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Unoccupied mounds of soil-feeding termites host diverse soil fauna both in primary and logged tropical forests

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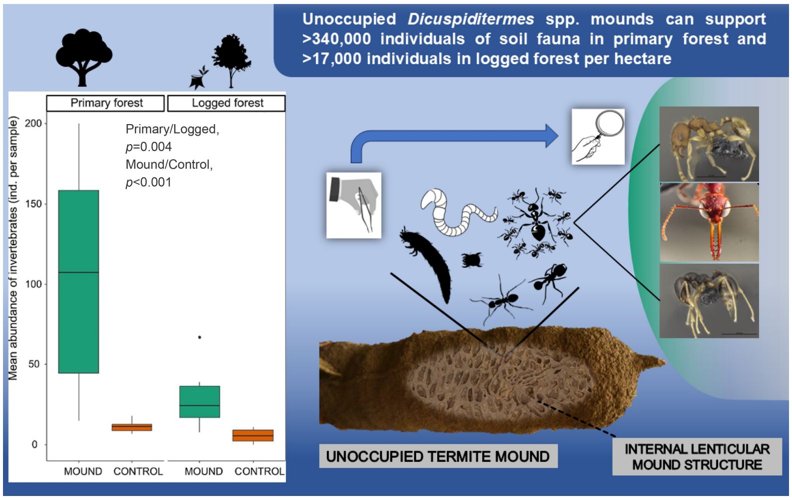
ABSTRACT

- We quantified soil fauna communities in unoccupied *Dicuspiditermes* spp. mounds.
- Mounds supported up to nine times more soil fauna individuals than control soil.
- Ants were the most abundant group with active colonies within the unoccupied mounds.



Many termite species create conspicuous, aboveground soil nest mounds. Once the resident termite colony disappears, the mound structure gradually disintegrates. The now empty mound, which is rich in nutrients, and stable in microclimate, potentially provides an important microhabitat for a different range of species. However, the communities in unoccupied termite mounds remain poorly explored, and the relative importance of these mounds in anthropogenically modified habitats is completely unknown. Here we quantify the invertebrate communities in unoccupied mounds of the soil-feeding termites *Dicuspiditermes* spp. in primary and logged lowland tropical rain forest in Malaysian Borneo and compare them to communities found in control soil. We also quantify the introgression of plant roots into the mounds. We found the unoccupied mounds support a range of invertebrate groups, with ants (Formicidae) having the highest abundances of any group across both habitats. Mounds supported significantly higher abundances of invertebrates overall in both primary forest (nine times more) and logged forest (five times more). However, the number of invertebrate taxa did not differ between mounds and control soils. Plant root mass was higher in control soils than in unoccupied mounds, possibly due to dominance of fine roots in the latter microhabitat. Using previous estimates of mound densities, we estimate that unoccupied *Dicuspiditermes* spp. mounds support >340000 invertebrate individuals in primary forest and >17000 individuals in logged forest per hectare. Our results indicate that unoccupied mounds are an important, although ephemeral, microhabitat for a range of invertebrate groups, in both pristine and anthropogenically disturbed habitats.

Keywords termite, *Dicuspiditermes*, Borneo, tropics, rainforest

1 Introduction

Termites play a key ecological role in many tropical and subtropical ecosystems. They are one of the main decomposers of plant matter in different stages of decay, including soil organic matter in the case of soil-feeding termites (Jouquet et al., 2011). Thus they accelerate nutrient cycling and strongly affect fluxes of methane, nitrogen oxides and carbon dioxide (Bignell et al., 1997; Khan et al., 2018). By building and maintaining their nests and mounds, termites substantially affect bioturbation levels, soil properties and nutrient distribution (Tuma et al., 2019, 2022) which further

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can lead to different patterns of plant communities (Okullo and Moe, 2012; Van der Plas et al., 2013; Erpenbach et al., 2017). In many regions, aboveground termite mounds are so abundant that they dominate the landscape and strongly affect ecological patterns (Meyer et al., 1999; Funch, 2015; Martin et al., 2018), even forming a distinct, termite-modified soil layer, called the termitosphere (Lavelle and Spain, 2001). The presence of termite nests and mounds in the environment can therefore affect a multitude of ecosystem properties and functions.

Termite mounds represent a unique type of microhabitat maintaining specific conditions not only for termites but also for other potential inhabitants. In this study we use the term *mound* when describing the whole physical protective structure termites build and nest in (that is the case of our focal genus), while the term *nest* is used when referring to the the place where a colony lives and which can be inconspicuous or without a single central location in many species. There are two main ways in which termites alter conditions in their mounds that are relevant to other potential inhabitants: manipulation of microclimate and changes in the availability of nutrients. First, in terms of microclimate, there is typically higher humidity, lower and more stable temperature within the mound interior (Grube and Rudolph, 1999). Termites collect water in form of wet soil aggregates either from deep soil horizons or during rain events. The protective mound layers then maintain the humidity inside the mound at higher levels than in the surrounding air (Grube and Rudolph, 1999; Bardunias et al., 2020). Temperature in the mounds is generally lower and fluctuates less than in the ambient air due to the mound's functional architecture. This allows ventilation by convective air flows and also the removal of metabolic gasses, which are poisonous for invertebrates in higher concentrations, from the mound (Vesala et al., 2019). Second, in terms of nutritional value, termite mounds have high levels of nutrients such as phosphorus, nitrogen or carbon from collected food resources or from deposited waste and termite faeces (Jouquet et al., 2017; Tuma et al., 2022). In the most extreme case, in soil-feeding and mound-building termites (e.g., *Dicuspiditermes*, *Cubitermes*), the whole mound structure predominantly consists of termite faeces, since these are used as the primary building material (Brauman, 2000; Holt and Lepage, 2000; Ndiaye et al., 2004). With this richness in plant-available nutrients, unoccupied mounds may be preferentially colonized by plant roots seeking nutrient-rich environments, especially in high competition settings such as rainforest soils (Muthert et al., 2020). Although several studies have highlighted the impact of termite mounds on vegetation cover and community, the root colonization of mounds has not yet been empirically well tested (but see Ackerman et al., 2007). Moreover, termites themselves represent a nutritious, poorly chitinised food source for a range of potential predators. The mounds are also sealed from the environment by protective soil or carton layers, so the mounds represent an enclosed and secure microhabitat. Taken together, termite mounds provide favourable, stable microclimatic conditions, are easily defensible from natural enemies, and have high nutrient levels. As a result, such enticing conditions attract other, non-termite animals and plants, especially in high-competition environments.

Although a range of animal groups, with differing degrees of specialisation, are able to exploit termite mounds in some way (Sheppe, 1970; Deligne et al., 1981; Tuma et al., 2020), when the colony is active, termites apply a wide range of effective defence mechanisms. The first line of defence is passive. The mound wall itself forms a sturdy barrier, often hardened by mixture of termite saliva with clay and other mineral particles, making the mound outer coating very hard to penetrate (Adepegba and Adegoke, 1974; Noirot and Darlington, 2000). The complex architecture of the mounds makes it challenging for intruders to navigate the maze of tunnels and chambers (Eggleton, 2011). In cases of termite species without a soldier caste or in situations when workers are directly attacked, termite workers then also defend mounds actively, fighting off intruders by either direct biting, defecating on the intruders, sacrificial explosion of termites (Noirot and Darlington, 2000; Šobotník et al., 2010), or by rapid sealing up the breakthrough points (Chouvenc et al., 2015). In termite species with soldier castes, these soldiers are recruited to the point of attack. Soldier termites possess a range of specialized mechanical and chemical defence mechanisms. These mechanical defences are reflected in the shapes and functions of soldier’s mandibles, which include piercing, slashing, crushing and a number of types of asymmetrical snapping mandibles (Prestwich, 1984). Chemical defence strategies of soldiers include squirting, daubing or smearing irritants, poisons, glues or anti-healing agents onto mound intruders. Many of these defence mechanisms are thought to be specifically adapted for dealing with ant ingression into colonies, as this group is one of the main termite predators (Jaffe et al., 1995; Tuma et al., 2020).

This complex defence system makes it challenging for other animals to intrude upon or establish nests within termite mounds. Nevertheless, a wide range of animal taxa uses termite mounds in many different ways (Redford, 1984). For example, large mammals such as rhinoceros or elephants use the mounds externally as preferential browsing and lick spots (Muvengwi et al., 2014; Charles et al., 2021). Birds use termite mounds as nesting and perching places and also feed on termites. For example, 179 bird species in Brazil opportunistically feed on termites (de Vasconcelos et al., 2015). Various reptile species also lay their eggs in termite mounds (Moreira et al., 2009; Hood et al., 2020). Even a larger number of invertebrate species from various taxa are reported to cohabit with termites. Those are called *termitophiles* in the case of non-termite invertebrates (which can be obligate or facultative), or *inquilines* in the cases when the mound intruder is another termite species living with the original builder of the nest or mound (Florencio et al., 2013; Hugo et al., 2020). Inquiline termites typically have non-aggressive or repellent interactions with the host species and only use existing spaces of the mound for their own colony development (Marins et al., 2016; Hugo et al., 2020). This kind of cohabitation includes several species of inquiline termites across different geographical regions along with cases of multiple inquiline species inhabiting the same host colony (Costa et al., 2019). There are also cases of obligate inquilinism, e.g., *Inquilinitermes microcerus* which is a termite species fully dependent on the host species for its colony development (Shellman-Reeve, 2010; Cruz et al., 2023). Other notable invertebrate termitophiles include both adult and larval beetles (Coleoptera) with Staphylinidae, Elateridae, and Carabidae being the most commonly reported; bees (Apidae) and wasps (Vespidae); earwigs (Dermaptera); spiders (Araneae), and centipedes (Chilopoda) (Da Cunha and Brandão, 2001; Costa et al., 2019; Hood et al., 2020). One of the most commonly reported groups of termite guests is the ants. Almost two hundred ant species have been recorded as nesting in termite mounds (Longhurst and Howse, 1978; Jaffe et al., 1995; Leal and Oliveira, 1995; Dejean and Fénéron, 1996; Schöning and Moffett, 2007; Hood et al., 2020; Tuma et al., 2020). The nature of the interactions between ants and the resident termites ranges from cohabitation to occasional or regular preying on termites (known as termitolesty). Ants typically seclude themselves in less occupied mound chambers where they actively build and maintain the barrier between their nesting space and the host termites in order to limit aggressive, dangerous encounters (Lubin and Montgomery, 1981).

When a mound is no longer inhabited by its resident termite colony, the active defences previously mediated by the termites no longer function. Consequently, the mound can then be used and/or colonized by a potentially different variety of animal species. This abandonment can be caused either by the death of the resident termite colony or when the colony moves (e.g. in the Termitinae subfamily where the colony spreads by budding into a new mound, while the original mound is abandoned). When the benefits of inhabiting a mound relate not to the interactions with termites but rather to dwelling in the mound itself, which is necessarily the case with unoccupied mounds, this is known as *termitariophily* (from the term "termitarium", sensu Araujo, 1970; Pisno et al., 2019), rather than termitophily. If the intruder is able to penetrate the outer coating or a mound wall of the unoccupied mound, then there is a pre-built, empty, relatively safe and often nutrient-rich niche available for foraging, temporary shelter or nesting. Unoccupied termite mounds sometimes attract aggressive occupants such as ants which will protect their new nesting site or foraging spaces (or perhaps expand their activities in the case of ants that previously cohabited with the previous termite colony). Nevertheless, there remain several outstanding knowledge gaps in relation to the ecological importance of unoccupied mounds.

There is almost no information about community succession in unoccupied mounds in the field (although see a laboratory experiment by Chouvenc et al., 2013). Generally, high competition for foraging and nesting spaces is predicted in environments with overall high competition such as tropical rainforests (Blüthgen and Feldhaar, 2010) so unoccupied mounds could represent valuable resources in these habitats. Furthermore, we do not know whether unoccupied mounds retain any importance in anthropogenically modified habitats, such as logged forests and plantations. Given that modified habitats often present more challenging microclimates (Williamson et al., 2022; Santos et al., 2024), and can be limiting in terms of resources generally (Rozak et al., 2018; Widyati et al., 2022), termite mounds are potentially important microhabitats in these landscapes. A limitation of previous studies exploring the importance of unoccupied mounds is that they depend only on limited data from dissections of the dead mounds, with typically no comparison with the background soil-dwelling arthropod communities (Redford, 1984; Costa et al., 2019; Hood et al., 2020). Furthermore, the importance of unoccupied mounds as a resource for plants, as characterised by the growth of roots from individuals elsewhere, has not yet been studied. Hence it remains unclear whether unoccupied termite mounds support elevated abundances of arthropods, different composition of taxa or higher amounts of plant roots relative to the rest of the soil. Furthermore, previous studies recording the secondary inhabitants of termite mounds focus largely on South America and Africa targeting mainly large Macrotermitinae mounds with much less attention having been given to the Indomalayan zoogeographic region. Additionally, some less well-known termite genera such as soil-feeding mound builders have not previously been investigated in this manner although their nest mounds are frequently found at high densities (Tuma et al., 2019).

In this study, we investigated for the first time how unoccupied mounds of the soil-feeding termite *Dicuspiditerme*s spp. differed in the presence and community composition of invertebrates, and colonisation by plant roots, relative to the rest of the soil in Malaysian Borneo. We also explored how these effects differed between primary lowland tropical Dipterocarp forest and selectively logged forest. Even though the mounds of this genus are abundant in forest habitats and have previously been shown to significantly contribute to bioturbation and nutrient accumulation (Abe and Matsumoto, 1979; Tuma et al., 2019, 2022), the secondary inhabitants of their mounds have never been studied. By taking the same volume of unoccupied mound and control soil samples we were able to compare the relative abundance and diversity of invertebrates between habitats. Using this approach, we asked following questions: 1. Do mounds host a higher abundance and diversity of invertebrates than control soil samples? 2. Do mounds serve as nesting microhabitats for ants? 3. Is the difference in abundance and diversity of non-termite invertebrates between the mounds and control soils higher in logged forest than in primary forest as we expect a reduction of nesting microhabitats in logged forest soils due to effects of logging? 4. Do the mounds contain more plant roots than control soils due to their higher nutrient content?

2 Methods

2.1 Field sites

Field sampling took place within the Stability of Altered Forest Ecosystems (SAFE) Project sites (Ewers et al., 2011 see the website of safeproject.net) in Sabah, Malaysian Borneo, in two types of forest. Primary lowland dipterocarp forest was sampled in Maliau Basin Conservation Area (MBCA, SAFE Project site 'OG2'; 4.747 133−116.972 182). The 58 840 ha MBCA forest has never been logged and is part of a larger continuous forest block of one million hectares of logged forest. The continuous selectively logged forest was sampled in the SAFE Project experimental area (SAFE Project sites 'LFE', 'B', 'LF1'; 4.729 231−117.616 939) which had been selectively logged at least twice at the time of sampling (Struebig et al., 2013). Note that all sites were sampled before any SAFE project-related experimental fragmentation. Data were collected from 9th July to 17th August 2016. This was during a two-year-long El Niño event, although no fires occurred in the study area. The area has an average annual temperature of 26.7 °C and receives on average 2 669 mm of rainfall annually. There is no strong seasonality (Walsh and Newbery, 1999).

2.2 Mound sampling

We investigated the mounds of the soil-feeding termites *Dicuspiditermes* spp. (Isoptera: Termitidae). Two species from this genus were identified during previous fieldwork in the sampling plots (Tuma et al., 2019), *Dicuspiditermes nemorosus* (Haviland, 1898) and *Dicuspiditermes minutus* (Akhtar and Riaz, 1992), which both build phallic-shaped mounds from a mixture of their faeces and a smaller fraction of mineral particles. Voucher specimens for these species were taken from active mounds of the same shape found nearby the unoccupied (sampled) mounds. Owing to difficulties identifying these species from the unoccupied mound structure alone, we combine them in this study (referred to as *Dicuspiditermes* spp. herafter). The identification of the respective termite species, including the non-*Dicuspiditermes* spp. termites present in mounds was done by David Jones at Natural History Museum (NHM), London. We classified the mounds as being unoccupied if they had been unoccupied by termites for more than one year, as determined through labelling and surveying for occupancy during a previous field season, in which plot-based mound turnover was estimated (Tuma et al., 2019). We chose mounds unoccupied by *Dicuspiditermes* spp. termites, based on the following conditions: 1. the mound had fallen and was touching the soil surface in a horizontal position, 2. when the mound material was gently investigated by digging two to three narrow holes, no termites were observed, and 3. the surface of the mound was covered by mosses. Note that the third condition was used only as supplementary evidence for mound status, since moss cover is not entirely reliable as an indicator of termite absence. We collected whole mounds in the field into sealed plastic bags and transported these to the field laboratory within six hours. We took the control samples 0.5 m away from the mound using a tubular soil corer of dimensions 4.0 cm in diameter and 5.0 cm in depth in a triangular layout, such that the three control samples were approximately 0.87 m apart from each other (see Supplement 1) in locations with no visible termite structures nearby. Before collection of control samples, litter was scraped away and the soil sample was checked for termite presence as there were often non-distinct termite nests below the surface. In those cases, another sample nearby was taken instead. This was done to ensure that the controls also comprised soils without living termite colonies. Thus our results should be interpreted as the impact of unoccupied termite mounds relative to nearby soils unoccupied by termites. We collected N=6 mounds per habitat with the same number of paired control samples. The average size of mounds from primary forest was 32 cm (SD=1.8) in height and 8 cm (SD=1.1) in diameter, for logged forest = 36 cm (SD=9.7) in height and 10 cm (SD=1.2) in diameter. There were no statistically significant differences in mound sizes between habitats (*t*-test). In the laboratory we took three samples per mound using the same method as for control samples. The volume of soil searched for animals equalled 188.4 cm^3 of mound or control soil material (in each cases comprising a composite sample of three 62.8 cm^3 subsamples; see Supplement 2).

2.3 Extraction of invertebrates from mound and control samples

In the field laboratory, we placed three subsamples from each mound or control sample into a plastic tray with high rims, and gently broke down the soil aggregates. During this time the samples were searched for invertebrates visible to the naked eye by a trained research assistant for ten minutes using a head torch. All invertebrates were collected using entomological tweezers and transferred into 96% ethanol. The animals were counted and identified to higher taxonomic levels (order: Araneae, Blattaria, Coleoptera, Diplura, Diptera, Isopoda, Pseudoscorpionida; infraorder: Isoptera; class: Diplopoda, Chilopoda, Insecta, Symphyla and subclass: Acari, Collembola, Oligochaeta). As ants (Formicidae) accounted for 79.3% of all individuals in the samples, they were also evaluated separately (Fig. 3, see the following). They were further identified to species or morphospecies level using genus level key by Fayle et al. (2014), a voucher collection of ants from the sampled area maintained by the lead author and reference species images from Antweb (AntWeb, 2024). When ants were found in the samples, we defined a colony as being present when there were both workers of a particular species and brood or queen (dealate) from the same species.

2.4 Assessing the potential of unoccupied mounds to host invertebrates

We combined the data on invertebrates inhabiting the unoccupied mounds of *Dicuspiditermes* spp. with the data from our previous study (Tuma et al., 2019) which investigated the distribution and turnover of mounds of the same termite species in the same plots (Table 1). Hence, we could calculate the volume of an average mound (measurements taken from *n*=30 active mounds) and relate it to the mean number of invertebrate inhabitants per mound. Then we multiplied the mean number of unoccupied mounds per hectare present in the forest by the mean number of invertebrates per unoccupied mound. Through this extrapolation, we estimated the total available space in unoccupied mounds and the total counts of invertebrates residing in those mounds in both primary and logged forest per unit area. Additionally, we applied the same calculation to the number of freshly unoccupied mounds per year, allowing us to estimate the annual number of invertebrates potentially moving into this newly available microhabitat. Note that if the system is in a steady state in terms of unoccupied mound densities, then these numbers would be balanced by the disappearance of equal numbers of existing unoccupied mounds, presumably as they break down further.

2.5 Measurement of root content

Root content was measured by collecting all plant roots visible to the naked eye in the mound or in the control soil samples during the search for invertebrates. The roots were cleaned of the soil particles, oven-dried at 60 °C for 24 h and weighted on analytical scales with 0.000 1 g precision.

2.6 Data analyses

A linear mixed effects model analysis, LMM - R packages “LMERConvenienceFunctions” (Tremblay and Ransijn, 2015), “lmerTest” (Kuznetsova et al., 2017) and “afex” (Singmann et al., 2015) with “lmer”, “afex::mixed” functions, was conducted to assess the relationship between abundance/taxonomic richness of invertebrates (separate analyses conducted at higher taxonomical levels for all soil fauna and species level for ants) and plant root content (response variables) in relation to the predictor variables: sample type (unoccupied termite mounds vs. control soils) and habitat (primary vs logged forest). Generalized linear mixed effects model with Poisson error family distribution (GLMM, R package “pscl” (Jackman et al., 2015) with function “zeroinfl”)) was fitted for zero-inflated data of ant colonies found in unoccupied termite mounds. Wald-type tests (R package “lmtest” (Hothorn et al., 2015) with “waldtest” function)) were used to assess the significance of each predictor variable, with *p*-values calculated from the summary output of the GLMM. We included an interaction between sample type and habitat and a random factor of sample (mound/control) in all original models. Initially, full models with both main effects and their interaction were fitted. If the model without the interaction had lower AIC, then the interaction was removed, and the main effect was also subsequently

Table 1 Predicted abundances of invertebrates in unoccupied termite mounds (either due to mound abandonment or death of the colony) in relation to mound density (per hectare and year) in primary and logged forest in Sabah, Malaysia.

Habitat	Number of unoccupied mounds (ha)	Mean volume of all unoccupied mounds (L ha^{-1})	Number of newly unoccupied mounds (ha year^{-1})	Mean volume of newly unoccupied mounds (L ha^{-1})	Average number of animals per unoccupied mound (sum of three subsamples, extrapolated, based on mound volume)	Total number of animals in unoccupied mounds (ha)	Number of animals in newly unoccupied mounds (ha) = **potential yearly increase of animals**
Primary forest	**197**	613	**61**	191	105	**341 496**	**106 263**
Logged forest	**61**	112	**45**	83	30	**17 820**	**13 234**

The data on unoccupied mound presence are from Tuma et al. (2019) and the data on invertebrate abundances come from the current study. The initial units of mound volume (cm^3) were converted to litres for easier comparison among categories.

removed from the model where appropriate in the same way. Log-transformation was applied to response variables to achieve normality of residuals in the case of all taxa abundance, ant abundance and root weight. These analyses were performed in R software version 4.3.0 (RStudio Team, 2016; R Core Team, 2023). Multivariate analyses were performed in Canoco v. 5.15 software (Ter Braak and Smilauer, 2018) to explore the relationship between the predictor variables and composition of higher taxa of soil fauna. Redundancy analysis (RDA) ordination was used, since the longest axis length was 2.7 SD units, to summarise the main patterns of variation in the response matrix (relative abundance of invertebrates) explained by a matrix of explanatory variables (type of the sample). Dataset included ants as family Formicidae here. For uncluttered visualization the habitats were plotted separately, although the ordination was only run once. Data were centred, standardized and log-transformed prior to multivariate analyses. Standardizing and centering by species data allowed the RDA to focus on relative abundances, eliminating biases from extreme absolute counts.

3 Results

In total, we collected 911 invertebrate individuals, with 808 individuals in termite mounds and 103 in control samples from 16 higher taxonomical groups (13 in mounds, 14 in controls; Fig. 1). The mean abundance of invertebrates was nine times higher in the mounds than in the controls in primary forest and five times higher in the mounds than in the controls in logged forest (effect of type of the sample−mound/control: LMM, $F_{1,21}$=32.18, p<0.001) and was higher in primary forest than in logged forest (effect of the habitat−primary/logged forest, $F_{1,21}$=10.42 p=0.004; Fig. 2A). However, there was no difference in the mean number of higher taxa between the mound and control (LMM, $F_{1,21}$=0.01, p=0.92; Fig. 2B) or between habitats (LMM, $F_{1,21}$=2.98, p=0.10). While the redundancy analysis showed no effect of habitat on community composition (pseudo-F=1.4, p=0.164), there was a significant effect of type of the sample = mound/control, contributing an adjusted 7.0% of explained variability (type of the sample, simple effect pseudo-F=2.2, p=0.008; Fig. 5, the following).

Ants were ubiquitous in the mounds (100.0% incidence) as well as in the control samples (83.3% incidence). The mean abundance of ants was fourteen times higher in the mounds than in the controls in the primary forest and eleven times higher in the mounds than in the controls in the logged forest (LMM, $F_{1,21}$=19.11, p<0.001). In total, we identified 22 species or morphospecies of ants, with *Pheidole* and *Carebara* being the most abundant genera. *Pheidole butteli* was the most ubiquitous species in the mounds across the two habitats (6 of the 12 mounds sampled). The median number of ant species in mounds was 1.25 times higher than in the controls (LMM, $F_{1,11}$=11.00, p=0.007; Fig. 3) with nine unique species (not shared with the control samples) in primary forest and four unique species in logged forest mounds (Fig. 3D and Supplement 1). The confirmed presence of ant colonies was evaluated separately. In total, we found 18 ant colonies from 12 species in our samples, with a total of 17 colonies found in mounds and only one colony in

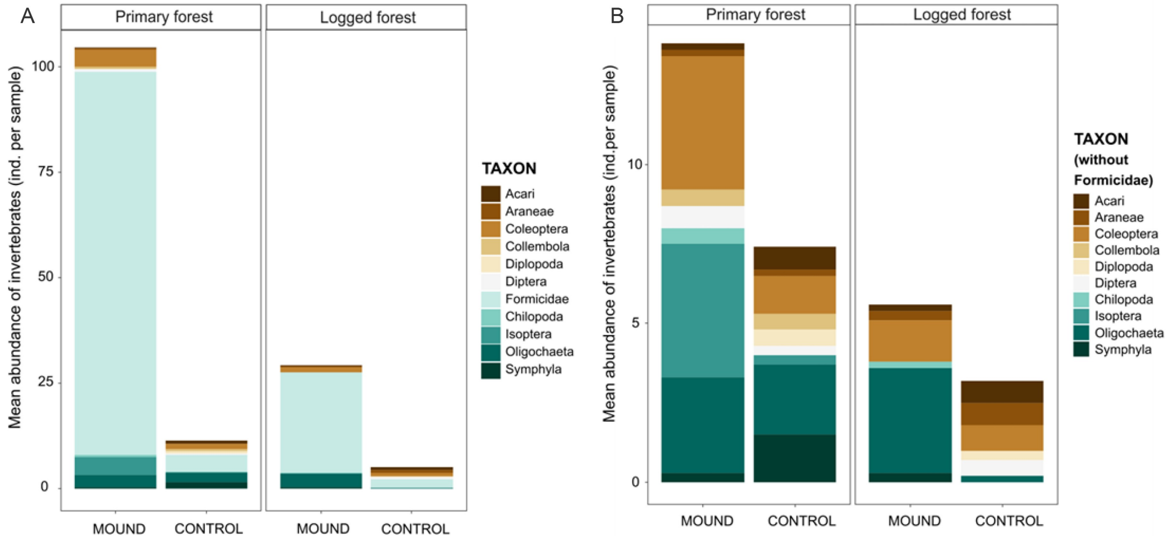


Fig. 1 Mean invertebrate abundances in unoccupied *Dicuspiditermes* spp. termite mounds and in control soil samples in primary and logged forest in Sabah, Malaysia showing the first eleven most abundant taxa for clarity. The full list of taxa is available in Supplement 1. (A) all recorded taxa; (B) the same dataset, without the data for ants (Formicidae) as this taxon obscured the patterns of the other taxa due to its high numerical dominance in the samples. Each individual sample comprises invertebrates sampled from 188.4 cm^3 of material.

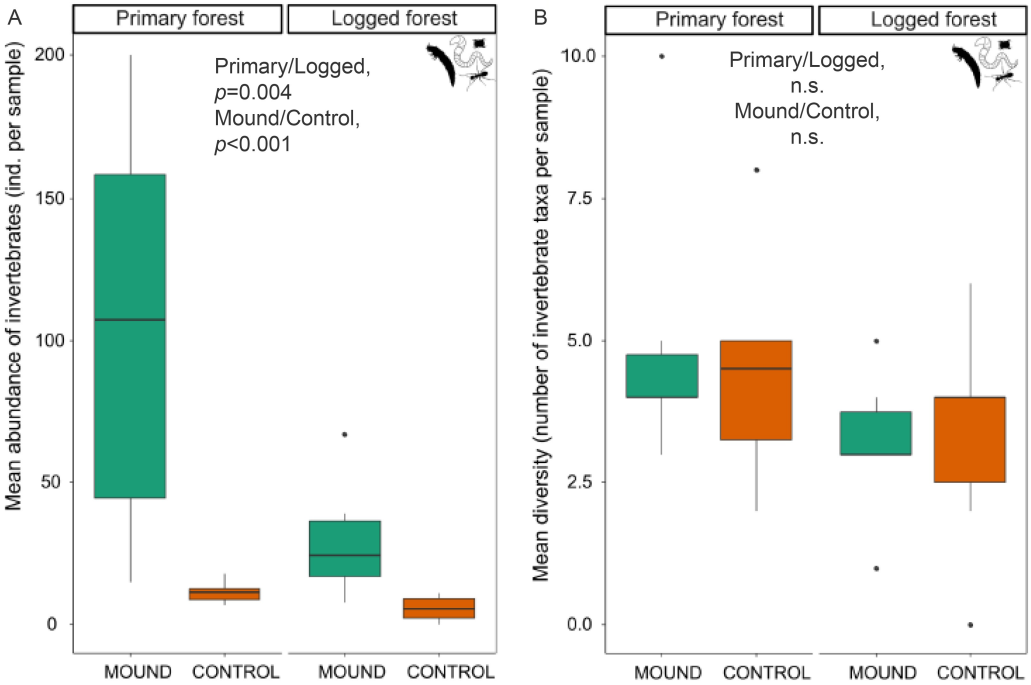


Fig. 2 (A) Mean abundance and (B) mean number of invertebrate taxa found in unoccupied mounds of *Dicuspiditermes* spp. and in control soils in primary and logged forest in Sabah, Malaysia. Medians are denoted by bold horizontal lines, the interquartile range box represents the middle 50% of the data, and the whiskers represent full data ranges. Outliers are represented by full points and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles. The significance tests originate from linear mixed models (LMMs) with a 0.05 threshold of significance. Each individual sample comprises invertebrates sampled from 188.4 cm^3 of material.

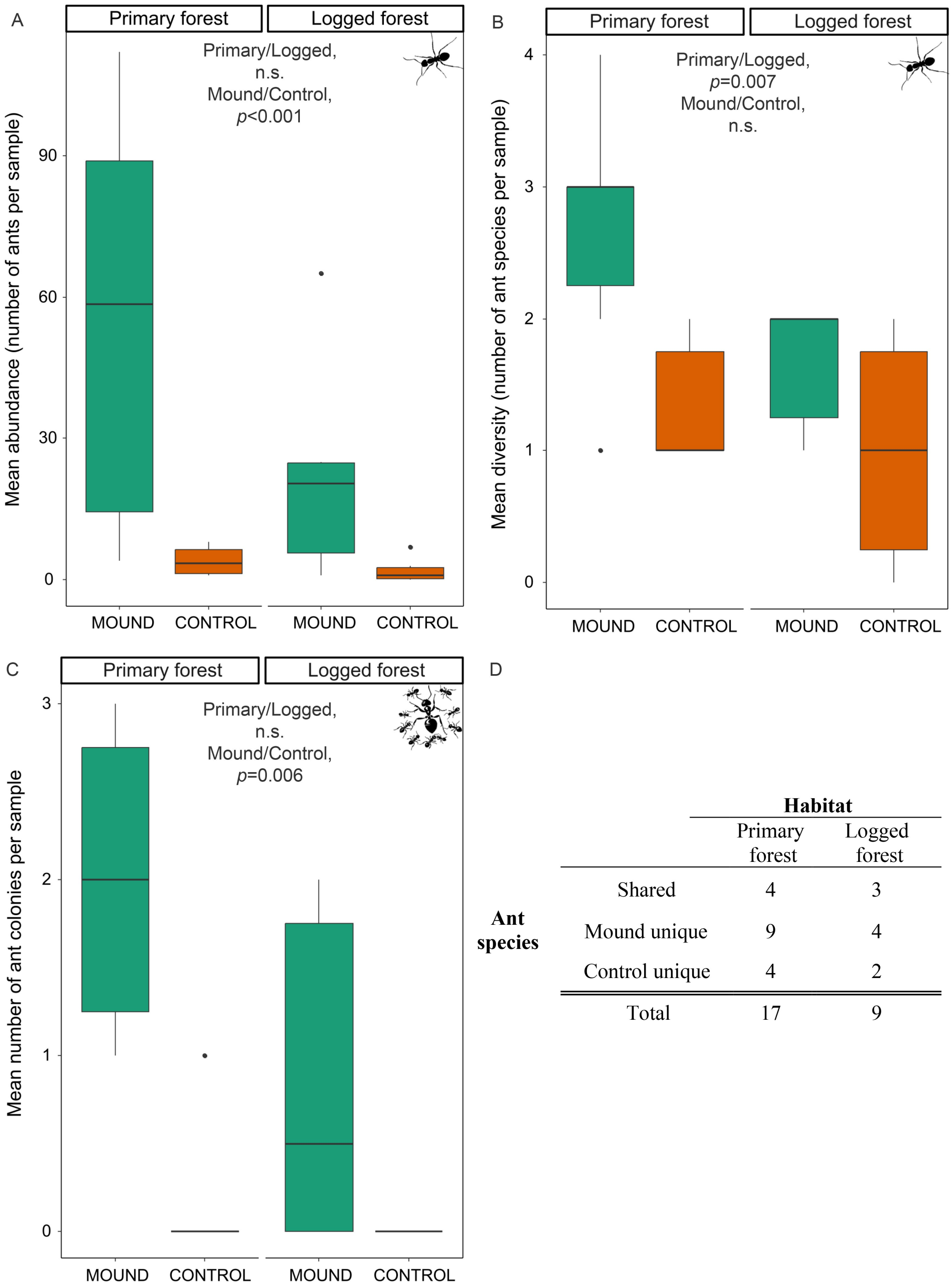
controls (GLMM, z-value$_{1,21}$=2.75, *p*=0.006; Fig. 4) with no difference between habitats (GLMM, z-value$_{1,20}$=1.82, *p*=0.069). The plant root content was generally lower in mounds than in control soil (LMM, $F_{1,22}$=7.40, *p*=0.013, Fig. 5).

4 Discussion

In this study, we showed that unoccupied mounds of soil-feeding termites in the genus *Dicuspiditermes* host a range of invertebrate taxa with mounds having five to nine times higher invertebrate abundance compared to the surrounding soil. This is the first time the relative importance of unoccupied termite mounds for providing living space for invertebrates and plant roots has been quantified. The difference that we found is probably caused by the properties of the mound itself since the mound is a pre-built, well-protected micro-habitat which can serve as a suitable foraging or nesting space for a range of secondary inhabitants. However, as the mound is constructed predominantly from termite faeces in this genus, it is rich in basic soil nutrients (Tuma et al., 2022) and it may also serve as a valuable food source for soil-feeding fauna.

4.1 Unoccupied *Dicuspiditermes* spp. mounds as habitats for a wide range of invertebrates

This could be the case of Coleoptera larvae which were the third most abundant group in mounds and can feed directly either on the mound material, on the fungi mycelia which were observed as well or on the intruding plant roots. Hence the termite mounds provide suitable microhabitats containing feeding substrates for Coleoptera larval development (Costa and Vanin, 2010; Potapov et al., 2022). Similarly, the second most common taxon in mounds, Oligochaeta (earthworms and enchytraeids) feeds on organic-rich substrates and we even directly observed the mound material in their guts. In two mounds we found a secondary termite inhabitant from a soil-feeding genus *Pericapritermes* (in one mound there was a colony, but in the second there was only one individual present which could be just an accidental forager). Thus the unoccupied mounds can serve as a secondary nesting space for other soil-feeding termite species or, as the cases described above, soil-feeding termites can also feed directly on the mound substrate. Cohabitation in the same mound is a common phenomenon among termites (Marins et al., 2016) and the unoccupied mound is not protected by its original inhabitants and is thus free to be occupied by other termites. However, the mound can be defended by its new, non-termite inhabitants as well (e.g.,



		Habitat	
		Primary forest	Logged forest
Ant species	Shared	4	3
	Mound unique	9	4
	Control unique	4	2
	Total	17	9

Fig. 3 (A) Mean abundance of ant individuals per sample, (B) species richness of ants per sample and (C) mean number of ant colonies of ants in unoccupied mounds of *Dicuspiditermes* spp. and in control soil in primary and logged forest in Sabah, Malaysia. The presence of an ant colony was confirmed in cases when one termite mound contained workers of a particular species with brood and/or a dealate queen. (D) Summary table of ant species found inhabiting mounds. The number of species present in both mounds and the control samples in each habitat is marked as *shared*, while *unique* denotes the species which were found only in either the mound or in the control soil. In graphs, medians are denoted by bold horizontal lines, the interquartile range box represents the middle 50% of the data, and the whiskers represent full data ranges. Outliers are represented by full points and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles. LMM models were used to evaluate the effect of habitat or type of the samples and their interaction in (A) and (B) while a GLMM model for zero-inflated data was used in the case of graph (C), with a 0.05 threshold of significance for all analyses. Each individual sample comprises invertebrates sampled from 188.4 cm^3 of material.

ants). In our previous studies, we occasionally recorded new structures being built within the unoccupied *Dicuspiditermes* mounds by other (unidentified) termite species (Jiri Tuma field notes, unpublished) so this may be a common phenomenon. Additionally, in a few cases, we observed the unoccupied mound serving as a base for a new mound growth, apparently in instances when the original colony proliferated by budding (common in Termitidae; Noirot and Darlington, 2000), although these were not included in our samples. Hence the temporal dynamics of the creation of unoccupied mounds and their colonisation might be even more complex.

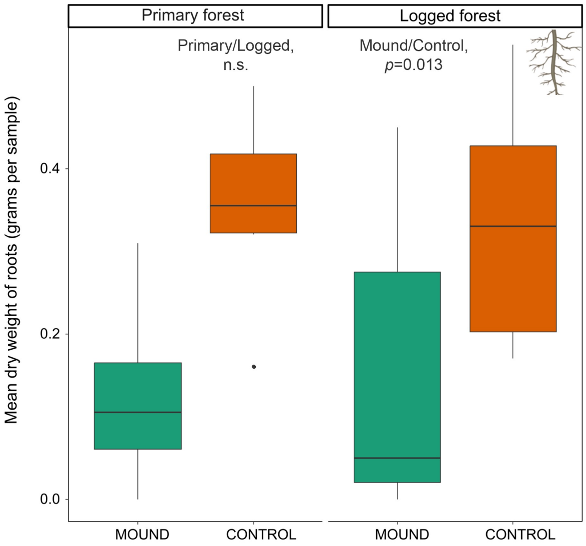


Fig. 4 The mass of plant roots found in unoccupied mounds of *Dicuspiditermes* spp. and in control soil in primary and logged forest in Sabah, Malaysia. Medians are denoted by bold horizontal lines, the interquartile range box represents the middle 50% of the data, and the whiskers represent full data ranges. Outliers are represented by full points and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles. The significance test originates from linear mixed model (LMM) with a 0.05 threshold of significance. Each individual sample comprises roots collected from 188.4 cm^3 of material.

4.2 Ants as the most abundant inhabitants of unoccupied *Dicuspiditermes* spp. mounds

The most abundant group in termite mounds were ants, comprising 79.3% of all individuals, and being present in 11 out of 12 mounds. Ants thus govern most of the patterns we observed between mounds and control soils but also between habitats (Figs. 2, 3). As there is a relatively high abundance of potential prey for ants, the unoccupied termite mounds may serve as suitable foraging spaces. However due to the high incidence of ant colonies (9 out of 12 mounds with at least one ant colony), the unoccupied mounds may primarily serve as a nesting space. This would correspond to the high pressure for nesting spaces in the rainforest in general (Sagata et al., 2010; Plowman et al., 2020) but also to the high levels of cohabitation between ants and termites observed even when mounds are active (Wheeler, 1936; Holt and Greenslade, 1980). However, this has not been described for *Dicuspiditermes* termites. Because of the high number of ant colonies established within the unoccupied termite mounds, we cannot rule out the possibility that some of the other invertebrates sampled are in fact myrmecophiles. Consequently, there might be an overlapping community of termito/termitariophiles and myrmecophiles. On the contrary, ants may protect the mounds they nest in as well. Therefore the ant presence in the unoccupied mounds may prevent other invertebrates from colonising the unoccupied termite mounds, especially in taxa susceptible to ant predation (Higashi and Ito, 1989; Jaffe et al., 1995; Tuma et al., 2020).

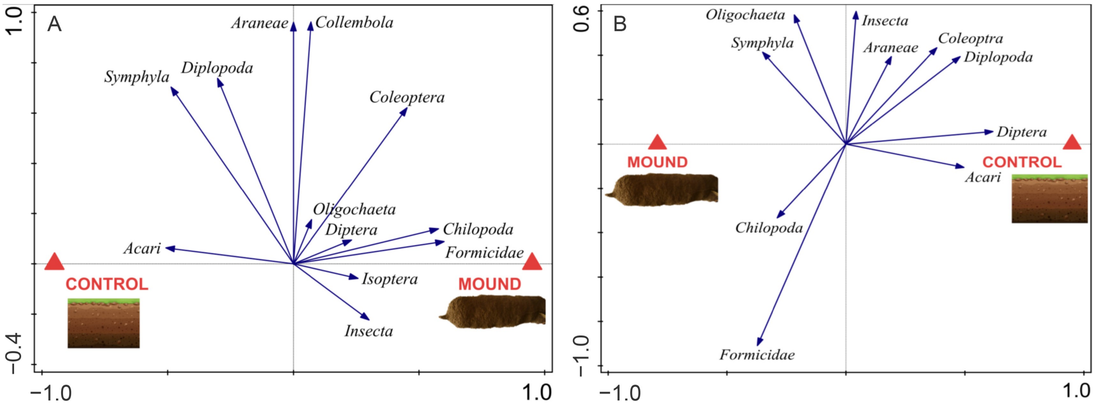


Fig. 5 A multivariate constrained Redundancy Analysis (RDA) summarising the main patterns of variation in the response matrix (abundance of invertebrates found in unoccupied *Dicuspiditermes* spp. mounds and in control samples) which is explained by a matrix of predicted explanatory variables (type of the sample) for (A) primary forest and (B) for logged forest, in Sabah, Malaysia. The full model including both habitat and type of the sample is given in the results section. Data represent proportional abundances and were standardised, centred and log-transformed to show relative differences among the higher taxa, so the species data are not skewed by the absolute magnitudes of abundances.

We found 17 species of ants in the unoccupied mounds and 11 in the control soils, and the mounds hosted twice as many unique species as the control soils. In addition to the ubiquitous opportunist genera *Pheidole* (with five species present in mounds) and *Monomorium*, we found species which live more cryptically or with less well-known nesting habits. These were typically of small body size (*Syllophopsis australica*, *Mayriella transfuga*, *Strumigenys* cf. *amasara* or *Carebara pygmaea*) while *Carebara atoma* being even one of the smallest ants known. Small body size might be of advantage when nesting and foraging within the rather narrow chambers of *Dicuspiditermes* spp. mounds and the colonies might also protect themselves better against larger invertebrates and other ants in such confined spaces. Similarly, we found two colonies of *Discothyrea bryanti*. Ants from this genus are tiny predators with small colonies and peculiar nesting habits. They have been found nesting in spider egg sacs or in the egg chamber of ant nests (Brown, 1957; Dejean and Dejean, 1998), in both cases feeding on eggs (Katayama, 2013). We found a whole colony enclosed in one lenticular chamber of the unoccupied mound. We speculate that they can feed on ant eggs as they occupied the same termite mound as a colony of *Monomorium* cf. *pharaonis*, or on mites which were present as well. Similarly, there is limited knowledge of the biology of the ant genus *Mayriella*. These ants are found in litter, soil or rotten wood (Wheeler, 1935; Shattuck and Barnett, 2007), but unoccupied termite mounds are also potential foraging or nesting habitats. Hence further exploration of unoccupied mounds of termites might contribute significantly to our knowledge of the natural history of less common or cryptically living ant species and other soil invertebrates. We cannot determine whether the ant species we found in unoccupied mounds previously preyed on or even displaced the original resident termites, but the abundant *Pheidole* spp., or *Carebara* spp. that are common in this system are well-known opportunistic termite predators (Tuma et al., 2020) and when active mounds are broken open they usually rapidly emerge and prey on exposed termites (Jiri Tuma, personal observation). In conclusion, although ants are well known to influence many core ecosystem processes (e.g., Del Toro et al., 2012; Farji-Brener and Werenkraut, 2017), there is still limited understanding of the specific microhabitats on which they rely. This gap in knowledge is particularly evident for cryptically living and nesting species. The occurrence and diversity of ants are closely tied to high microhabitat complexity (e.g., Bátori et al., 2020; Priest et al., 2021), where unoccupied termite mounds may represent an important resource.

4.3 Differences between primary and logged forest

The number of all invertebrates in the unoccupied termite mounds was higher in the primary forest compared to the logged forest. However, the control samples contained 50% fewer invertebrate individuals in the logged forest compared to the primary forest. There were also much higher densities (1.6 times more in primary compared to logged forest) in the primary forest of the unoccupied mounds. Consequently, we might expect this would mean that mound availability is no longer a limiting factor in this habitat, and hence the per-mound density/species richness would be lower. However, we found the opposite pattern to this, since invertebrate densities were higher in mounds in primary forest. Hence the kinds of resources that the mounds provide are clearly a limiting factor even in primary forest. Future research should include surveys of mounds in other simplified habitats such as plantations, which have generally lower invertebrate diversity than forested habitats (Turner and Foster, 2009, although note that soil-feeding termites are very rare in those).

4.4 Unoccupied mound availability in space and time

Although new unoccupied mounds become available in the given space, the ongoing breakdown of them through time means that unoccupied mounds are ephemeral microhabitats. Although new unoccupied mounds become available, they are likewise breaking down and the available space is vanishing. The breakdown of mounds is caused by rain and clearly accelerated by a range of animal taxa. We previously estimated there to be in mean 613 litres/ha of unoccupied mound space available in primary forest and 112 litres/ha in logged forest (Table 1 and Tuma et al., 2019). This assumes a steady state situation in which the mounds decompose at an unknown rate as well. Thus the colonization of these structures presumably begins shortly after abandonment, or perhaps even already when the resident termite colony is dying or moving out, with a maximum in terms of invertebrate density during the period when the mound still holds its shape and finally decreasing when the mound disintegrates. The taxa found in high abundances in mounds are rather mobile (ants and earthworms) and can presumably rapidly colonise and also abandon the mound structure. Coleoptera and Diptera probably use the structures more temporarily for their larval development. As the mounds have rather clumped spatial distribution in the forest, reaching up to 265 mounds per hectare, but also being completely missing in other locations (Matsumoto, 1976; Tuma et al., 2019), the available living space provided by them is not only ephemeral but also spatially uneven, making this type of microhabitat spatiotemporally heterogeneous for the species that rely on it.

4.5 Plant roots in unoccupied *Dicuspiditermes* spp. mounds

We found a lower amount of roots in mounds compared to the control soil. Despite the high concentration of nutrients in termite mounds (Tuma et al., 2022), other factors apparently play a more important role in the colonization of plant roots. There might be a slower progression of plant roots into these structures due to their mechanical properties (Rogers et al., 1999). We surveyed only lightly decomposed mounds, which still hold their structure and hence might be hard to penetrate. The mounds do not have as large a surface area in contact with the rest of the soil, since they are horizontal cylinders, compared to the control samples (which are completely surrounded). Hence, there may be fewer opportunities for roots to colonise. The mounds may be also more rapidly desiccating than the control soil, which is covered by a litter layer and thus is less suitable for root growth. In the mounds, we predominantly found fine roots, characterized by their relatively low biomass compared to the numerous thicker roots observed in the control soil. Fine roots are primarily responsible for nutrient and water uptake, while thicker roots play a role in resource transport and structural support of the plant. Fine roots tend to have a rapid turnover and offer less protection against predation (Eshel and Beeckman, 2013; McCormack et al., 2015). This suggests that plants may prioritize the production of fine roots in mounds to quickly absorb nutrients, despite the potential high risk from soil-dwelling herbivores. The presence of abundant soil fauna, such as Coleoptera larvae known for consuming substantial amounts of plant roots (Potapov et al., 2022), likely exerts predation pressure on the fine roots in the mounds. There are studies describing the preferential growth of certain plant species on large Macrotermitinae termite mounds (Traoré et al., 2008; Beaudrot et al., 2011). However, when root content was systematically examined across several species in the Amazon (Ackerman et al., 2007), a lower amount of roots was found in them compared to control soil, similar to our study. Due to their building process and consequent specific chemical composition, the mounds can also lack some limiting micronutrients such as boron (Mills et al., 2024) which can restrict the growth of plants. However, the micronutrient composition of *Dicuspiditermes* mounds had never been analysed. The supposed higher amounts of roots found during mound dissections of soil-feeding termites (Salick et al., 1983) may be just an artefact or an observational bias as the roots in the mounds are more prominent in plain mound material than in complex soil matrix. Nevertheless, this phenomenon is poorly explored and the root content may vary with the mound decomposition stage, where more decomposed structures are mixed with the soil matrix and the limiting factors suggested above may be reduced.

4.6 Outstanding questions and future research directions

Our work raises new research directions for exploring the dynamics of unoccupied termite mounds and interactions between mound-building termites and other soil biota. The sample size in this pioneering study is relatively limited so in the future larger numbers of mounds should be dissected, across different stages of decomposition, with active mounds as a starting point. To evaluate the decomposition rate of the mounds and hence the temporal availability of these microhabitats, observation of individual mounds should be conducted, starting from their abandonment and ending in their disappearance when they blend with the soil matrix. Moreover, there is no existing data on the inquiline species of *Dicuspiditermes* termites, and thus we cannot distinguish between inquilines of *Dicuspiditermes* colonies and secondary inhabitants of their unoccupied mounds. Similarly, a food web of the invertebrates in the unoccupied mounds could be reconstructed, which would shed light on the primary food sources of the mound inhabitants and their interactions (Hyodo et al., 2015; Potapov et al., 2022). This would indicate whether the inhabitants utilize the mound as a food source, foraging space and/or nesting microhabitat. Additionally, this would reveal which groups of invertebrates act as the mound decomposers, accelerating mound breakdown and hence further limiting the temporal availability of this microhabitat for other taxa. Unoccupied termite mounds thus should not be overlooked when performing biodiversity surveys, especially those targeting ants. If unoccupied termite mounds indeed serve as such important microhabitats, their ecological role could be even more significant in highly modified environments—such as extensive oil palm plantations. Management changes in these systems, such as retaining dead wood or even translocating live colonies of soil-feeding termites into modified habitats, could help harness the full range of ecosystem services provided by termites throughout the entire life cycle of their colonies. These services include soil bioturbation, accelerated decomposition and nutrient release, and, as highlighted in this study, the provision of both microhabitat and feeding substrate for a wide array of invertebrates.

5 Conclusion

This work presents new evidence about the invertebrate inhabitants of unoccupied mounds of the enigmatic soil-feeding termite *Dicuspiditermes*, which is common in forest habitats of South-East Asia but has a largely unexplored natural history. Together with our previous studies on this genus, we have confirmed its significance in accumulating soil nutrients, enhancing soil bioturbation levels and now in providing a suitable microhabitat for a range of soil and litter-dwelling invertebrates and nesting sites for ants. This microhabitat availability is likely to be important in maintaining biodiversity, especially in disturbed habitats. Even though soil-feeding termites contribute only a small portion of the total termite abundance in the Sabahan rainforest when measured by traditional transect methods (Eggleton et al., 1999), their unoccupied mounds are continuously appearing and breaking down and provide significant amounts of living space. Similarly to well-recognized microhabitats like dead wood (Seibold et al., 2021), unoccupied termite mounds of soil feeding species should be considered as important microhabitats for various soil and litter fauna, especially in areas where they are abundant, such as lowland tropical rainforests.

Data availability

Full datasets for all analyses in this paper are available at Zenodo (https://doi.org/10.5281/zenodo.15546812).

Conflicts of 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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Electronic supplementary material

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