



The impacts of tropical mound-building social insects on soil properties vary between taxa and with anthropogenic habitat change

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ABSTRACT

Ants and termites reach high abundances in the tropics and substantially affect the environment through a range of their activities. Because of foraging and decomposition of organic matter at their nesting sites, these locations show fundamentally altered soil properties compared to the adjacent soil. However, such changes are typically studied only within one species or taxon and in one habitat type. Consequently, it is not clear how these effects vary across different taxa and in relation to anthropogenic habitat change. In this study we assess the impacts of different mound-building taxa across a gradient of tropical habitat change in SE Asia comprising primary forest, logged forest and oil palm plantation. To do this we analysed chemical soil properties of mounds of multiple taxa of social insects, with some taxa spanning the full habitat change gradient, and where taxa differ in their mound construction type. Our results show that soils in mounds and adjacent soils have consistently different properties. However, these patterns differ both between social insect taxa and across habitat types. Specifically, mounds of soil-feeding termites *Dicuspiditermes* spp. were substantially enriched in basic soil nutrients such as C, N, P, especially in oil palm, while mounds of the leaf litter-feeding termite *Macrotermes gilvus* were depleted. Ant mounds did not show a clear pattern. This indicates that different social insect taxa in a particular habitat affect soil properties in differing ways, and furthermore that such impacts can change when a habitat is anthropogenically altered. Our research highlights the importance of termites for driving the heterogeneity of soil properties and nutrient redistribution across tropical landscapes.

1. Introduction

Ants and termites are two of the most abundant arthropod taxa worldwide, inhabiting most terrestrial ecosystems (Tuma et al., 2020). Although both groups are eusocial insects, they affect their environment in different ways through a wide range of activities. Ants are important predators, scavengers, and mutualists, and hence they substantially influence nutrient redistribution (Griffiths et al., 2018; Styrsky and Eubanks, 2007). Termites on the other hand are efficient decomposers of plant organic matter in various stages of decay, including highly decomposed plant material in the form of soil organic matter (Eggleton and Tayasu, 2001; Hyodo et al., 2011). Through predation, herbivory, organic matter decomposition and nest-building activity, ants and

termites significantly alter energy channels and nutrient distribution (Lobry de Bruyn and Conacher, 1990). Such altered conditions then increase resource heterogeneity (Jouquet et al., 2006) and affect occurrence or interactions between other organisms, making ants and termites important ecosystem engineers (Cammeraat and Risch, 2008; Jones et al., 1994; Jouquet et al., 2011).

Ant and termite nesting sites are the centres of their activity and thus soil properties and nutrient concentrations are substantially changed at these locations (Frouz and Jílková, 2008; Kaiser et al., 2017; Viles et al., 2021). Such effects have been predominantly studied in the soil nesting ants and termites that build conspicuous aboveground mounds, and it is on these that we focus here. Note that this excludes non-central-nesting termites, wood nesting termites and most of the nomadic army ants, in

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which quantification of their impacts on soils is more challenging. There are two main ways in which ants and termites affect soil properties. (1) The nest and the mound-building process itself. (2) The collection of food and other material from nearby, and transport of this to the nest. During the first of these processes, nest and mound-building, workers excavate and translocate soil material, usually to the upper levels of soil or aboveground to create space or protective structures for the reproductive caste and brood, food storage areas and symbiotic fungi. This is typical for ants where bulk density, soil texture or the number of macropores are affected by creating nest entrance holes and by translocating selected soil materials. Soil-feeding termites (e.g. *Dicuspitermes* spp.; *Cubitermes* spp. from feeding group IV sensu Donovan et al., 2001) build their nests with complex inner structure from their excrements and saliva, with low mineral but high organic matter content (Brauman, 2000). In contrast, litter-feeding termites (e.g. *Macrotermes* spp.; *Odontotermes* spp. feeding group II) use mineral particles from deep soil layers with high clay content, which they bind together with their saliva for mound construction (Eggleton and Tayasu, 2001). These differences are then expected to contrast with the chemical composition of the soil surrounding the mounds (Hedde et al., 2005; Shanbhag et al., 2017). These changes in soil can last for many years after colony abandonment, even when the physical presence of the mound is no longer apparent (DeSouza et al., 2009). During foraging activities, the second major way that social insects affect soil properties, ants collect large amounts of sugars, proteins, seeds or plant tissue, while termites collect mainly plant material in various stages of decay. These materials are then typically stored in the nest, processed and finally deposited within the nest body once they are no longer of use, thus affecting the properties of nest/mound material (Bottinelli et al., 2015; Holt and Lepage, 2000). As a result, increased concentrations of nitrogen, phosphorus and carbon, together with higher conductivity and more neutral pH levels are usually measured in social insect mounds (Boulton and Amberman, 2006; Farji-Brener and Werenkraut, 2017; Holt and Lepage, 2000; Mills and Medinski, 2021). However, trends in nutrients and soil properties are not uniform and vary significantly between species and feeding groups (Farji-Brener and Werenkraut, 2017; Rückamp, 2011). Additionally, we can expect that larger mounds, with a higher number of workers (Marins et al., 2016) would affect the soil properties comparatively more than smaller ones (Frouz and Jílková, 2008; Hesse, 1955). However, despite known differences in mound-building strategies and differences in the effect on soil properties between social insect taxa (Cerdá and Dejean, 2011; Contour-Ansel et al., 2000; Decaëns et al., 2002; Jiménez et al., 2008; López-Hernández et al., 2006), their relative effects on multiple soil nutrients are yet to be further explored, especially in relation to anthropogenic habitat change.

Human-caused habitat change is one of the main threats to biodiversity worldwide (McGarigal et al., 2005; Newbold et al., 2015). Logging and conversion of tropical forests to agricultural land adversely affect biodiversity, ecosystem functioning, and consequently the ecosystem services provided by species (Bommarco et al., 2013; Dislich et al., 2017). However, agricultural land represents an important part of tropical landscapes, is a driver of economic development, and management of these areas is one of the most challenging tasks for land owners, politicians and environmentalists (Fürst, 2021). One major effect of habitat change on ecosystem functioning is the alteration of soil quality, nutrient cycling, and carbon storage (Guillaume et al., 2018). The changes are pronounced in oil palm plantation as the soil is substantially altered during logging and plantation establishment operations (Corley and Tinker, 2015). Specifically, decreases in soil organic carbon (Kotowska et al., 2015), phosphorus content (Kurniawan et al., 2018b) or nitrogen availability (Allen et al., 2015) are observed. In response, plantation managers apply high amounts of artificial fertilizers to support nutrient balance to sustain high yields. However, these fertilizers are frequently flushed away from the plantations by rain into the rivers (Bah et al., 2014). As a result, recent research has highlighted the need for nutrient retention to sustain high productivity of

plantations (Kurniawan et al., 2018a). Ants and termites can affect nutrient pools and cycling and consequently, such impacts are reflected in the properties of mound soils (Frouz and Jílková, 2008; Holt and Lepage, 2000). Encouraging these social insects potentially reduces fertilizer inputs into tropical crops such as oil palm plantations, as mounds of ants and termites can act as nutrient pools, decreasing nutrient runoff from the system. Additionally, the mounds serve as a well-protected microhabitats and nesting sites for a number of animals such as amphibians, snakes, and spiders, but also for other ant and termite species (De Visser et al., 2008; Hood et al., 2020; Moreira et al., 2009). Hence presence of these mounds can potentially increase niche availability and thus species diversity even in intensively managed agricultural habitats.

It is vital to understand how habitat change affects ant and termite-driven ecosystem process. One way in which this might occur is through changes in the per-mound impacts of any species that persist in anthropogenically altered habitats. For example, there might be changes in activity rates driven either by altered abiotic conditions, such as microclimate or soil properties, or by biotic changes, such as presence of competitors or predators. However, comparisons of the impacts of the same ant or termite species on soil properties across different habitats are rare (Chen et al., 2021; Donovan et al., 2001; Schaefer et al., 2016) or are based on small sample sizes (Chisanga et al., 2020; Jouquet et al., 2017; Menichetti et al., 2014).

Here we assess the impacts of different mound-building social insect taxa across a gradient of habitat change in tropical SE Asia. To do this we analyse chemical soil properties of mounds of multiple taxa of social insects, with some taxa spanning the full habitat change gradient, and where taxa differ in their mound construction type. Hence, we are able to compare the effect of particular taxa on soil properties in different habitats. Specifically, we test the following hypotheses:

1. Ant and termite mounds will support higher levels of nutrients and conductivity with pH values closer to neutral than control soil.
2. The relative nutrient enrichment of the mounds of the same ant and termite taxa will be lower in logged forest and oil palm plantation than in primary forest.
3. Larger mounds will retain higher levels of soil nutrients than smaller ones.

2. Materials and methods

2.1. Sampling sites

Above-ground ant and termite mounds were sampled in Sabah, Malaysia (4° 40' 27" N, 117° 31' 40" E; see Appendix A for a map with sampling locations) within the Stability of Altered Forest Ecosystems (SAFE) Project sites (see Ewers et al., 2011 or www.safeproject.net for details) in three types of habitat. 1. Primary lowland dipterocarp forest in Maliau Basin Conservation Area (MBCA, SAFE Project site 'OG2'). 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. 2. Continuous selectively logged forest in the SAFE Project experimental area (SAFE Project sites 'LFE', 'B', 'LF1', 'A' and 'D') which has been selectively logged at least twice (Struebig et al., 2013). Note that all sites were sampled before any SAFE project-related experimental fragmentation. 3. Oil palm plantations, at SAFE Project sites 'OP1', 'OP2' and 'OP3'. OP1 and OP2 were planted in 2006 (nine years old at the time of sampling), and OP3 in 2000 (fifteen years old at the time of sampling). These are managed by the company Benta Wawasan Sdn Bhd (see Ewers et al., 2011). Data from all three habitats were collected from 22nd June to 18th August 2015 and from 9th July to 17th August 2016. All habitats were sampled in each year. 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 2669

mm of rainfall annually. There is no strong seasonality (Walsh and Newbery, 1999).

We obtained soil samples from 70 mounds of social insects, of which 27 were from the termite *Dicuspiditermes* spp. (9 in primary forest, 13 in logged forest, 5 in oil palm plantation); 27 from the termite *Macrotermes gilvus* (8 in primary forest, 7 in logged forest, 12 in oil palm plantation) and 16 from ants (12 in primary forest, 4 in logged forest). The ants were from five species: *Diacamma intricatum*, *Dinomyrmex gigas*, *Leptogenys mutabilis*, *Odontomachus* sp. and *Odontoponera transversa* (see Appendix B for species list with corresponding habitats). The ant species were combined for analysis as their mounds were morphologically similar across different species (see Appendix C for the field images showing this structural similarity), and there were not enough replicates of individual ant species per habitat for any statistical comparisons. The ant mounds with conspicuous aboveground part were found only in primary and logged forest habitats. Ant soil mounds in oil palms were as a rule formed only by a small amount of excavated material around the nest entrance so no ant data from oil palm are presented. Mounds from the three focal taxa were haphazardly selected for sampling during other fieldwork, with spatial scale of samples being comparable between the three habitats. *Dicuspiditermes* spp. mean mound height was 29 cm (range: 11–66 cm, SD = 12) and diameter 10 cm (range: 6–16 cm, SD = 3); *M. gilvus* mean height was 54 cm (range: 17–130 cm, SD = 34) and diameter 74 cm (range: 23–244 cm, SD = 46); Mean height of ant mounds was 7 cm (range: 2–24 cm, SD = 5) with a mean diameter of 23 cm (range: 4–60 cm, SD = 16).

2.2. Mound sampling

Soil samples were taken using a garden trowel or a parang (~6 cm depth and ~6 cm in diameter) after removal of coarse litter. Three types of soil samples, each comprising three manually mixed subsamples, were obtained from each mound and its surrounding area: 1. Mound samples were taken from the upper part of the mound, but below the uppermost slope of the mound (Fig. 1a; each of the three subsamples was taken in a triangular layout centred on the middle of the mound). Note that for *M. gilvus* mounds, the depth of the sample means that it contains the outer mound wall, not the fungus gardens or other inner nest chambers. 2. Base samples were taken at the base of the mound, where the mound structure met the surface of adjacent soil so the resulting sample consisted of non-mound soil. 3. Control samples were taken in a larger triangular layout where each of the subsamples was taken three meters from the mound centre (Fig. 1b) in areas with no sign of ant or termite activity, nest structures, or individual insects. The sampling depth of control samples (~6 cm) yielded a sample that contained a majority of soil organic matter but also a variable fraction of mineral subsoil. All the samples were visually checked for ant or termite presence and any individuals were manually removed before taking the sample. Note that ant mounds were less conspicuous than termite mounds and the boundary between the aboveground and belowground parts was often unclear, so the mound sample was obtained by shallow digging in the ant-modified soil when needed. Each of the mixed samples was transferred to the field laboratory, oven-dried at 80 °C for 3–5 days, stored at the room temperature in airtight, closed plastic bags and then

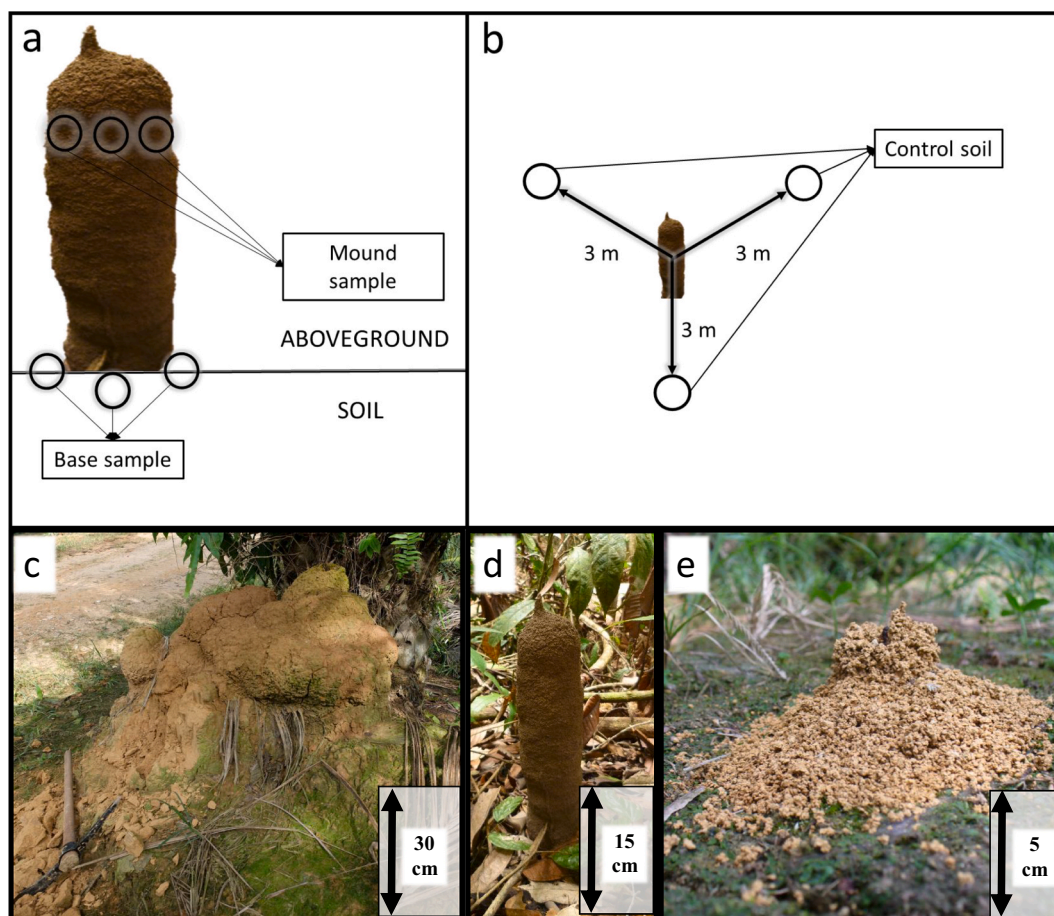


Fig. 1. Mound sampling design used to obtain a representative soil samples for soil chemical analyses of (a) the main body of a termite mound and its base and (b) control soil. Circles represent individual subsamples that were mixed together in order to obtain a combined soil sample for further analyses. A typically shaped *Dicuspiditermes* sp. mound is used in this example here. Typical mounds from (c) the termite *Macrotermes gilvus*, (d) the termite *Dicuspiditermes* sp. and (e) the ant *Odontoponera transversa*.

shipped in sealed plastic bags to the Czech Republic for chemical analyses.

2.3. Chemical analyses

Soil samples were homogenized and sieved through 2 mm mesh. A 1:5 soil:water ratio mixture was then shaken for 1 h. After shaking, samples were immediately filtered through filter paper (qualitative filter KA2, Papírna Perštejn, Czech Republic) and pH and conductivity were measured (Lab850 Shott Instruments, HI9033 Hanna Instruments). NO_3^- was also measured in the 1:5 soil:water ratio solution extract by spectrophotometer (UV/VIS Genesys 10, Thermo Scientific) at a wavelength of 210 nm. For analysing available phosphorus, soil samples were extracted in solution according to Mehlich 3 in ratio soil:Me3 = 1:10 and samples were shaken for 30 min. After shaking samples were immediately filtered through quantitative filter paper 474 (VWR). Soil extract was diluted at 1:10 and 1 ml of colouring solution was added. Released phosphorus formed molybdate phosphoric acid with ammonium molybdate in an acidic medium. This was reduced to phosphomolybdate blue in the presence of ascorbic acid and antimony. The intensity of the blue colour corresponds to the amount of phosphorus in the extract and was measured by spectrophotometer (UV/VIS Genesys 10, Thermo Scientific) at a wavelength of 889 nm. For C and N content, soil samples were milled using a ball mill (Retch 400) and additionally dried before analysis (40 °C, 12 h, Memmert). Samples were then packed in tin capsules and weighted using a microbalance (MX5, Mettler Toledo) with an accuracy of 0.001 mg. The total C and N content was determined in soil samples using an elemental analyser (CHNS/O Flash 2000, Thermo Scientific). We are aware that there might be some minor changes in the soil properties due to long-term storage of the samples before the analyses were performed. However, the nature of the chemical analyses we performed typically allows accurate results even on such samples providing they are dry, which we ensured by 80 °C drying and storing in double layered zip-lock bags. Once the samples are dried, any changes in measured soil properties over time are likely to be minor (e.g. 0.1 unit of pH) which is much less than the differences between treatments observed in our study, and this effect should apply uniformly across samples from different treatments.

2.4. Mound volume calculation

Mound volumes were measured because larger mounds are expected to more strongly influence soil properties (Frouz and Jílková, 2008; Hesse, 1955). The volume of termite mounds was calculated separately for *Dicuspitermes* spp., where the most representative diameter (the average of three vertically spaced measurements was taken as the mounds varied slightly in diameter along the vertical axis) and the mound height from the soil surface was measured, and for *Macrotermes gilvus* where the diameter at the base of the mound and the mound height from the soil surface was measured. For *Dicuspitermes* spp., the mound volume was then calculated by approximating the mound shape to a cylinder, using the standard formula for cylinder volume $V = \pi r^2 h$, while for *M. gilvus* the standard formula for cone volume $V = \pi r^2 h/3$ was used (Tuma et al., 2019).

2.5. Species identification

When the mound sample was taken, 8–10 individuals of ants or termites (including those from major/soldier castes if present) were collected and stored in 98 % ethanol. Termites were identified at Natural History Museum (NHM) London by David Jones. Note that species boundaries between *Dicuspitermes* termites were not clear in all cases, and so *Dicuspitermes minutus* (Akhtar and Riaz, 1992) and *Dicuspitermes nemorosus* (Haviland, 1898) were pooled as *Dicuspitermes* spp. Ants were identified by authors (JT and TMF) using a key of ant genera of Borneo (Fayle et al., 2014) with updates for recent taxonomy changes,

and the Antweb database (AntWeb, 2021). The species list is available in Appendix A.

2.6. Statistical analyses

In order to identify the most important factors explaining the variability in soil properties an overall redundancy analysis (RDA) with variation partitioning was used to evaluate the effect of habitat (primary forest, logged forest, oil palm plantation), sample type (mound, base, control) and social insect taxon (*Dicuspitermes* spp., *M. gilvus*, ants) on soil properties (carbon, nitrogen, nitrate, phosphorus, pH, conductivity). To test Hypothesis 1, that social insect mounds support higher levels of soil nutrients than control soil, ANOVAs with Tukey HSD post-hoc tests (where applicable) were used for evaluating the differences in values of individual soil properties in relation to habitat, taxon identity with a standard threshold of significance $p < 0.05$ (“stats” package, R Core Team, 2020). To test Hypothesis 2, that the effects of particular taxa on soil properties varies across habitats, we included an interaction in these models. Data were log-transformed to improve homogeneity in case of NO_3^- , P and conductivity for *Macrotermes gilvus* and P and conductivity for ants. Model reduction was conducted by stepwise removal of non-significant predictor variables. Because we were conducting a reasonably large number of statistical tests (18 separate taxon/soil property combinations), we ran a correction to minimise false positive (the false discovery rate correction, Benjamini and Hochberg, 1995), using the p.adjust function in the R “stats” package (R Core Team, 2020). We did this separately for the p-values relating to each of the two predictors (taxon and soil property). Where there was a significant interaction term, we used this in both analyses. No p-values that had been significant prior to the correction become non-significant ($p > 0.05$) after the correction. We report the original p-values, but present the corrected p-values in Appendix D. Redundancy analysis (RDA) was used to calculate and visualize the relationship between the values of soil properties in the mounds and in the control soil. The values of the control soil were subtracted from the values in the mound to obtain “net” mound enrichment or depletion in soil properties. This approach was used for all analyses/figures except Fig. 3, where the ratio of the soil properties for the mound versus the control sample (relative enrichment/depletion of the mound) was calculated by dividing the value of individual soil properties for the mound sample by the value of the control sample (according to Seymour et al., 2014). We did this to illustrate how many times were the mounds enriched or depleted in soil nutrients compared to the control soil. It was not possible to perform the RDA for ant mounds because of the small sample size and thus insufficient degrees of freedom. Data were centred and standardised for all multivariate analyses. The pairwise correlations between the net effect of the mound and the control soil on individual soil properties was performed using “corrplot” package (Wei and Simko, 2017) with Pearson correlation coefficient (r) at $p < 0.01$ as a threshold of significance because the aim of this analysis is to highlight only the most important correlations, while the Pearson correlation is susceptible to finding significant relationships with larger sample sizes even in cases of weak correlation (Zar, 2010). To test Hypothesis 3, that larger mounds will support higher levels of nutrients, we conducted simple linear regression models using package “lm” (“stats” package, R Core Team, 2020) with soil property values as response variables and mound size (log-transformed) as the explanatory variable. All analyses were carried out in R 4.0.2 (R Core Team, 2020), except for the multidimensional analyses, which were performed using Canoco software (Canoco 5.12., Ter Braak and Šmilauer, 2018). Complete data of this study are available online at: www.zenodo.org/10.5281/zenodo.6726306.

3. Results

3.1. Explained variation in factors affecting soil properties and pairwise correlations between soil properties

The greatest amount of variation in the soil chemical properties was explained by the position of the sample: mound, base of the mound and control soil, (RDA; Variation partitioning with simple effects = 31 %; Appendix E); closely followed by the taxon of insect which created the mound (30 %); the habitat where the mound was sampled (23 %) and the interaction between habitat and species (16 %). On average, 58 % of mounds of termites or ants had values of basic soil nutrients, conductivity and pH higher than the control soil, but this ratio was highly variable among the insect taxa and different between the habitats. Changes in soil properties in the individual mounds vary with properties of the soil in which the mound was located. Overall, soil properties correlated with each other more frequently in the control soil than within the body of the mound.

3.2. The effect of *Dicuspiditermes* spp. mounds on soil properties

In support of Hypothesis 1, *Dicuspiditermes* spp. mounds were greatly enriched in C and N compared to control soil (ANOVA, C: $F_{2,76} = 121.54$, $p < 0.001$, N: $F_{2,76} = 166.58$, $p < 0.001$; with Tukey HSD: mound – control, $p < 0.001$ for both C and N; Fig. 2, Fig. 3a) while the concentrations of these two nutrients were strongly correlated in the mound ($r = 0.93$, $p < 0.001$, Fig. 4). However, in support of Hypothesis 2, there was a difference in this enrichment between forested habitats (6.5 and 5.3 times higher concentration in the mound for C in PF and LF respectively and 5.2 and 4.9 times for N in PF and LF respectively) and oil palm plantations (10.7 and 11.0 times higher concentration in mound for C and N respectively, for complete results see Appendix F) with a decreasing concentration from mound through its base to the control soil (Tukey HSD: $p < 0.001$, for all pairwise comparisons see Appendix G). A similar, but weaker pattern was found in conductivity and pH, with the conductivity systematically decreasing from the mound towards the base until the control soil and pH being lower in control and base soil compared to mound soil (Figs. 2; 3a; Appendix C). The extractable NO_3^- showed different patterns across the habitats (ANOVA – habitat and soil sampling location interaction, $F_{4,72} = 6.71$, $p < 0.001$), with the mounds in oil palm being enriched in NO_3^- but mounds in primary and logged forest being depleted compared to control soils (Figs. 2; 3a). Furthermore, the mounds were enriched in NO_3^- on soils with high acidity, but low NO_3^- , C, P and conductivity (Figs. 4 and 5). Additionally, there was a weak peak in NO_3^- at the base of the mounds (Fig. 2). There was an interaction in the effects of habitat and soil sampling location on P concentration (ANOVA - interaction, $F_{4,72} = 3.53$, $p = 0.011$). However, mounds in all habitats were on average enriched in P by a factor of 3 (PF), 2 (LF) and 17 (OP). There was exceptionally high variability of P in termite mounds ($N = 5$ sampled mounds) found in oil palm habitat (mean = 35.8, SD = 16.6, Figs. 2, 3a). P concentration in mounds was higher on soils with low conductivity ($r = -0.58$, $p = 0.001$). However, in general and in support of Hypothesis 1, *Dicuspiditermes* spp. mounds accumulated C, N and P regardless of the concentration of those nutrients in the control soil (Fig. 5). Contrary to Hypothesis 3, the size of the mound was not correlated with the values of any of the soil properties in the mound for this termite taxon (Appendix D).

3.3. The effect of *Macrotermes gilvus* mounds on soil properties

Different patterns from those seen in *Dicuspiditermes* spp. were found for *M. gilvus* mounds. Contrary to Hypothesis 1, there was generally a lower concentration of C and N in the mounds compared to the control soils, especially in the two forested habitats (Fig. 3b). However, the

distribution of C differed among the habitats (ANOVA – habitat and soil sampling location interaction, $F_{4,72} = 4.41$, $p = 0.003$). The mounds were depleted in N in all the habitats (ANOVA, $F_{2,76} = 4.21$, $p = 0.019$) and were especially depleted in C and N where there was high concentration of C, N, or NO_3^- in the control soil (Figs. 4, 5) which would contrast the Hypothesis 2. The mounds were depleted in NO_3^- in forested habitats but there was on average twice the concentration of NO_3^- in oil palm in mounds compared to control soil (Figs. 2, 3b). Additionally, there was a significant peak in NO_3^- concentration at the base of the mounds (ANOVA, $F_{2,76} = 5.13$, $p = 0.008$, Tukey HSD: mound - base, $p = 0.006$). P concentration showed a distinct peak at the base of the mound (ANOVA, $F_{2,76} = 19.12$, $p < 0.001$, Tukey HSD: mound – base, $p < 0.001$, Fig. 2), and P concentration in the mound was significantly lower (Tukey HSD: mound – control, $p < 0.001$) especially when the control soil was rich in P ($r = -0.89$, $p < 0.001$, Figs. 4; 5). pH was unaffected by the presence of *M. gilvus* mounds, but the soils in general were more alkaline in logged forest, followed by oil palm with the most acidic being primary forest soils (ANOVA, $F_{2,76} = 24.51$, $p < 0.001$, Tukey HSD: PF - LF, $p < 0.001$; LF - OP, $p < 0.001$; PF - OP, $p = 0.014$, Fig. 2). However, the mounds were more acidic in relation to control soil when present on alkaline soils ($r = -0.73$, $p < 0.001$, Fig. 5). Similarly to pH, conductivity was generally higher in the logged forest than in primary forest (ANOVA, $F_{2,76} = 7.26$, $p = 0.001$, TukeyHSD: PF – LF, $p < 0.001$, Fig. 2), while the mounds in oil palm had on average six times higher conductivity than control soil (Fig. 3b). The conductivity levels in the mounds were positively correlated with pH and conductivity levels in the control soil ($r = 0.55$, $p = 0.003$ for pH and $r = 0.63$, $p < 0.001$ for conductivity, Fig. 5). In support of Hypothesis 3, there was a positive correlation between *M. gilvus* mound size and three soil properties in the mound, specifically C ($F = 5.895$, $t_{1,24} = 2.428$, $R_{2(\text{adj.})} = 0.164$, $p = 0.023$), N ($F = 17.58$, $t_{1,24} = 4.193$, $R_{2(\text{adj.})} = 0.399$, $p < 0.01$) and conductivity ($F = 9.264$, $t_{1,24} = 3.044$, $R_{2(\text{adj.})} = 0.248$, $p < 0.01$; Appendix H).

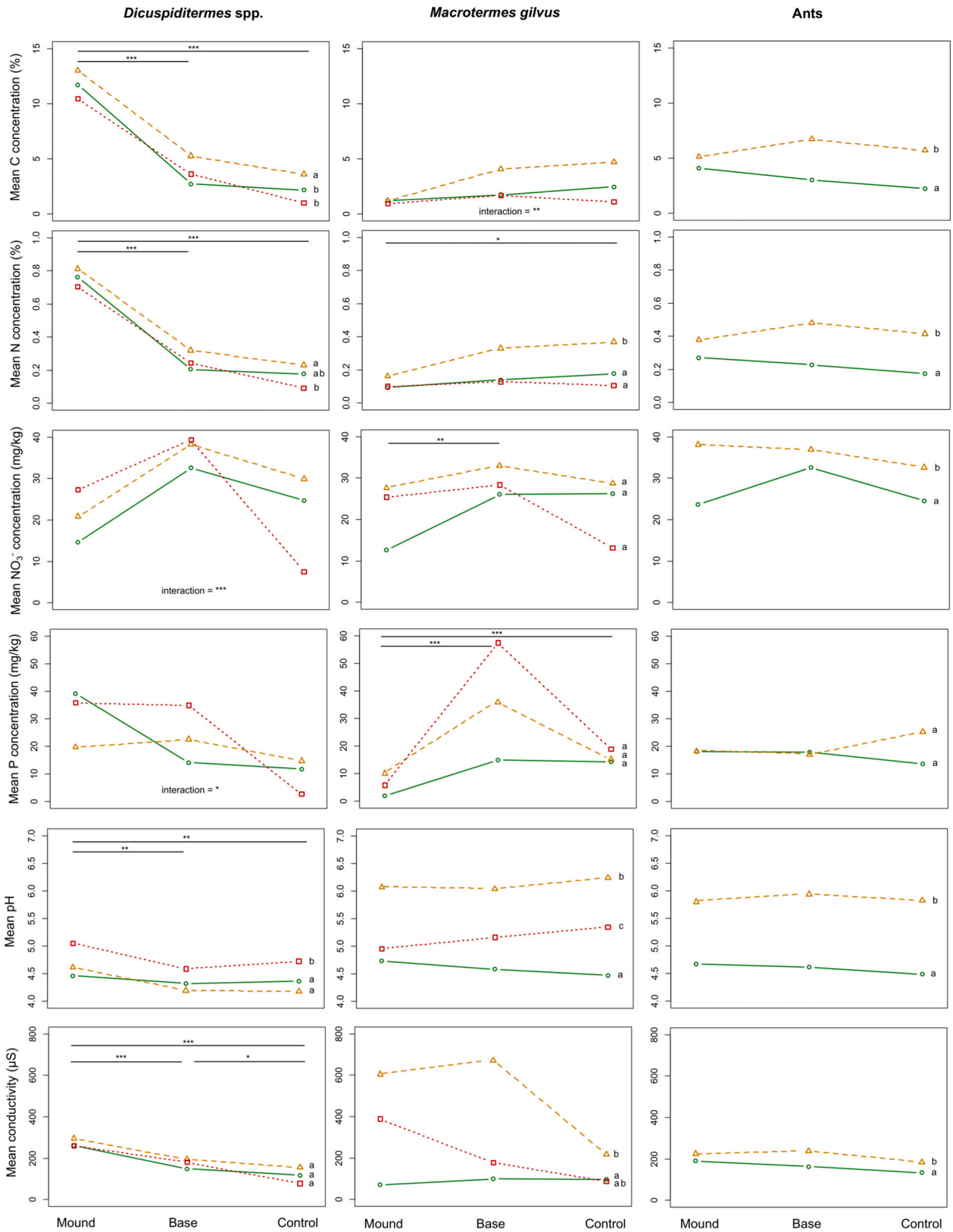
3.4. The effect of ant mounds on soil properties

Contrary to the Hypothesis 1, ant mounds showed no clear difference in any of the soil properties compared to adjacent soil. Additionally contrary to Hypothesis 2 the overall values of all samples were significantly higher in the logged forest than in primary forest with only P being an exception (Fig. 2; Appendix G). However, the C and N concentrations in the mound were higher in the primary forest, than in the control soil (C: 3 times higher, N: 2 times higher; Fig. 3c). Additionally, the P concentration in the mounds was lower when those were found on less acidic soils and those high in P ($r = -0.74$, $p = 0.001$ for pH and $r = -0.72$, $p = 0.002$ for P, Fig. 5).

4. Discussion

4.1. Social insect mounds affect soil properties differently across habitats and taxa

Previous studies have generally indicated clear differences between the soil properties in the mounds of social insects when compared to the adjacent soil. These mainly report higher content of C, N, P, and Ca^{2+} a shift towards neutral pH, higher clay content in case of termites and higher content of mineral or organic materials in the mound compared to adjacent soil (de Souza et al., 2020; Farji-Brener and Werenkraut, 2017; Frouz and Jílková, 2008; Holt and Lepage, 2000; Jiménez et al., 2008). Such studies often assume that the effects of a given species represent the effects of the whole group (e.g. termites) on soil properties. Our results confirm that soils in mounds and adjacent soils generally have consistently different properties. However, these patterns differ both between insect taxa and across habitat types. This indicates that different social insect taxa in a particular habitat affect soil properties in differing ways (Hulugalle and Ndi, 1993), and furthermore that the



Legend:

Primary forest	Logged forest	Oil palm
Significance of mound/base/control main effects and interactions		
* p ≤ 0.05	** p ≤ 0.01	*** p ≤ 0.001

(caption on next page)

Fig. 2. Interaction plot showing mean soil properties in termite and ant mounds, the base of the mound and in the control soil. Where there is an interaction between the effects of habitat and sample location (mound/base/control), then only this is stated at the bottom of the figure (main effect significance is not reported). Where there is no interaction, and hence it is possible to interpret main effects, then these are reported. Horizontal lines at the top of each panel denote significant main effects for the differences in soil properties between sampling positions. The number of stars denotes significance levels: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Lowercase letters denote significant main effects for differences between habitats in soil properties. Note that this is the only figure where the values for base of the mounds are shown. Complete results of statistical tests are available in Appendix G.

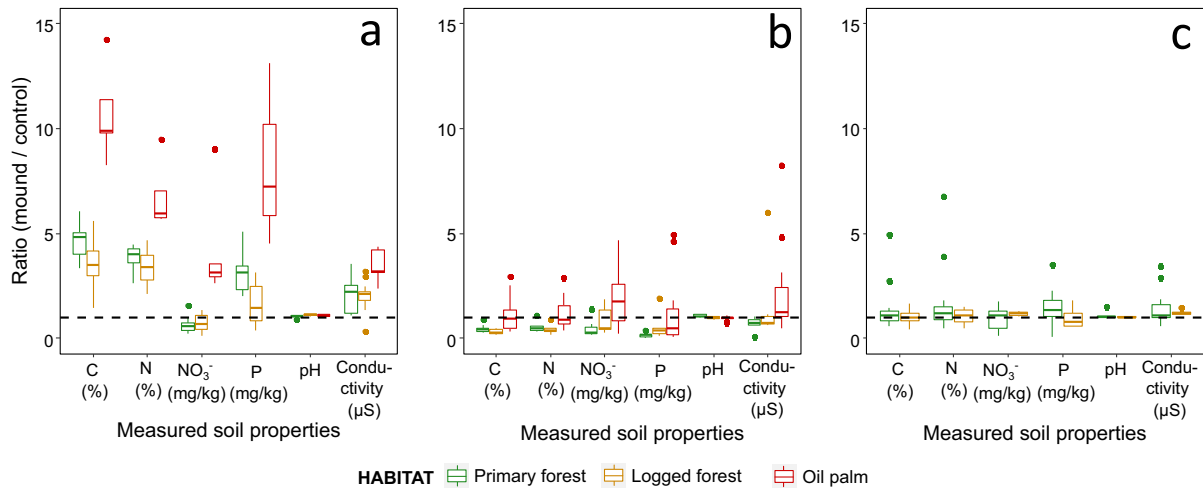


Fig. 3. The mean relative enrichment in soil properties in samples taken from the mounds of termites and ants for (A) *Dicuspiditermes* spp., (B) *Macrotermes gilvus* and (C) ants. The enrichment (ratio) was calculated as the value of that soil property in the mound divided by the value in the control soil. The dashed line indicates a threshold of one, so points above this line indicate that the value of a particular soil property was relatively higher in the mound. There are no data shown for ants in oil palm as there were no mounds with enough aboveground soil to analyse. In boxplots the median is denoted by a bold horizontal line, the interquartile range box represents the middle 50 % of the data and the whiskers represent the full data range excluding outliers. Outliers are represented by points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles. Note that outliers in A ($p = 16.6 \pm 11.0$) and B (Conductivity = 5.5 ± 10.8) are not plotted to increase legibility of the rest of the plot. The complete results are available in Appendix F.

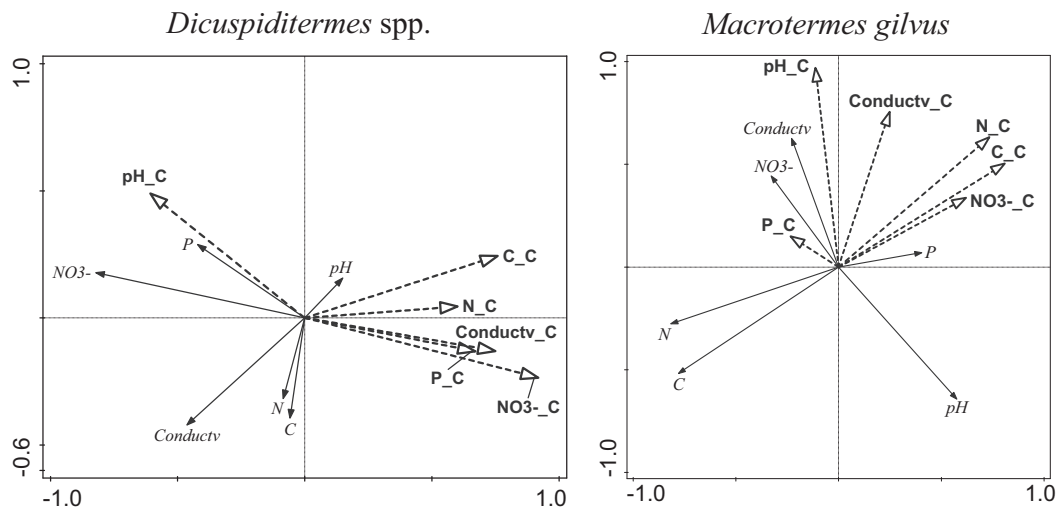


Fig. 4. Redundancy analysis (RDA) diagram showing the relationship between the increase in values of soil properties in termite mounds (difference mound – control, solid arrow and italicized font) of two termite taxa and the soil properties in the control soil (marked by “_C” suffix, by a dashed arrow line and bold font). All the axes were significant at $F_6 = 2.0$; $p = 0.007$ for *Dicuspiditermes* spp. mounds where explanatory variables accounted for 19 % of adjusted explained variation and at $F_6 = 9.2$; $p = 0.001$; for *Macrotermes gilvus* mounds where explanatory variables accounted for 65 % of adjusted explained variation (Appendix E). Abbreviations represents the following soil properties: “C” = C concentration in %, “Conductiv” = conductivity in μS , “N” = N concentration in %, “NO3-” = NO3- concentration in mg/kg, “P” = available P concentration in mg/kg. Note that it was not possible to perform the RDA for ant mounds due to small sample size and thus insufficient degrees of freedom.

impacts of any individual taxon can change when a habitat is anthropogenically altered.

4.2. The effect of soil-feeding termite mounds of *Dicuspiditermes* spp. on soil properties in different habitats

To our knowledge, this is the first study to assess multiple soil

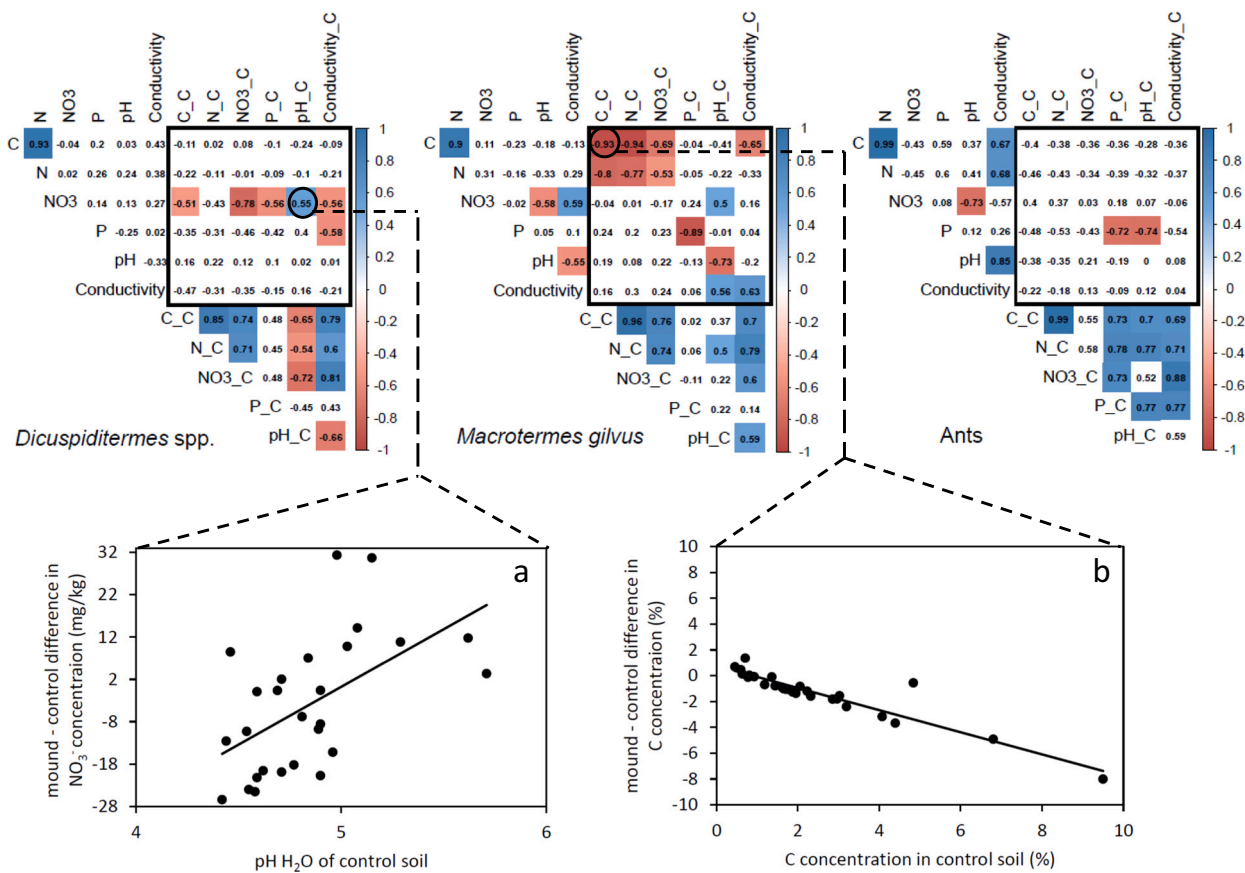


Fig. 5. Correlation coefficients between soil properties in control soil (denoted by suffix _C), and the impact of the presence of a mound on those soil properties (denoted by soil properties without suffices, calculated as the difference between mound and control soils) for the three social insect taxa. All values given are Pearson correlation coefficients. The black box shows the correlations between the shift in individual soil properties in mound and control soil and chemical properties of control soil. The fields outside the black square show Pearson coefficients for correlations between the shifts in different soil properties in the mound (left upper side) or between soil properties in control soils (lower side). Significant coefficients (at $p < 0.01$) are displayed in colour with the depth of colour indicating the strength of the correlation. Two typical examples of such relationships are presented in bottom of the panel. a) a positive correlation between the net effect of the mound on NO_3^- concentration and the pH of control soils for *Dicuspiditermes* spp. This show that the mounds were enriched in NO_3^- when found on less acidic soils, but depleted in NO_3^- when found on more acidic soils. b) a negative correlation between the net effect (mound – control soil) of the mound and the concentration of C in control soil for *Macrotermes gilvus*. This shows that the mounds are more depleted in C when found on soils rich in C. The complete p -values are available in Appendix I.

chemical properties of *Dicuspiditermes* mounds. The mounds of this soil-feeding termite were brown-black in colour, suggesting a high organic matter content (Jiménez et al., 2008; Kaschuk et al., 2006). In accordance with this, the C, but also N and P concentration (but not logged forest P) and conductivity were high in the mounds in primary and logged forest regardless of the concentrations in the adjacent soil. Interestingly, this relative enrichment was even higher in oil palm plantation. This can be explained by generally lower soil organic matter content linked with low N and C (Brady and Weil, 2001) in oil palm plantations as opposed to the rich upper soil horizon in forested habitats, so the enrichment of the mounds in basic nutrients in oil palm is relatively greater. This overall enrichment is probably caused by the manner of mound construction in soil-feeding termites. *Dicuspiditermes* termites selectively feed in the upper layer of soil on substrates rich in organic matter, i.e. highly decomposed plant material (Brauman, 2000; Tayasu et al., 2002). Their mounds are then built of their faeces and saliva and are low in mineral fraction thus they are rich in soil organic matter and macronutrients. However, Hyodo et al. (2001) did not find any difference between carbon composition (i.e. the ratio between labile and stable forms of carbon) in the mound and in the surrounding soil when measured using nuclear magnetic resonance. This could mean that *Dicuspiditermes* termites accumulate carbon in their mounds, but they do not change its composition.

NO_3^- distribution showed a weak peak at the base of the mounds. This nutrient stratification in the mound was also found in several termite species from different feeding groups by Kaschuk et al. (2006), where P, C, Ca_2^+ and K concentrations differed within the mound from top to bottom. This could be explained by leaching of this highly mobile anion from the mound matrix by rainwater down to the mound base. Additionally, in our study, the mounds themselves were depleted in NO_3^- in forested habitats so leaching could also be the cause here. However, this was not the case in oil palm where the adjacent soil was low in NO_3^- already (as the correlation with control NO_3^- but also with C, P, pH and conductivity in Fig. 3 show), meaning that the mounds were relatively enriched and may have been releasing available NO_3^- into the environment, especially when the nearby soil was less acidic (Fig. 5a). Available P concentration shows a similar pattern but with an even higher ratio (a mean factor of 17) in oil palm (Fig. 3a). This is important as P is generally a limiting nutrient in tropical forests (Vitousek et al., 2010) especially for microbial communities and thus limits organic matter decomposition (Cleveland et al., 2002). The mounds in logged forest show very similar patterns of soil properties to those of primary forest suggesting either insignificant disturbance (or disturbance and subsequent recovery) of soil caused by logging or that *Dicuspiditermes* spp. termites can maintain their effects on soil even in disturbed habitats. The latter speculation is supported by the similar absolute values we

observed for most soil properties in the mounds across the habitats.

Dicuspitermes spp. mounds thus accumulate essential macronutrients and increase soil chemical heterogeneity in tropical habitats (López-Hernández, 2001) and this effect is even more pronounced in human-modified habitats with poor soils such as oil palm plantations (Flynn et al., 2022). Mounds of this termite genus reach mean densities of 100 mounds per hectare in primary forest with relatively rapid turnover (Tuma et al., 2019) with the dead mounds gradually collapsing and thus releasing their nutrients into the environment (Kaschuk et al., 2006). Although there may be a greater per-capita effect of such mounds in oil palm, the mounds are rather scarce there, being found mainly in the vicinity of stumps and occasional deadwood left after the logging and clearance operations (personal observation), while other studies from this area do not report *Dicuspitermes* spp. from oil palm at all (Hardivinto et al., 2010; Keng and Rahman, 2012; Luke et al., 2014). We also lack any data about the turnover rate of these relatively scarce mounds in oil palm plantation, compared to forested habitats which is an important knowledge gap. Hence the overall impact of this taxon on soil properties in oil palm is likely to be less than in the forested habitats in which it is more abundant.

The soil properties of *Dicuspitermes* spp. mounds were not related to mound size. This could be explained by two factors: (I) the mound size variation was small, as our samples came only from mature, large mounds and/or (II) the mounds are constructed using a similar material throughout the mound. However, if nutrient leaching takes place in the mounds, then older and bigger mounds should contain less water-soluble ions, e.g. NO_3^- . Our observed lack of correlation between mound size and soil properties could be because termites visit the whole structure of the mound and they could additionally deposit faeces throughout its profile, or there might be more frequent repairs or successive growth of these mounds even when they are already large (Brauman, 2000). However, this is speculation, since our knowledge of the building and maintenance of mounds is incomplete for this termite group.

4.3. The effect of litter-feeding termite mounds of *Macrotermes gilvus* on soil properties in different habitats

The mounds of *M. gilvus* were in general depleted in basic soil nutrients. However, this relative depletion was prominent mostly in primary and logged forest, while mounds oil palm were generally only slightly depleted or even enriched (in the case of NO_3^- and conductivity; see Fig. 2, habitat*taxon interactions) These patterns can be explained by the way the mounds of this litter-feeding termite are built. In contrast to faeces-based *Dicuspitermes* spp. mounds, Macrotermitinae termites bring up material from deep soil strata, which is thus mainly mineral in nature, and bind the soil particles and aggregates with saliva (Contour-Ansel et al., 2000). This is demonstrated by the strongly negative correlation between *M. gilvus* mound impacts on C compared to the C concentration in the control soil, meaning that mounds are more depleted in C where found on C-rich soils (Fig. 5b). A similar pattern was found in *Macrotermes natalensis* in sandy soils in South Africa, where the mounds were enriched in carbon and higher in conductivity levels than the surrounding soils, which improved soil fertility (Mthimkhulu et al., 2019). Hence the main input of nutrients from the environment, leaf litter foraged by termites and subsequently decomposed by exosymbiotic fungi, is apparently not occurring in the mound walls at high concentrations. However, other studies have demonstrated nutrient stratification throughout the mounds of this termite genus (Erens et al., 2015; Menichetti et al., 2014). The nutrient concentrations are high in the centres of the mounds where the main biological activity and decomposition of plant material takes place, while the walls are comparatively depleted. This means that our samples (6 cm of depth) may reflect the soil properties of only the nutrient – depleted mound wall. Opposite to our expectation, the positive correlation of mound size with C, P and conductivity contrasts with the theory that smaller

mounds would have more of the “active” part of the mound relatively closer to the surface with a higher concentration of nutrients and conductivity near the fungus and storage chambers (Holt and Lepage, 2000). This sample bias and different topsoil legacy could be one explanation for contrasting claims from different studies that Macrotermitinae mounds are hotspots or coldspots of nutrients (Abe et al., 2011; Bera et al., 2020; Holt and Lepage, 2000; Jouquet et al., 2015; Menichetti et al., 2014). Finer spatial scale mapping of soil properties within these complex three-dimensional structures would be a fruitful direction for future research.

For the abovementioned reasons, we advise taking into account soil stratification when considering control samples. Our control samples consist of a mix of thick upper organic layer (in forested habitats) and mineral soil in various proportions. While the samples in the oil palm comprised a thin organic layer but a majority of mineral soil. This is an important factor when the differences between the mounds of different animal taxa are compared in different habitats with varying soil stratification. We point this out as such comparative studies are rare and future research should consider selecting the most appropriate control sample to disentangle the interaction of different habitats, animal taxa and soil types.

Nutrient leaching in *M. gilvus* mounds (in the same way as for the *Dicuspitermes* spp.) could cause the high concentration of NO_3^- , but more strikingly of P at the mound bases (Fig. 2). This difference would be driven by construction material used and thus structural stability differences between mounds made by the two termite taxa (Decaëns et al., 2002; Jouquet et al., 2015). As *M. gilvus* mounds are bound together only by saliva, the mounds erode faster than those of *Dicuspitermes* spp., and hence nutrient leaching to the lower levels and to the base of the mound is potentially more rapid (Contour-Ansel et al., 2000; Tuma et al., 2019). So soluble P and NO_3^- as well as P bound in the soil matrix, can partially accumulate at the mound base, together with eroded clay particles (Mills and Medinski, 2021), hence becoming available for plants growing near to the mounds.

Taken together, *M. gilvus* mounds are depleted in some of the basic soil nutrients. However, this finding does not refute their role in the ecosystem as important decomposers of plant organic matter and soil bioturbators (Ashton et al., 2019; Tuma et al., 2020). Their mounds also represent an important nesting microhabitat for a range of vertebrates and invertebrates including a number of ant and (other) termite species (Hood et al., 2020). Nevertheless, their main activities take place deeper in the mound profile, and hence the most commonly used sampling methods are likely to underestimate their effects on soil properties and nutrient availability. Additionally, other structures such as the soil sheetings that cover their foraging paths and food sources may have even larger (yet more difficult to measure) effects on soil properties than the mound themselves (Harit et al., 2017).

4.4. The effect of ant mounds on soil properties in different habitats

Ant mounds showed only a minor effect on the soil properties. In general, ant above-ground mounds were formed by loose excavated subsoil with no obvious structural or functional complexity. It would be expected that discarded food waste or deposited faeces could increase C, P, and N concentrations. However, enrichment in nutrients and effects on pH and conductivity were negligible or very moderate in the mounds (Fig. 3). This corroborates a tropical study on *Odontoponera transversa* where the differences between mound and control soil were significant, but also relatively small (Wang et al., 2017). One reason could be that the excavated subsoil diluted the ant-affected (and perhaps nutrient-rich) soil, and so our mound samples showed similar soil properties to the control soil (Holec and Frouz, 2006). Ants can also deposit their waste outside of the nest at a specific place so these nutrients would not be included in our mound sample (Farji-Brener et al., 2016). Alternatively, our mound sample could have been in fact an “inverted” version of the control sample as the mineral soil excavated by ants simply

overlayed the top organic layer of the original soil surrounding the ant nest entrance, thus resulting in a mixed sample with similar soil properties. This is supported by the fact that the mounds were particularly low in P when sampled on soils rich in P. The higher levels of soil nutrients and more alkaline soil in the logged forest compared to the primary forest (Fig. 2) could be caused by nutrient-release after forest disturbance and subsequent decomposition of accumulated deadwood or by higher litter input from pioneering plant species, or by different soil mineralogy (Pinard et al., 2000). High levels of soil bioturbation in logged forests can also bring up mineral soil to the surface and hence dilute acid organic layers and elevate pH (Holec and Frouz, 2006; Tuma et al., 2019). We sampled two mounds of ant *Leptogenys mutabilis* in logged forest which has an army ant lifestyle with regular colony migrations and nests rather temporary in ground cavities or in nests previously occupied by other ant species (Xu and He, 2015). Thus we cannot confirm that the mounds were originally created by this species but the sampled mound was occupied only by *L. mutabilis*. There is evidence that this genus can rebuilt and extend the secondarily occupied nest and use it for up to ten days (Maschwitz et al., 1989), but we cannot distinguish the effect of the incipient ant species and its army ant successor on soil properties.

We infer that most of the mound-building ant activity in Bornean lowland tropical forest that impacts soil properties takes place in underground nests, while the discarded soil is simply scattered around the nest entrances. Additionally, the excavated soil is easily washed away by heavy rains, especially in oil palm plantations where the soil surface is even, and lacking structural complexity (Tuma et al., 2019). However the impact of tropical ants on soil properties more broadly is widely reported (Lobry de Bruyn and Conacher, 1990; Schaefer et al., 2021). We thus advise to focus on the subterranean parts of the nests and the surrounding soil rather than the aboveground parts for these kinds of analyses in this region. The lack of complex aboveground soil mounds contrasts with some temperate ant species that build distinct aboveground mounds made from soil with various proportions of plant organic material and with a complex internal structure that has large impacts on soil properties (Viles et al., 2021). As tropical ant species do not need functional structures to cope with seasonal low temperatures (Kadochová and Frouz, 2013), they generally lack these long-lasting ant heaps. This also why their role in tropical soil bioturbation, as assessed using above-ground measurements, has been reported as being minor in natural habitats compared to earthworms or termites (Tuma et al., 2019).

5. Conclusion

We show that the effect of social insect mounds on soil properties in tropical landscapes differ between taxa but also across habitats. This is important as the effects of ants or termites are usually studied by the same methods only on one species or group of social insects and in the same habitat type. The mound-building, soil-feeding termites *Dicuspiditermes* spp. showed large effects on nutrient dynamics and accumulation even in highly managed habitats such as oil palm plantation. Conversely, *M. gilvus* mounds were in general depleted in basic nutrients but this depletion was less prominent in oil palm plantations, although more prominent on soils with an initial high concentration of these nutrients, meaning that this depletion is context-dependent. Ant mounds showed only minor effects on soil properties in this system, probably due to soil mixing and dilution effects. Therefore we emphasize the importance of soil-feeding termites in controlling soil properties, although this group is scarce in oil palm, compared to the primary or logged forest (Luke et al., 2014; Tuma et al., 2019) due to higher temperatures, lack of decaying wood and leaf litter and hence low densities of soil organic matter. The sustainability of oil palm plantations could be improved by the use of sustainable agricultural methods to encourage soil feeding termites among other biota. Our study gives another reason why termites should not be perceived as pest species in oil palm plantations, and

managers should be advised to not destroy termite mounds (Corley and Tinker, 2015). Recent research shows that leaving the undergrowth vegetation in the plantations can increase arthropod diversity generally (Luke et al., 2019). This management technique would also provide additional shade and litter, which are predictors for survival of more sensitive mound-building termite species (Bignell and Eggleton, 2000). Our work also highlights the potential importance of forest remnants within oil palm plantations as refuges for these and other termite taxa which could hence increase landscape spatial heterogeneity in soils.

Declaration of competing interest

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

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Appendices. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2022.104576>.

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