to this 'no soil contact' (hereafter NSC: without soil contact) treatment were placed individually on a white polyethylene plastic sheet measuring 15 cm (length) × 15 cm (width) × 10 mm (thickness). The remaining half of the blocks were placed in direct contact with the forest floor (hereafter WSC: with soil contact). We placed a total of twenty blocks in each of the four plots, five blocks for each treatment combination. Blocks were randomly assigned to treatments and arranged in a grid (2 mesh type × 2 soil contact type × 5 repeated segments = twenty grids) within each plot, with a 400 cm × 500 cm separation (400 cm × 5 repeated segments = 20 m, 500 cm × 4 treatments = 20 m) between each block. Because termites are the dominant wood-feeding insects throughout much of the tropics and subtropics and the lack of bark would have excluded many other wood-feeding insects, differences in decay rates between open and closed bags are assumed to be the result of termite activity (Cheesman et al., 2018; Griffiths et al., 2019; Law et al., 2019). After 24 months in the field, samples separate into two portions. One portion (about 20 g) was stored at -20 °C to quantify microbial biomass. The other portion was used to measure wood fauna and dried at 60 °C for five days to measure moisture content. The final dry wood mass was calculated by those two portions. We dissected blocks from the open bag treatments and removed all soil translocated into the wood by termites as well as termite fecal material before measuring final dry wood mass. The initial physicochemical properties of soil and wood used in this study are given in Appendices 2 and 3, respectively. The physical properties of wood at the end of the experiment are given in Appendix 4.

2.3. Phospholipid fatty acid (PLFA) analyses

To qualify microbial biomass at the end of the study, and to better understand the role of microbes in wood decomposition, we performed phospholipid fatty acid analysis (PLFA) after storing samples at -20 °C. Concentrations of each PLFA were calculated relative to the 19:0 internal standard concentration. We calculated microbial biomass (ng g⁻¹ dry wood material) for the following taxonomic groups as distinguished by fatty acid biomarkers: bacteria (B), fungi (F), Gram-negative bacteria (G⁻), Gram-positive bacteria (G⁺), actinomycetes (ACT) and arbuscular mycorrhizal fungi (AMF) (Appendix 5) (Olsson et al., 1999).

2.4. Wood fauna extraction

Wood fauna were extracted from wood immediately after returning the blocks from the field using the dry funnel method at the end of the study period (Crossley and Blair, 1991). To extract wood fauna, the collected wood was removed from mesh bags and added to Tullgren-funnels (with 5 × 5 mm mesh size) for three days (Carrillo et al., 2011; Wang et al., 2021). Animals were stored in 90% alcohol, counted using a binocular microscope, and identified to three subclass level: Collembola, Termites and Acari (Faber, 1991; Lavelle, 1996; Chomel et al., 2015; Ji et al., 2020; Wang et al., 2021). All other invertebrates were assigned to functional groups according to Moore et al. (2005). Wood fauna proportion is the total abundance of each taxon divided by the total abundance of all fauna on unit dry mass (per gram, g⁻¹) of wood (Ji et al., 2020).

2.5. Data analysis

All data analyses were performed using R (version 3.4.4). Results were determined as significant at $p < 0.05$. The proportional mass loss of each woodblock was calculated using equation (1):

$$\text{Proportional mass loss} = \left(\frac{\text{initial mass} - \text{final mass}}{\text{initial mass}} \right) \quad (1)$$

To account for differences among wood proportional mass loss of different wood blocks, we transformed wood mass loss data using natural logarithm, which was recommended for proportional data (Warton and Hui, 2011). Soil contact type (e.g., with or without soil contact), mesh type (e.g., open or closed bags), and their interaction on the wood proportional mass loss, microbial community and wood fauna were tested using two-way ANOVAs.

To further determine the relative contributions of termite and microbes to wood decomposition, we first calculated the mean wood proportional mass loss of closed bags and open bags with and without soil contact for each sample plot. We assumed that decomposition in closed bags was mostly attributed to microbes (although microfauna and mesofauna may also contribute to decay), and that wood decay in open bags was attributed to both termites (macro-invertebrates) and microbes (Cheesman et al., 2018; Griffiths et al., 2019; Law et al., 2019). Therefore, the proportion of wood mass loss attributed to termites was calculated by subtracting the mean proportional mass loss (mean \pm standard error) in closed bags from the mean proportional mass loss in open bags and then divided by the mean proportional mass loss in open bags.

3. Results

3.1. Wood decomposition

We found both the mesh type ($p < 0.001$) and soil contact type ($p < 0.001$) strongly affected wood decomposition in this study, and there was no significant ($p = 0.062$) interaction between the two treatment factors (Fig. 1). Open bags lost significantly (Tukey HSD, $p < 0.001$) more mass than closed bags regardless of soil contact type (Fig. 1). Similarly, wood with soil contact (WSC treatment) lost significantly

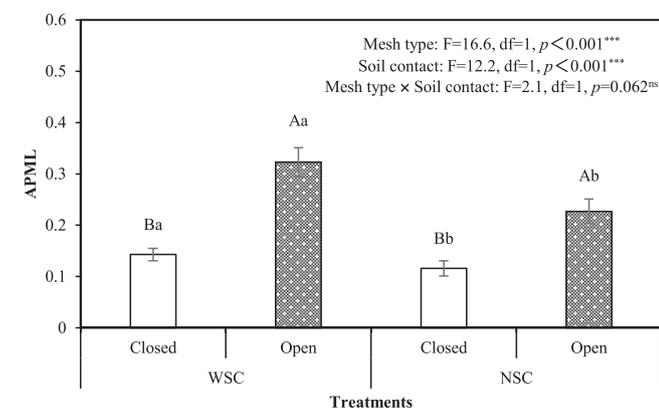


Fig. 1. Two-year average proportional mass loss of wood (APML) in the coniferous-broad-leaved mixed subtropical forest; values are means \pm SE for $n = 4$. For each soil contact type: mean proportional mass loss was calculated as the sum of the proportional mass loss of blocks within each plot divided by the number of blocks within each plot, $n = 4$ plots. Note: mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC). Different uppercase letters indicate significant differences among different mesh types (e.g., open vs. closed) of the same soil contact (e.g., WSC or NSC) at $p < 0.05$. Different lowercase letters indicate significant differences among different soil contact types for the same mesh type ($p < 0.05$). ns not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

more mass than wood separated from soil (NSC treatment) regardless of mesh type (Fig. 1). After two years, wood with and without soil contact lost $32.3 \pm 2.8\%$ and $22.7 \pm 2.4\%$ mass in open bags, and $14.3 \pm 1.2\%$ and $11.6 \pm 1.5\%$ wood mass in closed bags, respectively (Fig. 1). As a result, being in contact with the soil resulted in 1.42 and 1.23-fold greater mass loss compared to blocks separated from the soil for open bags and closed bags, respectively.

For closed bags (i.e., the colonization of macro-invertebrates was excluded), the wood mass loss attributed to microbes with soil contact was significantly (Tukey HSD, $p = 0.028$) higher than that under without soil contact (Fig. 2). Similarly, for open bags (i.e., the colonization of macro-invertebrates was allowed), the effect of termites on wood decomposition was also enhanced by the direct soil contact, with mass loss from wood with soil contact being significantly higher than wood without soil contact (Tukey HSD, $p < 0.001$).

For open bags where both termite and microbes affected wood decomposition, the relative contributions of termites and microbes to mass loss also depended on soil contact type. When wood was placed in direct contact with soil, termites exceeded microbes in importance, with their relative contributions to mass loss being $18.0 \pm 2.1\%$ (32.3% with open bags minus 14.3% with closed bags) and $14.3 \pm 1.2\%$ (closed bags), respectively. When wood was not placed in direct contact with soils, both microbes and termites contributed similarly to wood decomposition, with their relative contributions to the mass loss being $11.6 \pm 1.5\%$ (22.7% with open bags minus 11.1% with closed bags) and $11.1 \pm 0.8\%$ (closed bags), respectively (Fig. 1, Fig. 2). In other words, we found a significantly larger contribution from termites (55.7% mass loss) than microbes (44.3%) under with soil contact treatment (Tukey HSD, $p < 0.001$), and a smaller, but statistically similar, contribution from termite (48.9%) than microbes (51.1%) under without soil contact treatment (Fig. 2).

3.2. Microbial community composition

Soil contact (with soil contact vs. without soil contact) had significant effects on the concentrations of total PLFA, total bacteria, total fungi, G^+ bacteria, G^- bacteria, fungi, and AMF of the studied wood, with higher values observed with soil contact than without soil contact

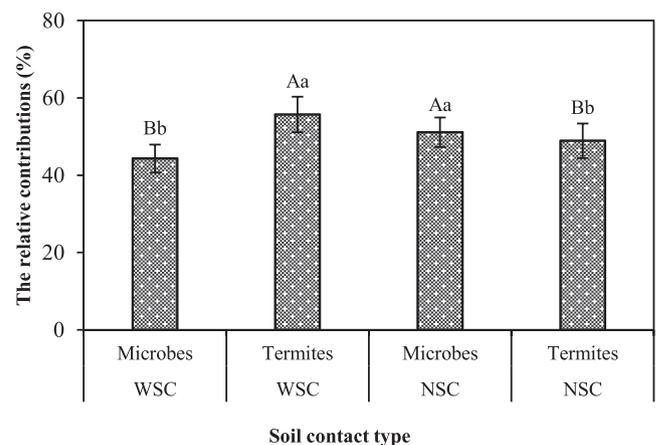


Fig. 2. The relative contributions (%) from microbes and from termites. The decomposition of closed blocks has been attributed to microbes (although microfauna and mesofauna may also contribute to decay), whereas decomposition attributed to termites has been calculated by the mean proportional mass loss of open blocks minus the mean proportional mass loss of closed blocks. Note: mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC). Different uppercase letters indicate significant differences among different decay agents (termites or microbes) of the same soil contact (e.g., WSC or NSC) at $p < 0.05$. Different lowercase letters indicate significant differences among different soil contact types for the same decay agent ($p < 0.05$).

Table 1

The phospholipid fatty acid (PLFA) (mean \pm SE; ng g⁻¹ dry wood material) signatures of the studied wood in the coniferous-broad-leaved mixed subtropical forest; values are means \pm SE for n = 4. Note: mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC). Different uppercase letters indicate significant differences among different mesh types (e.g., open vs. closed) of the same soil contact (e.g., WSC or NSC) at $p < 0.05$. Different lowercase letters indicate significant differences among different soil contact types for the same mesh type ($p < 0.05$). Total, total PLFA concentrations; B, bacterial PLFAs; F, fungal PLFAs; F/B, the fungal to bacterial ratio; G⁺, Gram-positive bacteria; G⁻, Gram-negative bacteria; G⁺/G⁻, ratio of Gram-positive to Gram-negative bacteria; AMF, arbuscular mycorrhizal fungi.

Soil contact	Mesh type	AMF	Fungi	Total Fungi	G ⁺	G ⁻	Total B	Total
WSC	Closed	12.2 \pm 2.1 Aa	45.5 \pm 5.5 Aa	57.7 \pm 6.3 Aa	10.8 \pm 2.6 Aa	15.5 \pm 3.8 Aa	26.3 \pm 5.4 Aa	94.1 \pm 10.7 Aa
	Open	12.6 \pm 1.9 Aa	45.8 \pm 5.1 Aa	58.4 \pm 5.9 Aa	11.1 \pm 2.2 Aa	15.7 \pm 3.2 Aa	26.8 \pm 6.1 Aa	94.9 \pm 12.2 Aa
NSC	Closed	6.3 \pm 1.7 Ab	31.5 \pm 5.1 Ab	37.8 \pm 7.1 Ab	8.7 \pm 1.4 Ab	11.1 \pm 2.1 Ab	19.8 \pm 2.5 Ab	66.2 \pm 9.9 Ab
	Open	6.5 \pm 2.7 Ab	31.8 \pm 4.6 Ab	38.3 \pm 6.8 Ab	8.9 \pm 1.1 Ab	11.4 \pm 1.8 Ab	20.3 \pm 1.9 Ab	66.8 \pm 9.1 Ab

(Table 1). However, mesh type (open bags vs. closed bags) had no effect on the microbial community (Table 1). In addition, the concentrations of fungal components (total fungi, fungi and AMF) of the studied wood were generally higher than that of bacteria components (total bacteria, G⁺ bacteria and G⁻ bacteria) (Table 1).

3.3. Fauna composition and abundance

We calculated wood fauna proportion as the total abundance of each taxon divided by the total abundance of all wood fauna on unit dry wood mass (per gram). In all plots, wood fauna was dominated by termites (Open bags: 52.34% and 25.82% with and without soil contact, respectively; Closed bags: None), Acari (Open bags: 29.53% and 12.56% with and without soil contact, respectively; Closed bags: 18.54% and 6.14% with and without soil contact, respectively) and Collembola (Open bags: 15.20% and 8.42% with and without soil contact, respectively; Closed bags: 4.52% and 1.94% with and without soil contact, respectively) (Fig. 3). Overall, the abundances of termites, detritivorous mites, collembola, herbivores and predators were higher for open bags and with soil contact (Fig. 3). Wood in open bags had 4.04- and 5.51-fold greater faunal abundance than closed bags with and without soil contact, respectively (Fig. 3). Wood with soil contact had 2.03- and 2.76-fold greater faunal abundance than wood without soil contact for

open bags and closed bags, respectively (Fig. 3).

Since open bags allowed the colonization of macro-invertebrates (dominated by termites in this study), both termites and microbes contributed to wood decomposition. Similarly, because closed bags excluded termites, microbes were primarily responsible for wood decomposition.

4. Discussion

This study represents the first attempt to experimentally disentangle the relative effects of soil contact, termites, and microbes on wood decomposition in a subtropical forest. We found that open bags lost significantly more mass than closed bags (Fig. 1). Since open bags allowed the colonization of macro-invertebrates (dominated by termites in this study), the result supported our first hypothesis that termites significantly accelerate wood decomposition. Previous studies also reported that the decay rate of wood was affected by termites in subtropical forests (Liu et al., 2015; Dossa et al., 2020). In open bags both termites and microbes contributed to wood decomposition. Therefore, we must acknowledge that the termite effect detected in our study might also include the possible superposition effect of soil microbes and termites.

We found that soil contact (the WSC treatment) resulted in 1.42 and

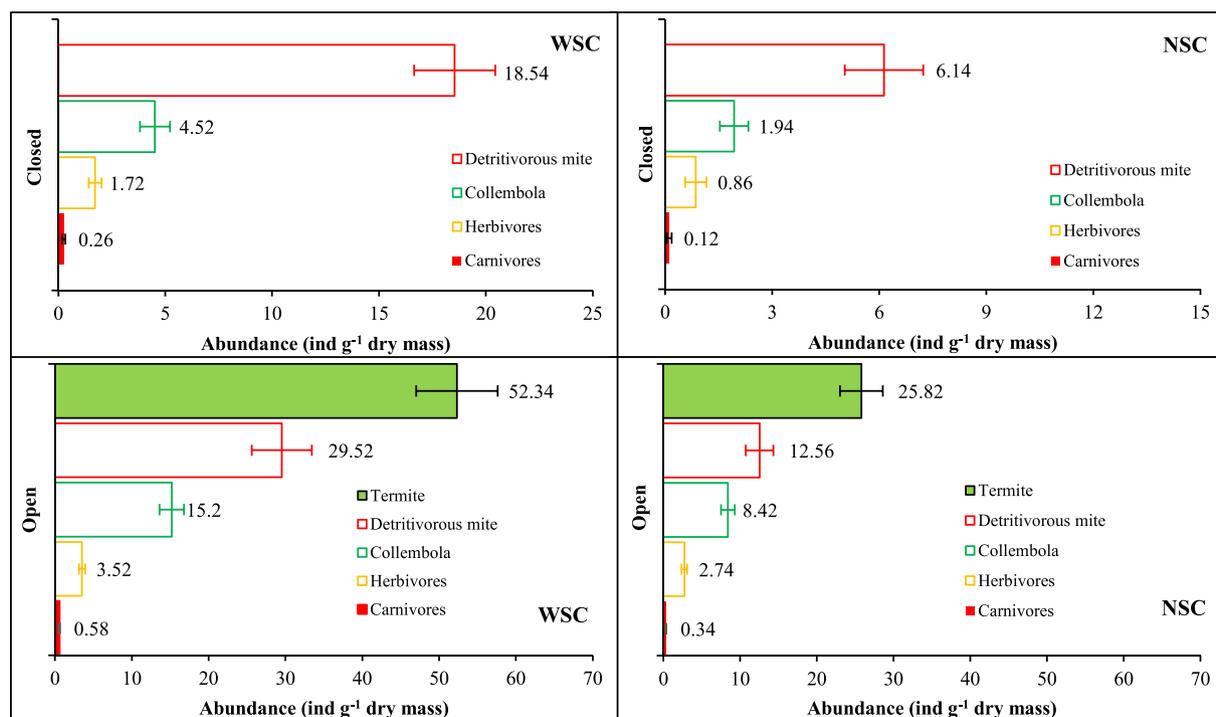


Fig. 3. Change in abundance of wood fauna functional groups present in the studied wood in the coniferous-broad-leaved mixed subtropical forest. Note: mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC).

1.23-fold greater mass loss compared to without soil contact (the NSC treatment) for open and closed mesh bags, respectively. Similarly, previous study also reported that direct contact with soils greatly enhances the decomposition of wood (Mäkipää et al., 2017; Law et al., 2019), which is responsible for a large amount of carbon flux from wood to the atmosphere and thereby regulates the global carbon cycle (Law et al., 2019). Our study confirmed that termite abundance in wood with soil contact was significantly higher than in wood without soil contact (Fig. 3). By placing wood on plastic sheets (e.g., without soil contact), we separated wood from the community of biotic decomposers active in the soil (Jacobsen et al., 2018; Law et al., 2019). Compared to the wood with direct soil contact, the wood separated from soil would be less likely discovered and colonized by both termites and microbes as these organisms are largely soil-dwelling (Lu et al., 2013; Mäkipää et al., 2017; Fukasawa et al., 2018; Law et al., 2019; Wu et al., 2019a; Čuchta et al., 2019; Dossa et al., 2020). These results supported our hypothesis that direct soil contact promotes decomposition and is particularly important for termite colonization.

We found that termites' relative contribution to wood decomposition with soil contact was larger when compared to that without soil contact (Fig. 2). Under the combination treatment of open bag and with soil contact, termites contributed about 56% of wood loss (Fig. 2). The result supported the hypothesis that termites can contribute more to wood decomposition than microbes. Furthermore, our study also found that soil contact type had significant effects on microbial community, with higher microbial biomass observed from wood with soil contact than in wood separated from the soil, especially for fungal components (Table 1). Previous studies indicated that microorganism communities play a key role in driving wood decomposition (Fukasawa et al., 2018; Wu et al., 2020). Therefore, our results suggest that the effects of wood on C and nutrient cycles in subtropical forests would be greatly enhanced by termites, especially when wood is in direct contact with soils. Termites can contribute more to wood decomposition than microbes.

The interactions between fungi and termites and transfer of decomposers between soils and wood with soil contact may act in concert to enhance wood decomposition (Kirker et al., 2012; Mäkipää et al., 2017; Cheesman et al., 2018; Stutz et al., 2019; Čuchta et al., 2019). For example, wood decayed by fungi can be attacked more readily by termites compared to undecomposed wood, possibly due to an increase in its nutrient availability and values (Waller et al. 1987; Cheesman et al., 2018; Griffiths et al., 2019). Previous studies also indicate that higher trophic levels (i.e. meso- and macro-fauna, including termites and mites) can contribute to the interaction between dead materials and microbial decomposer, and then accelerate the decay rate of dead materials (Milcu and Manning, 2011; Perez et al., 2013). In this study, wood blocks with soil contact hosted greater numbers of soil fauna and microbes (Table 1 and Fig. 3). For example, the abundance of termite and detritivorous mites greatly increased in wood blocks with soil contact compared to without soil contact (Fig. 3), and the microbial community of wood blocks with soil contact was also higher than without soil contact (Table 1), resulting in faster decomposition of wood blocks with soil contact treatment than without soil contact treatment. Therefore, our study demonstrated that soil contact, termites, and microbes all contributed significantly to wood decomposition, thereby affecting C and nutrient cycles in subtropical forest ecosystems. Finally, our study reinforces the view that both microbial-mediated and arthropod-mediated decay are important to wood decomposition, with important implications for the carbon cycle.

The generalization of our results may be limited given that we only studied one species (*C. camphora*) and the wood traits of this studied species (e.g., nutrient content and density) are likely differ from other species. For example, *C. camphora* is characterized by low wood density (Appendix 3) and may decompose faster by termites and microbes when compared to other species with higher density (Liu et al., 2015; Wu et al., 2019b; Dossa et al., 2020; Ulyshen et al., 2020). Additionally, our

studied species itself or its extracts attract insect colonization and thus accelerate wood decomposition (Wu et al., 2019b). Moreover, it is possible that insects may contribute even more to decomposition than our results indicate given the absence of bark from our blocks may have excluded many species of phloem feeding insects (Ulyshen and Wagner, 2013; Ulyshen et al., 2016; Dossa et al., 2018; Griffiths et al., 2019; Law et al., 2019). Therefore, future studies are necessary to determine whether our results are generally applicable to other species in subtropical forests. These studies should be aimed at understanding the roles of soil decomposers and other macro-invertebrates in wood decomposition process for various tree species with different wood traits, wood sizes, and soil properties (Ulyshen, 2016; Procházka and Schlaghamerský, 2019; Harmon et al., 2020; Kapusta et al., 2020).

Our study investigated wood decomposition during a two-year experimental period, which is a relatively short time span considering the turnover time of wood. Long term research would be better suited to determine the relative roles and contributions of microbes and termites in decomposing wood. Mesh bags may not be well suited for such long-term studies, however. They may deteriorate due to photodegradation (especially by UV) (Law et al., 2019) or animal activity and this could limit their value in long-term research. In addition, the potential for mesh bags to alter microclimate and ultimately decay rates remains a major challenge facing decomposition researchers (Kampichler and Bruckner, 2009; Stoklosa et al., 2016; Roh et al., 2018). Consequently, the above problems and possibly others significant challenges for conducting long-term experiments on wood decomposition.

Although mass loss was used to indicate decomposition, it cannot be assumed that all of the mass lost was completely decomposed and mineralized (Prescott et al., 2017). For example, it is possible that some mass loss resulted from the loss of wood material through the holes in the open bags. Similarly, our efforts to remove persistent termite fecal material could also have caused us to somewhat overestimate the contributions of termites to wood decomposition. Moreover, it is not clear how fecal materials may affect wood decomposition.

We must note that although termites have a higher assimilation efficiency than most soil fauna, it is still only about 50%, which means that about half mass of wood was consumed by termites was not decomposed, but rather converted to fecal material (Prescott, 2010; Prescott et al., 2017). In addition, the durability of faunal fecal material is supported by studies in many ecosystems (Wolters, 2000; Osler and Sommerkorn, 2007; Galvana et al., 2008). In this study, the persistence of faunal fecal material in wood could influence the estimates of wood decomposition. Therefore, we have an on-going incubation study to monitor the influence of faunal fecal material on the decomposition of those wood materials used in the study.

Finally, although our study clearly demonstrated a positive effect of soil contact on wood decomposition under our experimental conditions, many more studies may still be required to better understand the impact of soil contact on wood decomposition in forest ecosystems. First, soil contact is only one of many factors affecting wood decomposition, and its effects may vary among field sites, tree species, forest types, and environmental conditions. Second, the treatment effects on wood decomposition may depend on the wood size, and the observed effects in our study were derived from one specific wood size.

5. Conclusion

Our results demonstrate the importance of decomposers' movement from soil to wood, with direct soil contact facilitating decomposition. Furthermore, the relative contributions of termites and microbes to the decomposition of wood was also influenced by soil contact. However, wood blocks exposed to termites decomposed significantly faster than those protected from termites, regardless of soil contact treatment. Therefore, our results confirm the important role of termites and soil contact during the decomposition process. Results from our study should help further understand the relative importance and potential coupling

of major driving forces of wood decomposition in different forest ecosystems.

CRedit authorship contribution statement

Chunsheng Wu: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Writing - original draft, Writing - review & editing. **Michael D. Ulyshen:** Writing - original draft, Writing - review & editing. **Chunjie Shu:** Data curation, Formal analysis, Investigation, Software, Writing - original draft. **Zhijian Zhang:** Formal analysis, Investigation, Methodology, Resources, Software. **Yi Zhang:** Investigation, Methodology, Resources. **Yuanqiu Liu:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **G. Geoff Wang:** Conceptualization, Supervision, Writing - original draft, Writing

- review & editing.

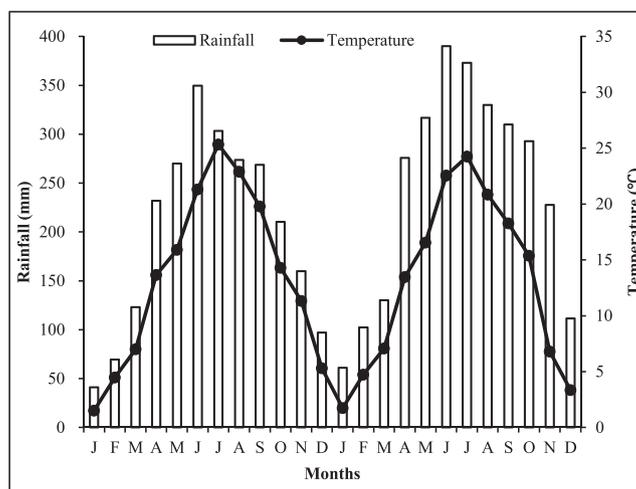
Declaration of Competing Interest

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

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Appendix A. Two-year average monthly air temperature and rainfall and from January 2017 to December 2018 in our research region. Note: J, A, S...was the abbreviation for each experimental month (from January 2017 to December 2018, 24 months in total).



Appendix B. Means of the initial soil physical and chemical characteristics (0–5 cm depth) in the coniferous-broad-leaved mixed subtropical forest; values are means ± SE for n = 4. Note: Mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC).

Soil contact	Mesh type	Organic matter (g/kg)	N (g/kg)	NO ₃ ⁻ -N (mg/kg)	NH ₄ ⁺ -N (mg/kg)	P (g/kg)	Available P (mg/kg)	pH	Moisture content (%)	Bulk density (g/cm ³)	Soil types
WSC	Closed	46.11 ± 4.21	2.05 ± 0.14	2.46 ± 0.22	1.75 ± 0.13	0.28 ± 0.03	3.88 ± 0.41	4.5 ± 0.3	41.36 ± 3.11	0.94 ± 0.16	Haplic alisols
	Open	46.17 ± 3.78	2.02 ± 0.11	2.43 ± 0.20	1.72 ± 0.11	0.27 ± 0.02	3.91 ± 0.45	4.4 ± 0.2	41.54 ± 3.37	0.94 ± 0.13	Haplic alisols
NSC	Closed	46.15 ± 4.01	2.01 ± 0.15	2.49 ± 0.18	1.77 ± 0.10	0.30 ± 0.02	3.87 ± 0.38	4.7 ± 0.2	41.76 ± 2.95	0.93 ± 0.13	Haplic alisols
	Open	46.23 ± 4.02	2.06 ± 0.16	2.50 ± 0.21	1.73 ± 0.15	0.29 ± 0.04	3.93 ± 0.40	4.6 ± 0.3	41.13 ± 3.28	0.95 ± 0.15	Haplic alisols

Appendix C. Initial chemical and physical properties of the wood used in this study by treatment, where TOC is total organic carbon, TN is total nitrogen, and TP is total phosphorus; nutrient ratios (C/N, C/P, N/P) are mass-based; values are means \pm SE for n = 4. Note: Mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC).

Soil contact	Mesh type	TOC (g/kg)	TN (g/kg)	TP (g/kg)	C/N	C/P	N/P	Lignin (%)	Cellulose (%)	Moisture content (%)	Density (g/cm ³)
WSC	Closed	423.23 \pm 9.73	5.78 \pm 0.68	0.21 \pm 0.04	73.22 \pm 3.99	2015.38 \pm 73.45	27.52 \pm 2.15	21.32 \pm 1.56	35.82 \pm 2.46	60.44 \pm 5.65	0.67 \pm 0.04
	Open	425.18 \pm 10.22	5.74 \pm 0.55	0.19 \pm 0.03	74.07 \pm 4.13	2237.79 \pm 81.17	30.21 \pm 2.31	22.11 \pm 1.27	36.05 \pm 2.35	60.87 \pm 6.13	0.64 \pm 0.03
NSC	Closed	418.66 \pm 9.23	5.76 \pm 0.66	0.20 \pm 0.03	72.68 \pm 4.32	2093.30 \pm 77.84	28.80 \pm 2.61	20.76 \pm 1.44	35.57 \pm 2.19	59.67 \pm 5.49	0.65 \pm 0.05
	Open	421.73 \pm 10.19	5.79 \pm 0.60	0.22 \pm 0.04	72.84 \pm 3.91	1916.95 \pm 83.01	26.32 \pm 2.11	22.05 \pm 1.61	36.32 \pm 2.27	59.11 \pm 6.22	0.68 \pm 0.04

Appendix D. The physical properties of wood at the end of the experiment. Values are means \pm SE for n = 4. Note: Mesh type (open or closed) and soil contact (with soil contact/WSC or without soil contact/NSC). Different lowercase letters indicate significant differences among soil contact (with soil contact/WSC or without soil contact/NSC) of the same mesh type (open or closed) at $p < 0.05$. Different uppercase letters indicate significant differences between different mesh types for the same soil contact ($p < 0.05$).

Soil contact	Mesh type	Moisture content (%)	Temperature (°C)	Density (g/cm ³)
WSC	Closed	74.47 \pm 6.87Aa	16.53 \pm 1.54Aa	0.53 \pm 0.05Ab
	Open	73.76 \pm 6.34Aa	16.57 \pm 1.61Aa	0.51 \pm 0.04Ab
NSC	Closed	65.19 \pm 5.07Ab	16.59 \pm 1.66Aa	0.59 \pm 0.06Aa
	Open	64.59 \pm 5.18Ab	16.58 \pm 1.69Aa	0.56 \pm 0.05Aa

Appendix E. Biomarkers of selected phospholipid fatty acids (PLFAs) used in this study.

Groups	Biomarker PLFAs	
Bacteria	15:0, i15:0, a15:0, i16:0, 16:1 ω 7c, i17:0, a17:0, cy17:0, cy19:0, 18:1 ω 7c	Frostegård & Bååth (1996) and Zak et al., 1996
G ⁺ bacteria	15:0, i15:0, a15:0, i16:0, a17:0, i17:0	Zelles (1999)
G ⁻ bacteria	16:1 ω 7c, cy17:0, cy19:0, 18:1 ω 7c	Zak et al. (1996)
Fungi	18:2 ω 6,9c, 18:1 ω 9c	Frostegård et al. (2011)
Actinomycetes	10Me 16:0, 10Me 17:0, 10Me 18:0	Zak et al. (1996)
AMF	16:1 ω 5c	Olsson et al. (1999)
Total biomass	15:0, i15:0, a15:0, i16:0, 16:1 ω 7c, i17:0, a17:0, cy17:0, cy19:0, 18:1 ω 7c, 16:1 ω 5c, 10Me 16:0, 10Me 17:0, 10Me 18:0, 18:2 ω 6,9c, 18:1 ω 9c	

AMF, Arbuscular mycorrhizal fungi.

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