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Spatio-temporal variations of carbon and nitrogen in biogenic structures of two fungus-growing termites (*M. annandalei* and *O. yunnanensis*) in the Xishuangbanna region

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ABSTRACT

Fungus-growing termites are abundant and play an important role in soil nutrient dynamics in the tropics due to their activities and unique effects on soil physical, chemical and biochemical properties. However, the mechanisms of termite mound turnover and the effects of such turnover on temporal and spatial patterns of nutrients in surrounding soils have rarely been studied. Here, we investigated the relationship between the stabilization and redistribution of soil nutrient properties and the chronological development of termite mounds (primary, secondary-occupied and abandoned mounds). The study was conducted to assess the concentrations of nutrients and water content in the biogenic structures produced by two fungus-growing termites (*M. annandalei* and *O. yunnanensis*) in different mound stages. Samples were collected along a transect at regular intervals proportional to the size of the biogenic structure. We found the concentration of NO_3^- in the following sequence: active mound, abandoned mound, and the surrounding soils. The concentrations of organic carbon (C_{org}) and total N in the active mounds were significantly lower than those in the surrounding topsoils, although a weak difference was observed with subsoils. The concentrations of C_{org} and total N in the abandoned mounds were significantly higher than those in active mounds, whereas no difference was observed with surrounding soils. The mean concentrations of nutrients were significantly different between fresh parts (sampling locations 1–3) and old parts (locations 4–6) of the secondary-occupied mounds. The nutrients in the fresh parts of the mound approached the values in the primary mound; whereas the nutrients in the old part of the mound approached the values in the abandoned mound. Our results indicate that nutrient concentrations change through the chronological development of termite mounds, which are hot spots of nutrients that subsequently affect ecosystem processes at specific spatial and temporal scales through the stabilization and redistribution of nutrients.

1. Introduction

Termites (Isoptera) are often considered major ecosystem engineers that alter soil properties through the selection, translocation and ingestion of organic and inorganic materials (Holt and Lepage, 2000; Sarcinelli et al., 2009; Levick et al., 2010). Termite mounds built by fungus-growing termites, which have a dominant role in tropical ecosystems, are numerous in the tropical forests of southeast China, particularly in areas converted to rubber plantations. Although many studies demonstrate that termites enrich the inside of their mounds with carbon, nitrogen, clay and exchangeable cations compared with the adjacent soils unmodified by termites (Mujinya et al., 2010; Seymour et al., 2014), the mechanisms of termite mound turnover and the effects of mound turnover on temporal and spatial patterns of nutrients in surrounding soils have rarely been studied for this region.

The effect of termites on the physical properties of soils, particularly the effects of fungus-growing species, is primarily related to burrowing and mounding activities through which the soil chemical and biochemical characteristics are also modified compared with original soils (Darlington et al., 1997; Mahaney et al., 1999; Mills et al., 2009). Fungus-growing termites build mounds constructed of a mixture of soil particles and saliva and also provide a protective enclosure around

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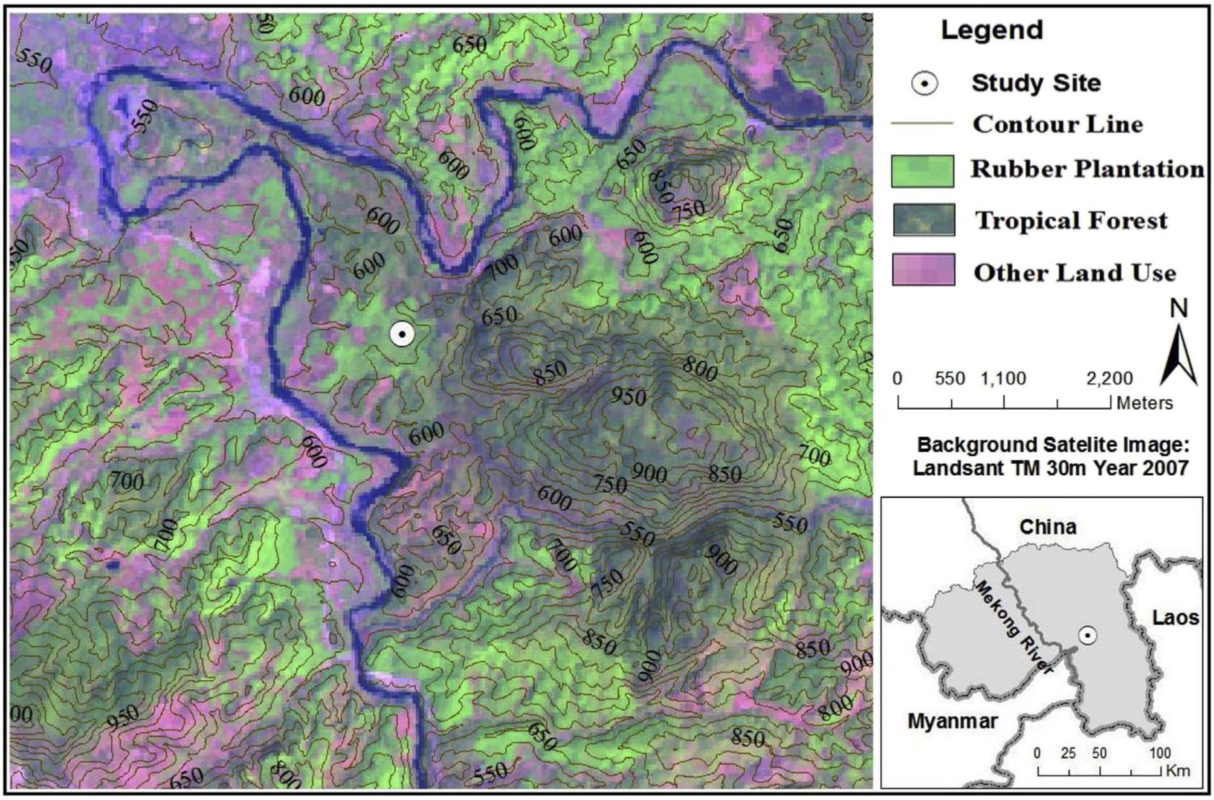

Fig. 1. Map showing location of the study site (21°55′39″N, 101°15′55″E) in Yunnan Province, southwest China.

potential food items within which feeding and foraging take place (Bagine, 1984). In general, termite mounds have increased levels of nutrients, including enrichment of N-based compounds (Seymour et al., 2014), phosphorus (Rückamp et al., 2010), and micronutrients (Seymour et al., 2014). In the mound structures of fungus-growing termite species, the quantity and quality of soil organic matter (SOM) are variable depending on the initial soil properties and on the specific species.

However, because of the low stability of termite mounds and the high rainfall in the study area, these types of biogenic structure (BS) are quickly recycled in soils. A decrease in nutrient contents may occur in the older or dead mounds due to weathering and organic matter decomposition or the activities of termites (Cammeraat et al., 2002; Roose-Amsaleg et al., 2005). For example, Congdon et al. (1993) and Schwiede et al. (2005) reported leaching of nitrates and ammonium from termite mounds into the surrounding soil. Moreover, recolonization of dead mounds is very common in populations of *Macrotermes*. Previous studies demonstrate that other colonies may occupy a mound after the death of the original builders, and these recolonizers may be the same or a different species or both (Pomeroy, 1976). Rückamp et al. (2009) found higher nitrate and ammonium concentrations and lower carbon fluxes in soil water leaching from older mounds inhabited by secondary termites than in water from mounds inhabited by primary termites or reference soils.

Because the activities of termites and environmental weathering both play important roles in nutrient cycling processes in tropical soils, which are notoriously nutrient deficient environments (Cerdà and Jurgensen, 2011; Menichetti et al., 2014), some researchers are attempting to understand the mechanisms and the evolution of termite mounds according to changes in nutrient distributions. For example, Menichetti et al. (2014) compared the concentrations of nutrients and biochemical activity of colonized and abandoned mounds of the litter-feeding termite (*Macrotermes* spp.) located in the Borana District, Ethiopia. They found that the abandoned termite mounds had higher microbial biomass and activity and displayed a redistribution of nutrients compared with the adjacent soils, whereas weakly significant differences were detected compared with mounds colonized by termites. Additionally, Rückamp et al. (2012) examined the chemical soil properties in and below mounds that were built by the primary termite (*Cornitermes silvestrii*) and the secondary colonizer (*Nasutitermes kemneri*) in tropical savannahs. The highest enrichment of chemical soil properties compared with the control soil was found in the mature or primary inhabited mounds, whereas the enrichment declined in older mounds but remained higher than that in the control soils.

Nevertheless, we are unaware of any studies that have been conducted on comparisons or relationships among the different stages or ages of mounds (i.e., the primary, secondary and abandoned mounds) in tropical soils, which are notoriously nutrient deficient environments (Garba et al., 2011; Miyagawa et al., 2011). Moreover, in the assessment of nutrient distributions, the structure of the mound as a whole is normally considered (Verchot et al., 2003; Holec et al., 2006), and few researchers have investigated different parts of the structure, particularly those of the secondary mounds with drastically varied physical and chemical properties in different parts of the structure. These omissions prevent obtaining a better understanding of the magnitude and persistence of termite-induced effects on soil primary properties and functions and in general, on the evolution of termite mounds. Thus, the goals of our study were to (1) assess the spatial and temporal variability of organic matter and nutrient contents of the biogenic structures produced by termites; (2) understand the effect of two dominant termite species feeding guilds on soil genesis in the Xishuangbanna area; and (3) evaluate the contents of organic matter and nutrients as indicators of chronological development in different states or ages of mounds, i.e., the primary, the secondary-occupied and the abandoned mounds.