

RESEARCH ARTICLE

Activity-density and spatial distribution of termites on a fine-scale in a tropical rainforest in Xishuangbanna, southwest China

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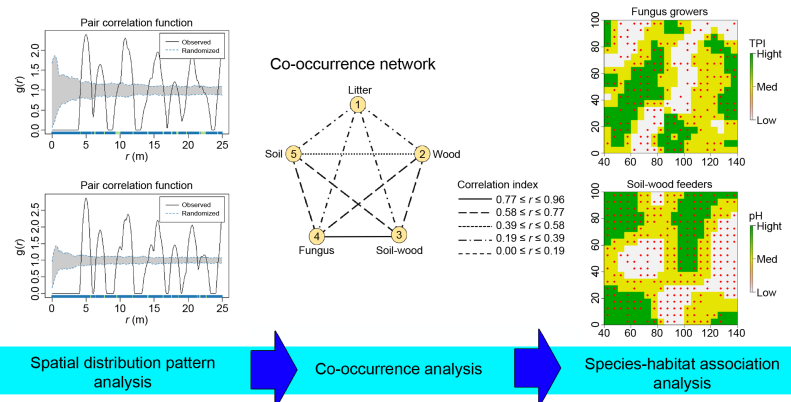
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HIGHLIGHTS

- Strong associations among soil-wood feeders and fungus growers were observed.
- Weak associations between litter feeders and other feeders were observed.
- TPI and pH had effects on all feeding groups of termites.
- Plant biomass influenced soil-wood feeders and wood feeders.
- Litter mass influenced fungus growers, litter feeders, and soil feeders.

GRAPHICAL ABSTRACT



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ABSTRACT

The community composition and activity-density of termites can influence nutrient cycling and other ecological functions. However, the spatial distribution and the activity-density of termites on a fine-scale in tropical forests are still unknown. We checked the spatial distribution patterns of the feeding groups and species of termites and their co-occurrence pattern in a 1-ha (100 m × 100 m) plot, and their correlation with the environmental factors. We used a standard protocol to collect termite assemblages and classified them into five feeding groups based on their preferred diet: fungus growers, litter feeders, soil feeders, soil-wood feeders, and wood feeders. We measured the environmental factors: soil pH, litter mass, aboveground plant biomass, and topographic position index (TPI). Soil-wood feeders showed the highest activity-density, followed by wood feeders, fungus growers, soil feeders, and litter feeders. Soil-wood feeders and fungus growers demonstrated a strong correlation while litter feeders showed weak correlations with other feeding groups. Termite feeding groups and most of the termite species displayed a positive association with the high TPI

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and the low soil pH patches. Our results indicated that the examined environmental factors influenced the termite community assemblages and distribution patterns on a fine-scale in tropical rainforests.

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1 Introduction

Soil fauna are essential for sustainable forest ecosystems and significantly influence soil quality (Donovan et al., 2001, 2007). Termites constitute up to 95% of the biomass of the overall soil insect biota in tropical ecosystems (Bignell and Eggleton, 2000; Donovan et al., 2007; Vasconcellos, 2010; Jouquet et al., 2011; Koné et al., 2018) and the function as “ecosystem engineers” (Davies et al., 2013; Canello et al., 2014). They perform a variety of ecosystem services, such as litter decomposition, nutrient cycling, soil structuring, and microbial activity stimulation (Sugimoto et al., 2000; Donovan et al., 2001). Termites comprise diverse and varied feeding groups, such as wood feeders, grass harvesters, soil feeders, soil-wood interface feeders, humus feeders, and litter feeders, which may not respond in the same way to environmental factors (Donovan et al., 2001; Dosso et al., 2010; Canello et al., 2014). The identification of the community composition of species or groups is essential in revealing the underlying mechanisms among biotic and abiotic factors (Gao et al., 2020).

Depending on the functional or taxonomical focus, previous studies have investigated termite distribution at different spatial scales from global (Abe and Higashi, 2001; Eggleton and Tayasu, 2001), regional (Dambros et al., 2017) to local (Davies et al., 2013) levels. Various studies have applied different sampling protocols to understand the diversity and relative abundance of termites (e.g., Donovan et al., 2007; Avitabile et al., 2015; Dosso et al., 2017; Dahlsjö et al., 2020; Scholtz et al., 2021). However, there is very limited information about the diversity, abundance, and spatial distribution patterns of termites in tropical rainforests, especially on a fine-scale which is defined as the scale from a few to tens of meters to investigate the biotic interactions occurring on smaller scales (Wiens, 1989; Xia et al., 2015; Niittynen et al., 2020). Hence, the concept of activity-density introduced for flying insects (Jouveau et al., 2020; St. Clair et al., 2020) could be adopted for termites.

Activity-density (activity-abundance) of the insects is the number of collected or trapped individuals during a certain period or within a specific area since the collected numbers depend not only on the absolute population density but also on movement activity (Thiele, 1977; Perner and Schueler, 2004). Since termites search for favorable food resources on the forest floors, we defined their activity-density as the total number of active individuals collected within a specific surface area. Understanding the community composition and activity-density of functional groups of termites is important for the global assessment of nutrient cycling under climate change (Scholtz et al., 2021). As termites play a

critical role in biogeochemical processes, such as carbon mineralization and methane emissions (Sugimoto et al., 2000), and nitrogen fixation (Slaytor, 2000), it is essential to assess the community composition and the activity-density of different feeding groups of termites to better understand the impact of termites on global soil carbon and nitrogen cycling. Moreover, the percent composition of different feeding groups of termites can indicate the capacity of nitrogen added to the soil (Hojo, 2019) which in turn benefits the health of forest soils. Nevertheless, little is known about the activity-density and composition of termites in tropical rainforests on a fine-scale.

Since tropical forests have a high diversity of plant species and environmental heterogeneity (Atapattu et al., 2020; Osborne et al., 2021), the diversity of litter and fallen wood creates a variety of food choices for termites. Termite species diversity can be greatly influenced by the climatic conditions at the regional level, while it can be influenced by soil texture and chemical composition at the local level (Dambros et al., 2017). In addition, altitude, rainfall, nitrogen content, and light intensity were the major determinants of the diversity and abundance of termites (Pratiknyo et al., 2018). Some studies have stated that lower termite density was found at higher elevations (Gathorne-Hardy et al., 2001; Palin et al., 2011; Nunes et al., 2017; Betz et al., 2020). However, previous studies have focused on the potential impact of environmental factors on termite communities or some termite species on large-scales (> 1 ha). Empirically, the small spatial scales were radical to distinguish the biotic processes, such as dispersal, and intra- and inter-specific interactions (Gao et al., 2020). In tropical forests, fine-scale distribution captures the heterogeneity of soil nutrient and environmental attributes that impact species activity and fitness, and determines individual species response to environmental fluctuations in a small area (Wiens, 1989). But it remains unclear how environmental factors influence the spatial distribution of termite communities on a fine-scale.

The present study examines the spatial distribution patterns, the composition of feeding groups and species on a fine-scale, and the association between termite species abundance and the above-mentioned environmental factors. These environmental factors showed spatial heterogeneity and were substantially important for the termite activity and distribution on the fine-scale (Xia et al., 2015). The objectives of this study are to understand: (1) the activity-density and spatial distribution pattern of termites, including feeding groups and species, within a 1-ha plot in tropical rainforest; (2) the association and competition among feeding groups; and (3) the environmental factors influencing the activity-density and spatial distribution of feeding groups.

2 Materials and methods

2.1 Study area

This study was conducted in the Center for Tropical Forest Science 20-ha dynamic plot (21°37'08" N, 101°35'07" E) in Xishuangbanna Dai Autonomous Prefecture, China (Fig. 1). The mean annual precipitation is 1221 mm, and the mean annual temperature is 21.7°C, varying from 14.8°C in January to 25.3°C in June (Yang and Chen, 2009). The vegetation type is tropical rainforest with 468 tree species (Xia et al., 2015; Atapattu et al., 2020). The soil is mainly lateritic red earth derived from siliceous rocks, equivalent to Oxisols based on the United States Department of Agriculture Soil Taxonomy, and the soil pH ranges between 4.5 and 5.5 (Cao et al., 2006; Soil Survey Staff, 2014). The samples were collected within the 1-ha plot (100 m × 100 m) with elevations ranging from 711.3 to 736.6 m at the south-east corner of the 20-ha plot (Xia et al., 2015).

2.2 Sample collection and analysis

In the 1-ha plot, 400 contiguous 5 m × 5 m quadrats were laid out (Fig. 1). All available termite individuals inside each quadrat were collected by 4 persons simultaneously (2.5 m × 2.5 m subquadrats per person) following a standard protocol (Jones et al., 2003). The potential termite activity patches for termite inhabitants were searched: accumulations of litter and humus at the base of trees and between buttress roots; inside of tree stumps, dead logs, branches, and twigs; soil within and beneath decomposing logs; carton sheeting and runways on vegetation up to a height of 2 m above ground level. According to their feeding substrates or microhabitats, samples were recorded and kept in a separate container for

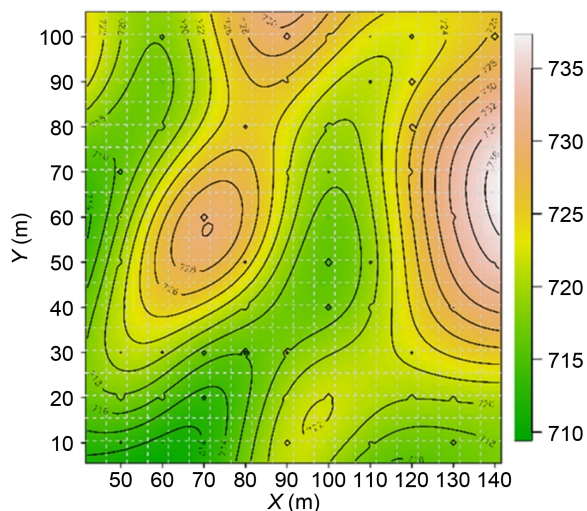


Fig. 1 Topography of the study site and position of sampling quadrats. The white dotted squares represent 5 m × 5 m quadrats for the termite sampling.

species identification. Termites were collected in August, 2016 for 10 consecutive days from 9 a.m. to 4 p.m. The identification of termite species followed the nomenclature of Cai and Huang (1980) under the microscope (Leica DM2000). All the captured termites were classified into different feeding groups, resulting into fungus growers, litter feeders, soil feeders, soil-wood feeders, and wood feeders, based on the species and the type of microhabitats they were observed and their prevailing diet (Eggleton et al., 1997; Dosso et al., 2013; Liu et al., 2019). Termites building prominent epigeal mounds and cultivating fungi only to degrade lignin for the efficient use of cellulose were called fungus growers, and those building belowground nests and cultivating fungi for their consumption were termed soil-wood feeders. Litter feeders were defined as the termites consuming leaf litter or lichens growing over trees and fallen litter substances. Termites invading and excavating damaged or fallen wood were called wood feeders and those consuming on the organic rich soil (humus) were named soil feeders.

In the same 1-ha plot, TPI was calculated following Jenness (2006) in which positive TPI values were associated with upslopes, negative values with downslopes, and zero with midslopes (Xia et al., 2015). The aboveground plant biomass was based on the species, wood density, and diameter at breast height of each tree in the plot (Chave et al., 2014). Soil samples were collected at 5-m intervals (361 soil samples in total) and five soil cores were collected, from a depth of 0–20 cm after removing the litter layer, using a core sampler (4 cm diameter × 10 cm depth) from each quadrat across the plot. The collected soil samples were mixed and air-dried for 30 days. After that, these air-dried samples were ground and sieved through a 2-mm mesh. Soil pH was measured by the 1:2.5 water suspension method using a pH meter (PHS-3C, Shanghai Precision Scientific Instrument Co., Ltd., China). Litter was collected every two weeks from January 2011 to December 2013 using 1 m² litterfall traps at 1 m above ground. Twigs were removed from the collections due to the low proportion of the total litter and low nutrient content. Annual litter mass was calculated by averaging the total amount of litter mass. More detailed descriptions of the experimental design were prepared by Xia et al. (2015).

2.3 Statistical analysis

All statistical analyses were performed in R software v 4.1.1 (R Core Team, 2021). We calculated descriptive statistics and checked the community composition at the feeding groups and species levels. To visualize the spatial distribution pattern of feeding groups and selected species, the ordinary kriging maps were generated with the *krige* function in *gstat* package following Pebesma (2004).

Species association analysis (co-occurrence analysis) was executed using the *sp.assoc* and *sp.pair* functions of the *spaa* package at the feeding group level and species

level, respectively (Zhang and Ma, 2013). The co-occurrence network among feeding groups was generated by the *plotnetwork* function of the same package using *Ochiai* method to visualize the simple network association. Niche width and niche overlap were calculated by the *niche.width* function using the *Shannon* method and the *niche.overlap* function using the *levins* method. Niche width is a measure of uniformity and the maximum niche width results from low discrimination (common) among different patches, while minimum niche width results from the high specialization of a species or a feeding group (Colwell and Futuyma, 1971). A lower niche overlap (< 0.6 threshold) represents weak or no competition between two communities (Zaret and Rand, 1971; Martins et al., 2020). The values of niche overlap lie at a minimum of 0 at no shared distribution and a maximum of 1 at the proportionately shared distribution of the two species (Colwell and Futuyma, 1971).

Species-habitat association analysis was performed using the *shar* package to understand how individual feeding group and species respond to the heterogeneity of environmental variables by defying spatial autocorrelation at small-scale environmental conditions (Hesselbarth, 2021). Environmental variables were transformed into raster images by the *raster* function under the *raster* package, and the termite data were transformed into spatial point pattern objects using the *ppp* function under the *spatstat* package. The resulting raster images were classified into 3 classes (high, medium, low) by the *classify_habitats* function. Point pattern data of termites were randomized by gamma-test and pattern reconstruction using the *fit_point_process* and *reconstruct_pattern* functions. The distribution pattern of termites (regular, random, or clustered) was identified by gamma tests at 99 permutations by using the *fit_point_process* function. Based on the graph generated by the pair correlation function $g(r)$, distribution patterns can be interpreted as clustered ($g(r) > 1$), random ($g(r) = 1$) and regular ($g(r) = 0$ for small r values and $g(r) > 1$ for large r values, significant fluctuations around 1 are possible) (Illian et al., 2007; Grohmann et al., 2010; Wiegand and Moloney, 2013). Species-habitat association results were calculated for the pattern reconstruction test using the *results_habitat_association* function. Exceptionally, we removed individual species observed in less than 10 quadrats (accounting for less than 1.49% of the whole community) in the species level analyses for the feasibility of the models.

3 Results

3.1 Relative abundance and community composition of termites

A total of 50 937 termite individuals from 24 species at 337 quadrats were recorded, comprising 10 genera and 3 families (Fig. S1). The occupancy of feeding groups decreased in the order of soil-wood feeders (283 quadrats), fungus growers (195 quadrats), wood feeders (80 quadrats), soil feeders (38 quadrats), and litter feeders (9 quadrats) (Table 1). The soil-wood feeders were the most dominant feeding group (51%), followed by wood feeders (22%), fungus growers (21%), soil feeders (3%), and litter feeders (2%) (Table 1). Fungus growers, soil-wood feeders, and wood feeders consisted of 6 species each, while soil feeders and litter feeders were composed of 4 and 2 species, respectively (Table 1; Fig. S1). All feeding groups showed very high coefficients of variation (CVs) (Table 1).

Among the 24 species, ten species showing occupancy in more than 10 quadrats were *Odontotermes formosanus* (OF), *Macrotermes barneyi* (MB), *Odontotermes hainanensis* (OH), *Odontotermes angustignathus* (OA), *Peribulbitermes jinghongensis* (PJ), *Ancistrotermes dimorphus* (AD), *Pericapritermes tetraphilns* (PT), *Havilanditermes orthonasus* (HO), *Macrotermes yunnanensis* (MY), and *Pericapritermes latignathus* (PL). These species represented over 94% of the total abundance: OF (35.5%), MB (19.5%), PJ (13.9%), OH (8.8%), OA (5.9%), AD (2.6%), PT (1.7%), HO (5%), MY (0.8%) and PL (0.5%) (Table S1).

3.2 Spatial distribution patterns of termite feeding groups and species

At the 5 to 25 m scales, soil-wood feeders and fungus growers showed comparatively regular distribution patterns, while wood feeders and litter feeders showed clustered distribution patterns, and the soil feeders showed a random distribution pattern (Figs. 2, 3). At the species level, OF, MB, and OH showed regular distribution patterns, while OA, PJ, and HO showed clustered distribution patterns, and AD, PT, MY, and PL showed random distribution patterns (Figs. S2, S3).

Table 1 Descriptive statistics of total termites and different feeding groups of termites in a 1-ha plot.

Group	No. of quadrats sampled	No. of species	Mean	SD	Min	Max	Relative abundance	CV
Total termites	337	24	151	159	5	1288		
Soil-wood feeders	283	6	92.3	104	1	691	51.26	1.29
Fungus growers	195	6	55.2	64	4	393	21.13	1.16
Wood feeders	80	6	140	186	3	1268	22.02	1.39
Soil feeders	38	4	44	56	9	332	3.25	1.34
Litter feeders	9	2	132	172	3	566	2.33	1.31

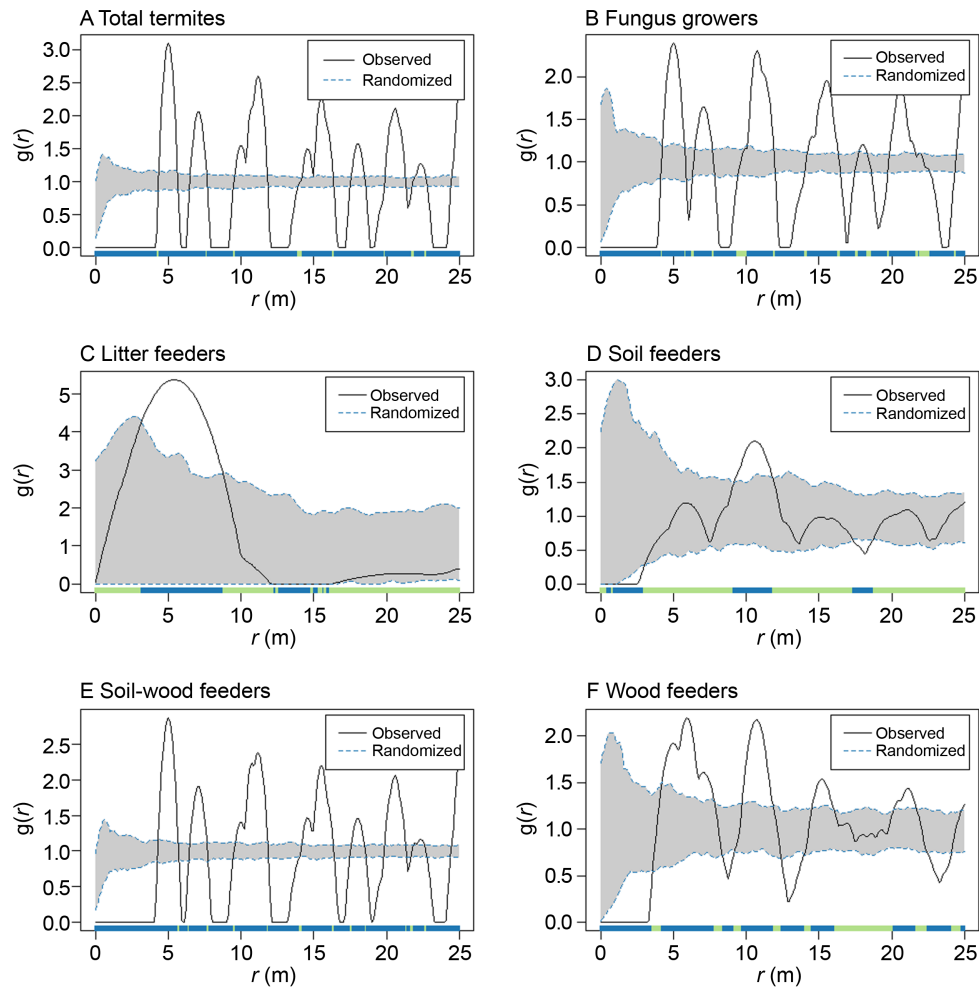


Fig. 2 The spatial distribution pattern by pair correlation function of (A) all collected termites, (B) fungus growers, (C) litter feeders, (D) soil feeders, (E) soil-wood feeders, and (F) wood feeders. The grey boundary shows the randomized pattern of distribution, and the black line represents the observed pattern of distribution.

3.3 Competition and co-occurrence among termite feeding groups and species

The niche width index of soil-wood feeders was the largest (5.87), followed by the fungus growers (5.22), wood feeders (4.03), soil feeders (3.38), and litter feeders (2.29) (Table 2). For individual species, *OF* showed the largest niche width index at 5.36, and *PL* showed the smallest niche width index at 2.2 (Table 2). Niche overlap mainly occurred among dominant groups and other groups. At the species level, relatively high niche overlap was found between *OF* and *MB*, the two most dominant species in our study plot, while relatively low overlaps were observed among other species (Table S2).

Co-occurrence network showed that weak associations ($r \leq 0.39$) existed between litter feeders and other feeding groups (Fig. 4). Wood feeders showed slightly strong association ($0.39 \leq r \leq 0.58$) with soil feeders and strong associations ($0.58 \leq r \leq 0.77$) with soil-wood feeders and fungus growers (Fig. 4). Similar associations were observed between soil-wood feeders and soil feeders, and between

fungus growers and soil feeders (Fig. 4). The strongest association ($r \geq 0.77$) was observed between soil-wood feeders and fungus growers (Fig. 4).

3.4 Effect of environmental factors on termite distribution

All termites (total and all feeding groups) showed positive associations at the high TPI and the low pH environment (Table 3; Figs. S5, S8). Soil-wood feeders and wood feeders illustrated positive associations at high plant biomass patches, while fungus growers, litter feeders, and soil feeders demonstrated positive associations at high litter mass patches (Table 3; Figs. S6, S7). At the species level, most of the species displayed positive associations at the high TPI with the low pH patches (Table S3; Figs. S9, S12). *OF*, *OH*, *OA* and *HO* presented associations in moderate to high biomass patches (Table S3; Fig. S10a, c, d, h). Similarly, *PJ*, *AD*, *PT*, *HO*, and *MY* showed associations in moderate to high litter mass patches (Table S3; Fig. S11e, f, g, h, i).

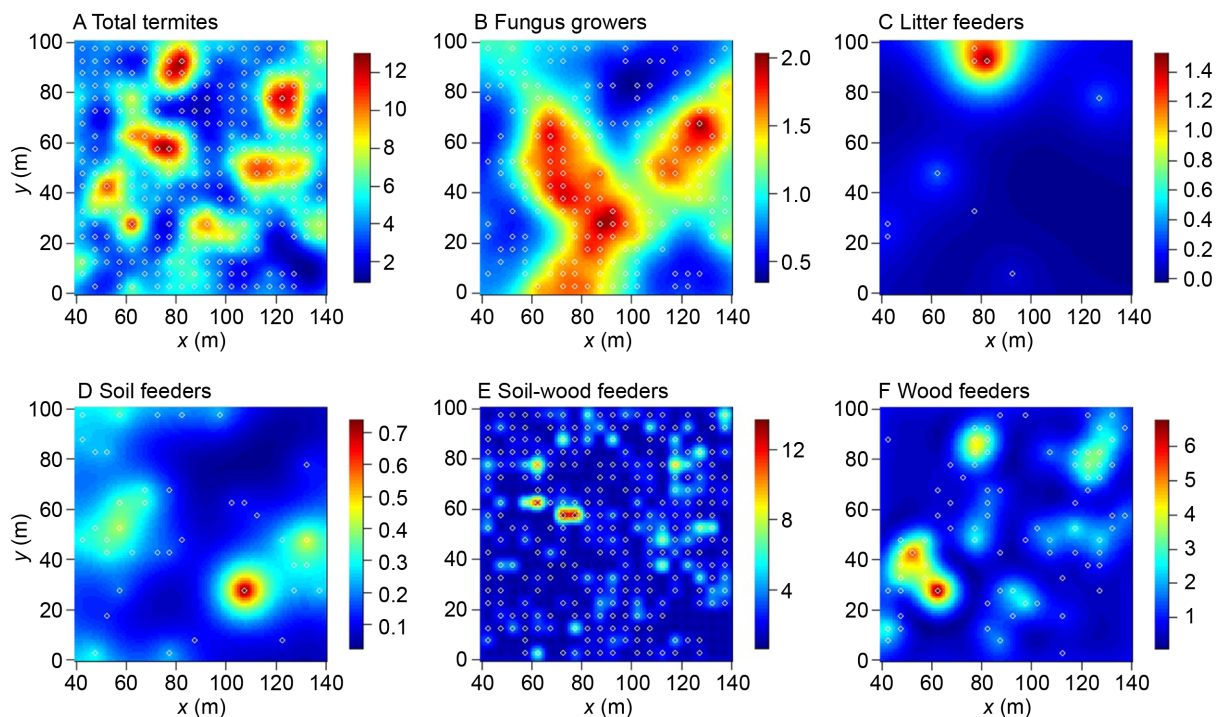


Fig. 3 The spatial distribution map of (A) all collected termites, (B) fungus growers, (C) litter feeders, (D) soil feeders, (E) soil-wood feeders, and (F) wood feeders in the 1-ha plot. The scale bar represents the number of termite individuals in the 1 m² quadrat. The white circles represent the points at which termite groups were observed.

Table 2 Niche widths of termite feeding groups and 10 most abundant species.

Feeding group/Species	Niche width index
Fungus growers	5.22
<i>M. barneyi</i>	5.10
<i>M. yunnanensis</i>	2.55
Wood feeders	4.03
<i>A. dimorphus</i>	3.03
<i>H. orthonasus</i>	2.84
<i>P. jinghongensis</i>	3.20
Litter feeders*	2.29
Soil feeders	3.38
<i>P. tetraphilns</i>	3.07
<i>P. latignathus</i>	2.21
Soil-wood feeders	5.87
<i>O. angustignathus</i>	3.94
<i>O. formosanus</i>	5.36
<i>O. hainanensis</i>	4.47

*No data at the species level because of few individuals.

4 Discussion

4.1 Relative abundance and community composition of termites

The total relative abundance of soil-wood feeders and

fungus growers accounted for over 70% of the total abundance in our study (Table 1). Similar results indicated that these feeders were dominant and represented 70%–90% of the total abundance in different forest types (Hemachandra et al., 2014; Dosso et al., 2017; Koné et al., 2018; Liu et al., 2019). Since both the soil-wood feeding group and fungus growing group were represented by a different single genus, we can simply refer to the genus *Odontotermes* as the soil-wood feeders and *Macrotermes* as the fungus growers for better comparisons and explanations. *Odontotermes* was not only dominant in our study plot (Table S1), it can also be found commonly in the Xishuangbanna area (Long et al., 2010), on Taiwan Island (Chiu et al., 2018), in India (Jouquet et al., 2015; Shanbhag et al., 2017) and across the Afro- and Indo-tropics (Cheng et al., 2011). *Macrotermes*, the second dominant genus in our study plot, also showed a wide distribution and high composition in southern China (Li et al., 2021), Thailand (Hyodo et al., 2003), Malaysia (Fajar et al., 2021), Kenya (Vesala et al., 2017), and Congo (Mujinya et al., 2014). The dominance of these two feeding groups, specifically *Odontotermes* and *Macrotermes*, has a profound influence on decomposition and soil nutrient turnover by tunneling and burrowing mechanisms since these genera are known for building mounds by transporting soil particles.

Notably, the wood feeding group, the second most abundant group in our study plot, showed the highest generic diversity comprising 5 genera from 3 families. *Peribulbitermes*, *Havilanditermes* and *Ancistrotermes* were the three most dominant genera and represented over 21%

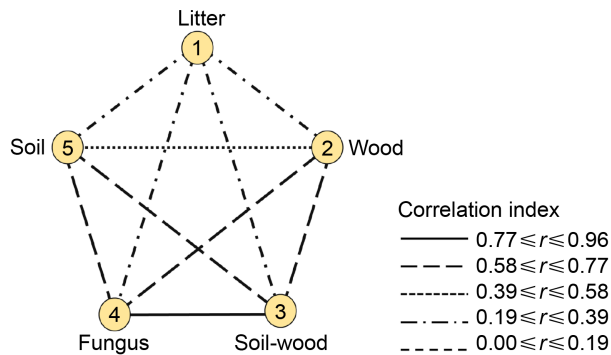


Fig. 4 Co-occurrence network among different feeding groups of termites calculated from coefficients of closeness. A high index denotes high co-occurrence and a low index denotes low co-occurrence among feeding groups.

of the total abundance (Table 1). Although wood feeding termites were composed of 26% of the genera and 56% of all species (Bignell, 2018) and were reported in Cameroon, Peru and Malaysia (Dahlsjö et al., 2015) and in India (Harit et al., 2021), we still have little knowledge about their relative abundance especially at the generic or specific level. The remaining two feeding groups, namely soil feeders and litter feeders, were composed of 4 species at 3% relative abundance and 2 species at 2% relative abundance in our study plot respectively (Table 1). These feeding groups have lower representation possibly because: (1) our sampling method was designed to detect the active termites on the surface of the soil that can limit the occurrence of soil living termites; and (2) the free and fast moving termites, such as, litter feeders can escape from being captured due to their surface wandering behavior and range of moving distance up to tens of meters (Miura and Matsumoto, 1997; Syaukani et al., 2016).

4.2 Spatial distribution patterns of termite feeding groups and species

Two major feeding groups, soil-wood feeders and fungus growers showed regular distribution patterns and shaped the spatial distribution pattern of the total termite community in the study plot (Fig. 3). As the soil-wood feeders (*Odontotermes*) and fungus growers (*Macrotermes*) were functionally closely related (Šobotník and Dahlsjö, 2017), the range and behavior in search of food resources might be similar. Regularity is commonly reported for mound-building termites and such regularity indicates inter- or intraspecific competition (Grohmann et al., 2010; Mujinya et al., 2014; De Souza and Delabie, 2018). However, regular distribution patterns were rarely found in previous termite studies; instead, clustered distribution patterns were commonly reported not only for termites (Donovan et al., 2007; Scholtz et al., 2021) but also for other soil-modifying taxa, such as earthworms (Jiménez et al., 2001, 2011; Valckx et al., 2009) and mites (Zhang et al., 2015).

The clustered distribution patterns of wood feeders and

litter feeders were greatly influenced by fallen trees and associated litter substances. Due to their specialized food selection and excavation strategy, they might be observed in patches favorable for them, such as fallen wood or leaf litter of some plant species (Bignell, 2018). Most of the soil- or tree-inhabiting insects showed clustered distribution patterns, for example ants (Mgocheki and Addison, 2010) and nematodes (Robertson and Freckman, 1995). The random distribution patterns of soil feeders might be due to a random appearance of soil feeders over the surface of the soil since they normally live in the organic rich layer of the soil.

4.3 Competition and co-occurrence among termite feeding groups and species

The dominant feeding groups (soil-wood feeders and fungus growers) showed large niche widths that were twofold higher than those of litter feeders, meaning that soil-wood feeders and fungus growers had a wider range of resource acquisition activity (Table 2). This result also indicates that soil-wood feeders and fungus growers were the generalists (Colwell and Futuyma, 1971). Moreover, soil-wood feeders showed niche overlaps with litter feeders, soil feeders, wood feeders, and fungus growers from high to low order (Table S2). Two major patterns were observed, in which soil-wood feeders (largest niche width) have the relatively large niche overlap with litter feeders (smallest niche width) while they have the relatively low niche overlap with fungus growers (2nd largest niche width). To understand whether there is competition or association between termite groups, we need to consider the pattern of distribution, type and amount of food resources, co-occurrence, niche width, and niche overlap. These results indicate that the generalists, soil-wood feeders, may compete for food resources with other generalists, fungus growers. However, they might have low competition with other specialists, especially litter feeders, possibly due to their different interests in resource types. Conversely, *OF* and *MB* had relatively high niche overlap although both showed the largest niche widths and were major species of soil-wood feeders and fungus growers (Tables 2, S2). Except for these two species, niche overlaps among other species were generally low. However, interactions among feeding group level and species level were relatively low and sometimes considered negligible since the niche width falls below 0.6 significant thresholds (Martins et al., 2020). Competitions were observed even between species of sympatric and sharing similar ecosystems (Korb and Foster, 2010), possibly due either to the heterogeneity of environmental factors or stochastic processes (Jiménez et al., 2011). Specifically, competition may arise over the sharing of finite and restricted resources (Scholtz et al., 2021).

Based on the resource acquisition and utilization strategy of each feeding group, we classified the hierarchical order of the feeding class by assuming litter feeders and wood

feeders as primary feeders, soil-wood feeders, and fungus growers as secondary feeders, and soil feeders as tertiary and final consumers. Co-occurrence network showed that litter feeders had low correlations ($r \leq 0.39$) with other feeding groups since they occur in patches with high litter mass but their unique open-air feeding habit is different from that of other feeding groups (Miura and Matsumoto, 1997; Syaukani et al., 2016). Unlikely, wood feeders showed stronger associations with the remaining feeding groups ($0.39 \leq r \leq 0.77$). Since wood feeders are systematic occupiers and utilizers of woody materials for a long period, they need more time to colonize and excavate the woody substances. After successful infestation, both soil-wood feeders and fungus growers could be able to access partially broken-down cellulosic materials and other substances. Both feeders can utilize those matters to grow fungi and consume them (Hyodo et al., 2003). Finally, soil feeders can utilize humus-forming substances after resource selection and translocation of soil-wood feeders and fungus growers. Since fungus growers and soil-wood feeders are functionally closely related (Šobotník and Dahlsjö, 2017), they showed the strongest correlation ($r \geq 0.77$) compared to the other feeding groups in our study plot.

Soil-wood feeders showed strong spatial associations (the species level) accompanied by low niche overlaps (individual level) with fungus growers providing that these two groups were occurring alternately in the study plot (Table S2). This implies the competition between these two feeding groups, although they co-occur by sharing a greater number of individuals than any other feeding group in the study plot. Similar occurrences were reported in teak plantations in Malaysia (Fajar et al., 2021) and *Macrotermes* sometimes outcompete *Odontotermes* for food resources (Grohmann et al., 2010). Since litter mass was significantly associated with plant biomass and both feeding groups were secondary consumers after litter and wood feeders, i.e., litter oriented and woody parts oriented, they also may appear at

the same resource accumulation patches but with different concerns on the type of food. Nevertheless, we only discussed possible competition or co-occurrence among the feeding groups and species of termites and further spatial or temporal investigations are still needed.

4.4 Effect of environmental factors on termite distribution

As abiotic factors, all termites (total and all feeding groups) preferred high TPI and low pH environments (Table 3; Figs. S5, S8). Previous studies have shown that higher elevations can significantly affect the diversity and abundance of termites in tropical rainforests (Gathorne-Hardy et al., 2001; Palin et al., 2011; Nunes et al., 2017; Betz et al., 2020). From these studies, we can understand that a decrease in temperature at increasing elevations can limit termite diversity and abundance. However, since the elevation range of our study site lies between 710 m and 735 m asl (Fig. 1), there is a low possibility of detecting the effect of changes in climatic conditions, such as temperature, rainfall, or humidity, within such a small range, in termite diversity. However, the presence of waterways in lower microhabitats can encourage termites to choose higher TPI patches. Moreover, more plant biomass at higher TPI can create more litter mass that can attract more termites than lower patches (Fig. S4). Additionally, high plant biomass and litter mass at higher TPIs can prevent intense direct sunlight to the surface of the soil (Pratiknyo et al., 2020). All the feeding groups of termites chose low pH patches in our study since termites have a tendency to raise soil pH in originally acidic soils and are clearly observed in acidic soil environments (Donovan et al., 2001; Li et al., 2017).

As biotic factors, high litter mass microhabitats attracted fungus growers, litter feeders, and soil feeders, while high plant biomass microhabitats attracted soil-wood feeders and

Table 3 Correlation between termite feeding groups and environmental factors at 0.05 significance level.

Environmental variables	Habitat	Total	Fungus	Litter	Soil	Soil-wood	Wood
TPI	High	+	+	+	+	+	+
	Medium	NS	NS	NS	+	NS	-
	Low	-	-	-	-	-	-
Biomass	High	+	NS	NS	-	+	+
	Medium	+	+	+	NS	NS	NS
	Low	-	-	-	+	-	-
Litter	High	+	+	+	+	-	+
	Medium	+	+	NS	-	+	+
	Low	-	-	NS	-	-	-
pH	High	-	NS	NS	NS	NS	-
	Medium	-	-	-	-	NS	-
	Low	+	+	+	+	+	+

Note: positive correlation (+), negative correlation (-), not significant (NS).

wood feeders (Table 3; Figs. S6, S7). For the litter mass dependent feeding groups, the amount of litter mass added to the surface of the ground was consumed by fast and freely locomoting litter feeders (Syaukani et al., 2016). In addition, fungus growers were also known for their efficient leaf litter decomposition (Eggleton and Tayasu, 2001; Jouquet et al., 2015). Soil feeders, as the final level consumers, might utilize all the residual litter remnants after these two feeders. Since the average annual litterfall in this study plot was reported at 7.3 Mg ha⁻¹ year⁻¹ (Atapattu et al., 2020), litter dependent feeding termites could obtain food resources more efficiently than wood dependent feeding groups. For the plant biomass dependent feeding groups, wood feeders have a specialized behavior of selecting wood to be infested, colonized, and reproduced while soil-wood feeders may utilize the decayed woody portions afterward. Wood feeders were not only associated with high plant biomass patches, but also showed an association with high litter mass (Table 3; Fig. S7f). Although wood feeders were commonly observed in places rich in woody materials (Dosso et al., 2017), they were also observed in patches rich in litter mass since litter mass showed a significant association with plant biomass (Fig. S4).

In summary, our study indicated that not all sympatric feeding groups compete for food resources, and not all separated groups have impact or interactions with others. Moreover, all abundant or dominant species are not ecologically important and small groups can even exert vital regulating functions upon ecological imbalances. Our study revealed that a small change in the fine-scale environmental conditions can have a great influence on the distribution, diversity, and activity-density of termites. This study provides useful information on the activity-density and species composition of termites within a 1-ha plot in a tropical rainforest. However, further studies are needed to understand the interactions of termites and the effects of seasonal shifts and different land-use.

5 Conclusion

This study explored the pattern and mechanism of the activity-density of termites on a fine-scale within a 1-ha plot in a tropical rainforest. We found a high diversity and regular distributions of the major termite communities in the study plot, which were dominated by soil-wood feeders (*Odontotermes*). Generally, soil-wood and wood feeders showed preference of high plant biomass microhabitats, whereas fungus growers, litter, and soil feeders showed preference of high litter resource patches. All groups showed preference of high TPI and low pH environment. This study suggests that the interactions among termites, under the influence of feeding habit differentiation, contribute to maintaining high termite alpha diversity.

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Competing interests

The authors declare that they have no conflicts of interest.

Author contributions

XDY, LSJ, XSW, and MT designed the experiment. MT and LXB conducted the experiments, MT analyzed the data, and wrote the manuscript. XSW and CM provided the basic data of the research plot. XDY and AJA helped to revise the manuscript. All authors reviewed and commented on the manuscript.

Electronic supplementary material

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