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# The non-additive effects of temperature and nitrogen deposition on $CO_2$ emissions, nitrification, and nitrogen mineralization in soils mixed with termite nests

Yaowen Hu [a], Ling Zhang [a,b,*], Bangliang Deng [a], Yuanqiu Liu [a,b], Qian Liu [a], Xiang Zheng [a], Liya Zheng [a], Fanqian Kong [b,c], Xiaomin Guo [a], Evan Siemann [d]

[a] *Key Laboratory of Silviculture, Co-Innovation Center of Jiangxi Typical Trees Cultivation and Utilization, College of Forestry, Jiangxi Agricultural University, Nanchang 330045, China*
[b] *Lushan National Forest Ecosystem Research Station, Jiujiang 332900, China*
[c] *Lushan National Nature Reserve, Jiujiang 332900, China*
[d] *Department of Biosciences, Rice University, Houston 77005, USA*

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## ABSTRACT

Global warming and nitrogen (N) deposition are important factors impacting soil carbon (C) and N cycling. Termites are important ecosystem engineers that can also strongly affect C and N cycling, potentially in interaction with warming and N deposition. In addition, non-additive effects that magnify or reduce their impacts on soil element cycles may occur when termite nests and adjacent soils are mixed due to their divergent properties but this has not been investigated. Here, we collected termite nests and trails built in wood ("termite nest soils") and adjacent control soils in forests at Lu Mountain (Jiangxi, China) to investigate effects of termites, warming, and N deposition on C and N processes. We measured $CO_2$ emissions, $N_2O$ emissions, net N mineralization, and net nitrification when soils were incubated at different temperatures (15 °C, 25 °C, or 35 °C) and levels of N deposition (control vs. 4 g N $m^{-2}$). Termite nest soils were characterized by higher dissolved organic C and $CO_2$ emissions. $CO_2$ emissions decreased with N addition and increased with temperature. $N_2O$ emissions increased with N deposition and increased with temperature, especially in termite nest soils and mixed soils. Net N mineralization rates increased with temperature but increases were smaller and more gradual in control and mixed soils than in termite soils. Mixing termite nest soils and control soils imposed synergistic (N mineralization: up to 57% higher than expected; nitrification: up to 170% higher; $N_2O$ emissions without N addition: 18% higher) and antagonistic ($CO_2$ emissions: 7% lower; $N_2O$ emissions with N addition: 28% lower) mixing effects, indicating termite impacts on soil C and N cycling might be under- and over-estimated, respectively, based on each soil alone. In light of the remarkable abundance of termites, the effects of mixing termite nest soils and the control soils on soil C and N cycling should be considered in the context of global change.

## 1. Introduction

Soils contain large carbon (C) and nitrogen (N) pools associated with carbon dioxide ($CO_2$) and nitrous oxide ($N_2O$) emissions, and N transformations (Raich and Schlesinger, 1992; Bremner, 1997). $CO_2$ and $N_2O$ emitted from soils are two important greenhouse gases, contributing substantially to atmospheric radiative forces and global climate change (IPCC, 2014). In addition, warming and N deposition are two important global change factors, which may interact with changes in soil C and N characteristics, further impacting C and N cycling (Luo et al., 2001; Janssens et al., 2010). Soil fauna (e.g. termites in forest ecosystems) and their activities also play important roles in regulating soil $CO_2$ and $N_2O$ emissions (Sanderson, 1996; Sugimoto et al., 2000; Jouquet et al., 2011; Dahlsjö et al., 2014) and N transformations, such as nitrogen mineralization and nitrification (Ndiaye et al., 2004b; Ngugi et al., 2011).

Termites are functionally important ecosystem engineers that often dominate the arthropod communities in subtropical ecosystems due to their frequent occurrence and high abundance (Eggleton et al., 1999; Abe et al., 2000; Bignell and Eggleton, 2000; Dahlsjö et al., 2014). Termites can have strong effects on ecosystem C and N cycling both directly through their metabolic activities (Sanderson, 1996; Yamada et al., 2006; Brauman et al., 2015; Majeed et al., 2015) and indirectly via impacts on soil characteristics (Jouquet et al., 2005; Brümmer et al., 2009; Neupane et al., 2015). For example, $N_2O$ emissions from termite

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* Corresponding author at: Key Laboratory of Silviculture, Co-Innovation Center of Jiangxi Typical Trees Cultivation and Utilization, College of Forestry, Jiangxi Agricultural University, Nanchang 330045, China.
*E-mail address:* lingzhang09@126.com (L. Zhang).

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guts have been observed in soil-feeding termites (Ngugi and Brune, 2012). But, the quantity of $N_2O$ emissions by termites have also been found to be substrate dependent (Brauman et al., 2015). In addition, runway building activities by savanna termites substantially alter denitrification and nitrification potential (Ndiaye et al., 2004b), which may alter soil N transformations. Moreover, $N_2O$ emissions from whole mounds of the soil-feeding termite *Cubitermes fungifaber* were reported to be two orders of magnitude higher than those from surrounding termite-free soil during the dry season (Brümmer et al., 2009). Therefore, soil C and N cycling may vary with C and N incorporation (Yamada et al., 2006; Ngugi et al., 2011; Dahlsjö et al., 2014), soil physicochemical characteristics (Ackerman et al., 2007; Abe and Wakatsuki, 2010; Jouquet et al., 2015), and microbial communities (Ndiaye et al., 2004a; Ngugi and Brune, 2012) induced by termite activities (Fig. 1). Meanwhile, warming and N deposition could directly enhance soil microbial activities and N incorporation, respectively, driving C and N cycling in termite nests (Grabherr et al., 2009; Deng et al., 2016). Soil C and N processes may also change in response to termite activities or soil disturbances, especially under the context of warming and N deposition (Fig. 1).

Under natural conditions, however, soils associated with termite nests (structure or trails supported by soil, henceforth “termite nest soils”) and surrounding termite-free soils (henceforth “control soils”) may create mixtures of control and termite soils (henceforth “mixed soils”). This is especially likely for termite nests built in decomposing materials (Ndiaye et al., 2004b), which contribute significantly to the decomposition of organic matter in forest ecosystems. As decomposition progresses, the wood collapses and falls onto the forest floor, mixing termite nest soils together with the surrounding soils. The divergent characteristics in soil physicochemical properties, C and N status, and microbial composition between termite nest soils and control soils could alter C and N cycling rates in soil mixtures (Kuzyakov et al., 2000). Moreover, element cycles in these mixed soils may not simply be an additive function of the component soils. Rather, if there are non-additive effects of mixing, the net effect of termites on element cycles may be systematically over or underestimated depending on whether non-additive effects are negative or positive. Termites have been shown to be more important in decomposing dead wood than beetles in subtropical forests (Wood and Sands, 1978; Liu et al., 2015). For example, the genus *Reticulitermes* that imports soil into decomposing wood occurs in Asia, Europe, Africa and North America, with at least 112 species in eastern Asia (Bourguignon et al., 2016; Dedeine et al., 2016). During the decomposition of wood, soils imported by *Reticulitermes* might be enriched by elements released by decomposing organic matter (Neupane et al., 2015) and hence cause priming effects on soil C and N cycling when they are mixed with termite-free soils. However, studies on such mixing effects are lacking, limiting our understanding of soil C and N cycling as affected by termite activities.

Here, we collected termite nest and control soils from evergreen broadleaf forests in Lu Mountain (Jiangxi, China) to examine changes in soil C and N cycling with warming and N deposition. We hypothesized that: 1) termite nest soils differ from the surrounding termite free soils in soil $CO_2$ emissions, $N_2O$ emissions, N mineralization, and nitrification rates; 2) mixing termite nest soils with the surrounding soils will impose non-additive effects on soil $CO_2$ emissions, $N_2O$ emissions, N mineralization, and nitrification; and 3) warming and N deposition effects on $CO_2$ emissions, $N_2O$ emissions, N mineralization, and nitrification will be altered by soils mixing with termite nest soils.

## 2. Materials and methods

### 2.1. Study area

Lu Mountain (“Lushan”) is located in the northern part of Jiangxi province, in subtropical China (29°32′ N, 115°46′ E), with an annual mean temperature of 11.6 °C and precipitation of 2070 mm (Fig. 2). The elevation of Lu Mountain ranges from 30 m to 1474 m above sea level with vegetation changing from evergreen broadleaf forests to deciduous forests with increasing elevation (Liu and Wang, 2010). The three most common tree species are *Castanopsis eyrei*, *C. sclerophylla* and *Lithocarpus glaber* (Liu and Wang, 2010). The large amount of decomposing wood in the evergreen broadleaf forests following natural disturbance (e.g. freezing rain and snow disaster or cutting) provides an ideal environment for termites (Ulyshen et al., 2016). Standing wood eventually decomposes and falls onto the forest floor, mixing termite nest soils with the surrounding termite-free soils. *Rhinotermitidae* is one important termite family in this area, which generally nests and feeds in decomposing wood. In this family, one genus (*Reticulitermes*) has been frequently observed, including the species *R. longicephalus* and *R. leptomandibularis* (Liu and Wang, 2010). Termite nests assessed in the study were built in decomposing wood that consisted of runways and other structures under the bark or inside the decomposing wood.

### 2.2. Experimental strategy

We collected termite nest soils and control soils, and produced mixed soils in the lab. We used these soils to determine the differences in greenhouse gas emission rates ($CO_2$ and $N_2O$) and N transformation rates (nitrification and N mineralization) among termite nest soils, mixed soils and control forest soils, and their responses to global change. We incubated soils in the lab with or without global change treatments and measured both greenhouse gas emission rates ($CO_2$, $N_2O$) and N transformation rates (N mineralization, nitrification) of each soil type. We also determined soil physicochemical characteristics to understand GHG emission and N transformation results.

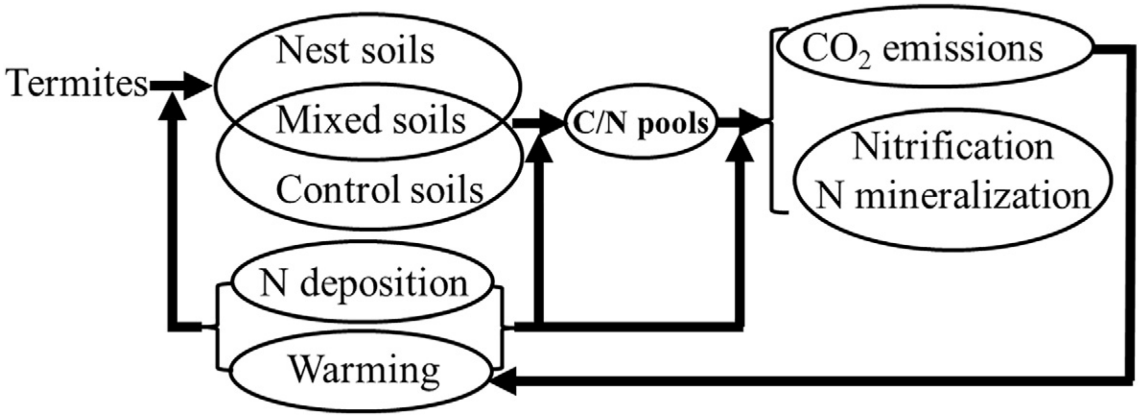

**Fig. 1.** Schematic diagram of potential interactions among termites, soil C/N, and global change. Arrows indicate directions of effects.