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The effect of tropical land use change on soil-dwelling ants and termites, their interaction and on ecosystem processes they affect

Ph.D. Thesis

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Annotation

In this thesis I explore the role of tropical soil-dwelling ants and termites in driving ecosystem processes, their mutual interaction and their responses to tropical land use change. To do this I use a combination of methods, including a full review of the ant-termite interaction literature, field sampling for ants and termites, DNA barcoding-based inference of ant predation on termites, and creation and implementation of a new protocol for measuring terrestrial bioturbation. I found that the literature mainly documents anecdotal observations of interactions between ants and termites, the vast majority of which are predatory. Many of these appear to be opportunistic predation of termites by non-specific ants, although some ant species have developed sophisticated methods that enable them to specialise on termite predation. My field sampling demonstrated that soil ants and termites are susceptible to habitat degradation, with logging having minimal impacts, but conversion to oil palm affecting both groups to a greater extent. The predation rate of ants on termites differs between ant taxa, but seems to be stable across habitats. Finally, termites are important for soil bioturbation in all habitat types, but overall, this ecosystem function relies only on few species in oil palm plantations, raising concerns about susceptibility of this function to future extinctions. My work emphasizes the importance of maintaining the diversity of these two trophically linked groups for the ecosystem functions they provide.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 2.2.2020

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Jiří Tůma

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List of papers and author contributions

The thesis is based on the following papers:

I. **Tuma, J**., Eggleton, P. & Fayle, T.M. (2019) Ant-termite interactions: an important but under-explored ecological linkage.

Biological Reviews (in press). DOI: 10.1111/brv.12577 (IF= 10.288)

JT, and TMF collated the literature. PE reviewed defence strategies of termites and with TMF significantly contributed to the manuscript writing and synthetizing the ideas and knowledge gaps. TMF performed the calculation of biomasses and created ant and termite distribution maps. JT led the manuscript writing and synthetized the interaction concepts and future research directions.

II. **Tuma, J**., Luke, S. H., Davies, R. G., Eggleton, P., Klimes, P., Jones, D. T., Konvickova, H., Maraví, P. M., Segar, S., Fayle, T. M.: How does rainforest logging and conversion to oil palm affect soil-living ants and termites and ant-termite predation rate? (Manuscript).

JT was responsible for the fieldwork, identification of ants, analysing the results, writing the manuscript and interpreting the results. DTJ and PE were responsible for identifying termite species. HK, PMM, SS performed the DNA barcoding and termite phylogeny aligning. SHL and RD created the sampling protocol and advised on data collection. PK provided lab support, was involved in sample collections and photographing ant voucher specimens. TMF provided field support, advised on data analyses and writing of the manuscript and on ant species delineations. All authors commented and edited at least one manuscript version.

III. **Tuma, J**., Fleiss, S., Eggleton, P., Frouz, J., Klimes, P., Lewis, O.T., Yusah, K.M. & Fayle, T.M. (2019) Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation.

Applied Soil Ecology 144, 123–133. DOI: 10.1016/j.apsoil.2019.07.002 (IF=3.445)

JT designed the sampling protocol, performed the sample collections, identified the species, analysed the data and wrote the manuscript. SF assisted with sample collection and contributed to manuscript writing. OL supervised SF and contributed to manuscript writing. JF contributed to the study design and field sampling. PK, PE and TMF participated in writing the manuscript and to the analyses. PE identified termite species. KMY supported JT as a local collaborator and advised on sampling design.

Co-author agreement

Tom M. Fayle, the supervisor of this Ph.D. thesis and co-author of chapters I - III, fully acknowledge the major contribution of Jiří Tůma to these manuscripts.

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Dr. Tom M. Fayle

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INTRODUCTION

INTRODUCTION

The effect of tropical land use change on soil-dwelling ants and termites, their interaction and on ecosystem processes they affect.

Habitat loss and its cause

Habitat loss resulting from habitat conversion is the most important threat for biodiversity, ecosystem stability and nature conservation worldwide (McGarigal et al., 2005; Meffe and Carrol, 1997; Sala et al., 2000). It is predominantly caused by human activities such as the conversion of original habitats to production land. It has been estimated that to date, 22 % of total terrestrial land area has been completely converted to human-used land (Hoekstra et al., 2005), with much of the remaining area being affected by other pressures such as selective logging and livestock grazing. Land-use change affects key environmental conditions, drives habitat fragmentation and thus causes species loss and changes in species community composition, with subsequent effects on ecosystem processes and services provided by species (Bommarco et al., 2013; Dobson et al., 2006).

Concerningly, the tropics are among the most strongly affected regions by human-caused habitat change while also being global biodiversity hotspots (Brooks and Spencer, 1997; Myers et al., 2000). Tropical biodiversity is currently threatened by land-use change far more than other threats, such as climate change (Sala et al., 2000). In fact, 80 % of new agricultural land is established on areas converted from primary tropical forests (Gibbs et al., 2010). Logging and conversion mainly to agriculture land such as pastures for cattle or for various crops such as soya or oil palm are the main drivers of tropical habitat loss (Geist and Lambin, 2001; Kissinger et al., 2012) and this process is predicted to accelerate in the near future (Laurance et al., 2004).

Palm oil and oil palm plantations

Palm oil is one of the most important sources of plant-derived fats in the world (Figure 1). It is used in a wide variety of commercial products, mainly in food, biofuels, cosmetics and industrial oils (Fitzherbert et al., 2008). Oil palm (*Elaeis guineensis*) is grown in lowland tropical areas with high rainfall (Corley and Tinker, 2015). The highest production of palm oil is in South East Asia which accounts for 85 % of the world’s palm oil production (FAO, 2017), mainly in Indonesia and Malaysia (Basiron, 2007).

Oil palm plantation is an intensive type of agriculture. The typical land use trajectory that results in establishment of an oil palm plantation is as follows. First, an area undergoes several rounds of selective logging where trees of the highest economical value are harvested first, then fast re-growing trees are harvested in the following rounds. The land is then cleared of the remaining vegetation, terraces are built and topsoil is moved and levelled using bulldozers and rollers in hilly areas. After the clearing, oil palm trees are planted. Pesticides and herbicides are used regularly on plantations to suppress pests and undergrowth. Additionally, high doses of

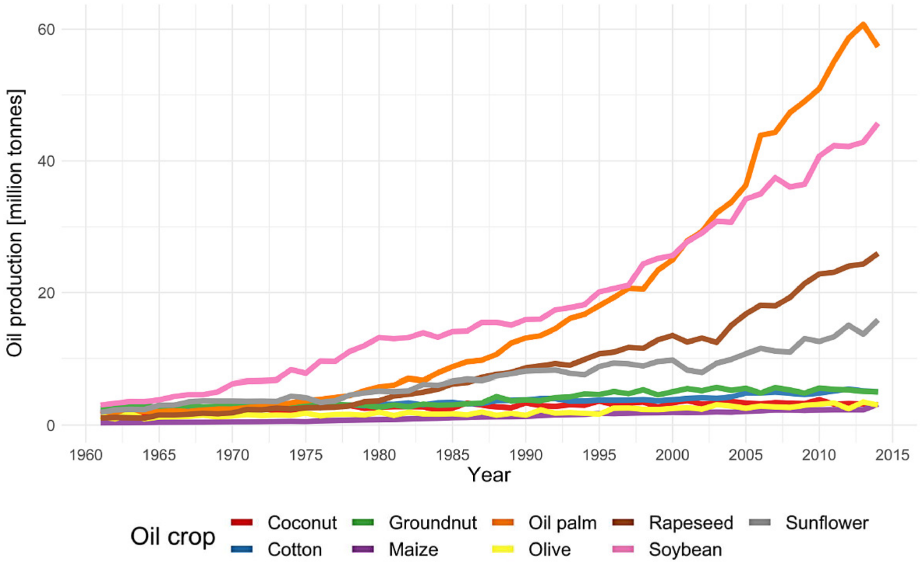

Figure 1. Main vegetable oil crops. Oil production from 1961 to 2014 (reproduced from Meijaard et al., 2015). Artwork reproduced under CC-BY Attribution 4.0 International licence.

slow-release artificial fertilizers are placed close to palms during the whole of the oil palm lifecycle. The first crop can be harvested around the fourth year after planting of the oil palm. After the production peaks (approx. 25 years), the palm trees are cut down, stumps uprooted, the land is levelled again and the cycle of the oil palm plantation repeats (Basiron, 2007; Corley and Tinker, 2015). Schemes for sustainable palm oil production are now being implemented in an effort to mitigate some of the negative impacts of oil palm production. The largest certification body - RSPO (Roundtable on Sustainable Palm Oil) certifies palm oil producers and requires sustainable principles which ensure transparency of the oil supply chain, reduced pollution, land-owners rights or minimize deforestation (RSPO, 2018). Nevertheless, only 21% of palm oil is produced under sustainable schemes and this does not include the largest palm oil producers (RSPO, 2018; ZSL, 2018).

As a result of such changes, oil palm plantation has strikingly different conditions compared to either primary forest or selectively logged forest (Figure 3). The plantation has a simplified, single-story open canopy, with high temperature and low humidity. There are low densities of deadwood, leaf litter and understory vegetation. The only organic materials left are palm fronds (leaves) piled in rows between the palm trees and patches of scattered used oil palm fruit bunches. Otherwise, the soil is generally bare or with moss cover, with thin or no layer of humus (pers. observation Tuma et al., 2019b).

Species diversity is vital for ecosystem functioning (Schmidt et al., 2009). An ecosystem that is reliant on only a small number of species to provide ecosystem services is more susceptible to failing to provide these in altered conditions (Jackson and Sax, 2010). In general, oil palm plantation supports a very low diversity of a range of different taxa compared with natural forests. According to a review (Turner et al., 2011), 25 of 27 different studies concerning various animal taxa demonstrated a decline in species richness in oil palm compared to other habitats. However, species abundance was influenced less predictably, as some taxa increased in abundance. This increase could be due to open habitat specialists, invasive species, or disturbance-tolerant species with low conservation value (Fayle et al., 2013). Fitzherbert et al. (2008) concluded that the changes in species diversity also have many side effects for the ecosystem such as over-usage of fertilizers and pesticides with consequent soil and water pollution, water and wind erosion of soil, or increasing vulnerability to invasive species.

Oil palm expansion causes deforestation in SE Asia

The demand for palm oil products is rising, due to diversification of its use, high profitability and relatively low price (Henderson and Osborne, 2000; Koh and Wilcove, 2007). Oil palm plantations are very productive yielding comparatively more oil while occupying less area compared to similar crops like soya or olive plantations (Basiron, 2007; Poore and Nemecek, 2018). Nevertheless, the recent rising demand for biofuels as a substitute for crude oil is expected to drive further expansion of oil palm plantations (Koh, 2007). Thus more land will be needed for establishing new plantations, which will lead to clearance of primary or logged forests at increasing rates. This is a major contributor to large-scale deforestation in South-East Asia, which is among the highest of any other tropical region (Figure 2). It is predicted that by 2100, there will remain only one quarter of the original forests in SE Asia (Sodhi et al., 2004). 94 % (1 040 000 ha) of the total deforestation in Malaysia from 1990 to 2005 was caused by oil palm expansion (FAO, 2009). This is important as primary and also selectively logged forests retain high biodiversity and maintain vital ecosystem functions.

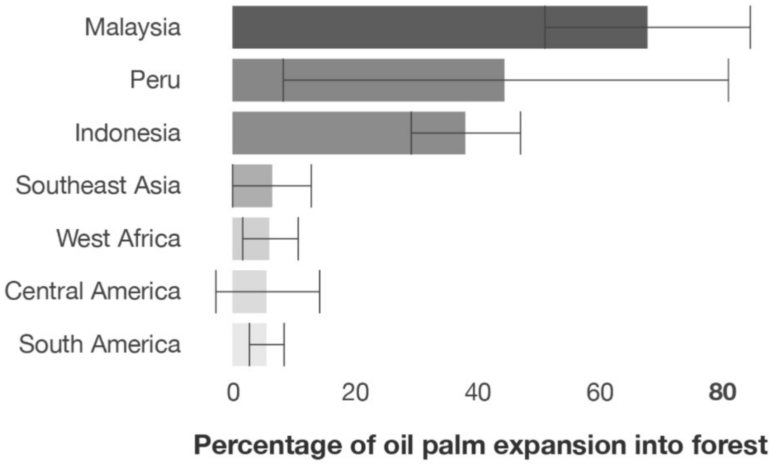

Figure 2. The role of oil palm in deforestation. The figure shows the percentage of all oil palm expansion that was immediately preceded by clearing of forest. Southeast Asia (SE Asia) excludes Indonesia and Malaysia, which are shown separately, while South America excludes Peru. Bars indicate the standard deviation of the sample mean weighted by study area (reproduced from Meijaard et al., 2020). Artwork reproduced under CC-BY Attribution 4.0 International licence.

Logged forest are not simply "degraded areas"

In Malaysia, logged forests (legally, semi-legally or illegally logged primary forests) are typically considered as "degraded" habitats, assigned as areas suitable for cultivation by local authorities (Casson, 2000). This is a legal first step for oil palm plantation establishment. Such an approach also allows the Malaysian government to claim no primary forest loss at the expense of oil palm when confronted with this issue by consumers like the European Union (FAO, 2006; Kanter, 2008). This poses a long-term risk for both primary and selectively logged forests. However, Malaysia could meet the demand for oil palm using only real "brownfields" such as former rubber plantations, instead of converting forests into new oil palm (Corley, 2009; Koh and Wilcove, 2008). Furthermore, selectively logged forests still preserve relatively high biodiversity and show fast recovery of vital ecological functions (Bowles and Rice, 1998; Douglas, 1999; Edwards et al., 2010; Fitzherbert et al., 2008; Woodcock et al., 2011). So logged forests can be of high conservation value, especially with comparison to oil palm plantations.

The importance of ants and termites for ecosystem functioning with an emphasis on the soil environment

Ants and termites are both highly developed, eusocial insects. They are known as ecosystem engineers because they play important roles in ecosystem processes and thus influence other organisms (Jones et al., 1994). Their complex behavioural patterns emerge from simple rules followed by individuals. These small individual decisions together create an exceptional behavioural scheme, called "collective intelligence" (Johnson, 2002). During their activities, they create new habitats, access nutrients for other organisms and change the characteristics of the environment. This contrasts with "keystone" species, where only the role in the food chain is typically considered (Jones et al., 1994; Meysman et al., 2006). With this advanced behaviour and high abundance and biomass, both ants and termites substantially affect their environment.

Impact of ants on the soil environment

Ants are present in the most of the world environments and they affect numerous ecosystem functions. Their diversity is highest in the tropics and subtropics and they contribute a significant portion of the world's terrestrial animal biomass (Tuma et al., 2019a Chapter 1, this thesis). Although their importance differs from habitat to habitat and from species to species, the main impacts ants have on ecosystems lies in their predatory, scavenging and seed dispersing activities, in their diverse mutualistic relationships, and in the mediation of herbivory and granivory. Ants also significantly influence nutrient cycling, soil processes and bioturbation and thus alter soil fertility and development (note that ant influences on soil bioturbation are further discussed in Chapter III in this thesis).

Impact of ants on the physical soil environment

Most ant impacts on the soil environment are caused by nest construction activity, nest maintenance and food storage. As ants maintain a higher relative humidity inside the nest, this provides stable conditions favourable for various decomposing soil flora. These organisms also have access to an ample source of nutrients to decompose in the form of ant excreta and food item remnants (Wolters, 2000). The nest material can also contain organic matter, which can decompose once the soil is moved up to more oxic conditions. Furthermore, ant nests are commonly well-aerated structures and sometimes even ants themselves use soil flora as symbiotic organisms in the nest construction process (Schlick-Steiner et al., 2008).

Ant impacts on water regimes

The influence of ants on water regimes is variable. The most important ant activity with respect to water regimes is the creation of nest entrances and the tunnels and chambers that can act as macropores for water conduction (Lobry De Bruyn, 1997; Wang et al., 1995). One study reports that *Aphaenogaster barbigula* can "cover" 0.9% of the ground surface in nest entrances (Eldridge, 1993). This activity can be more important in areas with water repellent soils and those in which water episodically accumulates on the surface (Lobry De Bruyn, 1997). However, ants also deposit materials with different grain size on the soil surface. These can be washed down to block existing soil macropores (Wang et al., 1995). These materials can also act to repel water, or even create a "crust" on the top of the nest (Nkem et al., 2000). So the effect of ant on water regimes depends on type of substrate for nest building and specific conditions in the nesting site.

Ants impact on soil properties

Ant nest soil often has different nutrient composition compared to adjacent soil. Macronutrients are often measured in such studies, such as N, P, K, Mg, Ca (Cammeraat and Risch, 2008; Carlson and Whiteford, 1991; Dostál et al., 2005; Holec and Frouz, 2006; Mandel and Sorenson, 1982; Nkem et al., 2000). Such differences might result either from impacts of ant colony construction on the soils, or from founding ant queens choosing nest sites with higher nutrient concentrations. However, Dostál et al. (2005) failed to find support for the latter theory in long-term observations of nesting habits of the yellow meadow ant *Lasius flavus* in mountain grassland, Slovakia. Davis-Carter & Sheppard (1993) stated that increased amounts of Mg, K could be caused by elevation of clay particles, which bind these nutrients. Similar enrichment in Ca ions in nests is caused by translocation of calcium-rich substrates from deeper soil layers (Levan and Stone, 1983). Ants can also increase the amount of N, P and organic matter content (Boulton and Amberman, 2006). Concerning carbon content, the situation is less clear. One possibility is that we can find more C in the nest originating from food remnants and ant excreta (Dostál et al., 2005). However, owing to burrowing and subsequent movement of mineral soil from deeper layers up into the higher levels of the nest during nest construction, the accumulated C is "diluted" by less carbon-rich soil (Frouz and Jilková, 2008). This relative drop could be up to 50% (Levan and Stone, 1983).

Ants typically shift the pH values towards neutral in the nest (Frouz and Jilková, 2008). Thus they influence the availability of some nutrients as a result of these changes, for example phosphorus (Frouz et al., 2003). There is a higher rate of mineralization of several nutrients, primarily higher nitrogen and phosphorus in ant nests in comparison with surrounding soil (Cammeraat and Risch, 2008). The rate of mineralization could also be accelerated by the more stable humidity in the nest (Holec and Frouz, 2006).

Furthermore the physical properties of the soil are also influenced (see also discussion of impacts on water regimes above). By creating tunnels and chambers, ants increase macro porosity, aeration and lower the bulk soil density. For example, bulk density did not increase in the nest of *Lasius flavus* with increasing soil depth in comparison with the adjacent soil (Dostál et al., 2005).

Ant impacts on plants via changes in soils

The nutrient stock in the nest is only partially accessible to plants and larger decomposers while inhabited by ants. However, trees are to be able to utilize these nutrients to some extent (Frouz and Jilková, 2008). After the nest is no longer occupied (due either to abandonment or death of the colony), nutrients spontaneously leak to the environment (Nkem et al., 2000). Wang et al. (1995) stated that abandoned nests of *Lasius neoniger* resist decomposition for less than one year in North America.

Because ant nests have differing soil structure and properties to surrounding areas, they support differing seedling recruitment and plant growth. There are two main activities that affect plant growth and distribution: nest construction and the gathering of food items. For example, the ant *Atta vollenweideri* accelerates rate of vegetation spread by nest construction in salt savannah in Uruguay by preferential recruitment of shrubs on ant nests, which contained more sodium, provided higher moisture and were less compacted than adjacent soil (Sosa and Brazeiro, 2010). In Patagonia, the presence of nests of *Acromyrmex lobicornis* facilitate the vegetation even during dry periods, where refuse dumps created by these ants supported seedling recruitment, by providing higher moisture and nutrient content for seedlings growth (Farji-Brener and Ghermandi, 2004). *Atta* sp. can support rain forest regeneration by providing nutrient rich, vegetation free and high insolation microhabitats for new seedlings (Farji-Brener and Illes, 2000). Vlasáková et al. (2009) found a similar pattern in nests of *Lasius flavus* in mountain grasslands for establishment of Norway spruce (*Picea abies*) seedlings.

The impact of termites on the environment

Termites are phylogenetically nested within the cockroaches (Inward et al., 2007) They differ from ants by the source of their diet. Termites can be found mainly in tropical and subtropical regions and their abundance and diversity peaks in the wet tropics (Bignell and Eggleton, 2000). Two main features of termite colony life determine their impacts on the environment: The foraging and digestion of their main food source – cellulose, lignin or materials containing organic matter in various states of decomposition (i.e. organic matter-rich soil) and the construction and maintenance of immense, often long-lasting nests (Wood and Sands, 1978).

Termites are responsible for significant litter, soil humus and deadwood decomposition. For example in Queensland dry savannah, they are responsible for decomposition of up to 20% of total dead plant material (Holt and Coventry, 1990). This decomposing activity is provided by the wide range of interactions with Archaeal, bacterial, fungal and protozoal symbionts living in the termite digestive tract, as well as the enzymes they produce themselves (Abe et al., 2000). As a result, there are significant fluxes of methane, carbon dioxide and even H_2 out of termite nests (Noirot and Darlington, 2000). Through this process, termites mediate 2-5% of global terrestrial carbon fluxes (Sanderson, 1996). However, a significant share of the methane produced can subsequently be trapped and oxidised in the nest walls (Nauer et al., 2018).

The termite nest (here we refer mainly to epigeal and hypogeal nests since these are likely to have the greatest impact on soil environment) is an adaptive structure with the main purposes of preserving colony homeostasis and protecting its inhabitants. It serves as a passive air-conditioner for maintaining constant temperature and humidity, as well as to effectively ventilate the emerging gasses from food digestion (Worall, 2011). Since the main breakdown processes take place in the nest and the collected food items are stored there, the nest represents a nutrient-rich hotspot in the environment (Ali et al., 2013; Brossard et al., 2007; Jouquet et al., 2004). Below I survey the literature on the impact of the termite nest as living, dynamic structure on soil biota and nutrient.

The impact of termites on the soil environment

Termites influence the amount of micro and macronutrients (Semhi et al., 2008). They also alter soil pH, although there is no general directional trend in this effect across different studies (Donovan et al., 2001; Holt and Lepage, 2000; Lobry de Bruyn and Conacher, 1990). The most alkaline level of 12.5 in any biological system was found in termite guts (Brune and Kühl, 1996). Significant amounts of calcium and sodium originating from digested plant material can be found in termite saliva and faeces (Bagine, 1984). In addition, termite guts host nitrogen-fixating bacteria, through which they contribute to the total soil nitrogen pool (Yamada et al., 2006). It has been suggested that the presence of termites fixating nitrogen can substitute up to 22-32% of the usual amount of ammonia fertilizers applied to agricultural fields (Evans et al., 2011). As a result of these processes there are clear patterns of increased carbon, nitrogen Ca2+, Mg2+ and K+ in the nest in comparison to adjacent soil (Holt and Lepage, 2000; Lee and Wood, 1971; Lobry de Bruyn and Conacher, 1990; Mujinya et al., 2010). The P content (generally a deficient nutrient in the tropics) seems to be influenced differently across different termite feeding groups (Rückamp et al., 2010).

The activity of building and maintaining a suitable living environment inside the nest influences the nest soil in various ways. Generally, the material for nest construction is mined from deeper soil layers and termites actively select soil particles for its creation. Jouquet et al. (2011) states that termites usually prefer finer soil particles for nest construction. However, fungus-growing termites select soil particles from upper layers for common tunnels and chambers, but for the fungal chamber, they choose clays from deeper soil layers for its better water-holding capacity (Jouquet et al., 2002; Konaté et al., 1999; Mujinya et al., 2010; Susumu, A. et al., 2012). In addition, through their burrowing activity, specifically the creation of chambers and tunnels often connected with the soil surface, termites significantly influence soil porosity (Holt and Lepage, 2000; Mando et al., 1996), water regime and runoff by the creation of preferential flow paths (Léonard and Rajot, 2001).

Termite impacts on plants via changes in soil properties

The impact of termites on the soil environment results in altered conditions for plant growth and diversity. Soil organic matter accumulation, higher microbial activity, altered nutrient content and availability, soil water accumulation and higher content of clay minerals leads to increased plant growth in the area surrounding the nest (Jouquet et al., 2011). Affected plants can also cope better with herbivory, as termite mounds provide sufficient amounts of nutrients to regenerate leaf area and survive (Brody et al., 2010). Furthermore, the spatial distribution of termite nests in the environment can result in altered vegetation patterns, and generate increasing patchiness (Jouquet et al., 2005; Pringle et al., 2010) and consequently increase habitat biodiversity. Moreover, nest sites can serve as protected areas from fire and flooding as well as regeneration spots for tree regrowth (Choosai, 2010; Traoré et al., 2008).

Ant – termite interactions

Exploring animal interactions is one of the basic tasks of ecology. Understanding networks of interactions is important, because their structure affects ecosystem stability and resilience to future disturbance. Furthermore, although each individual organism has its effects on the environment, the interaction between them can greatly influence the environment. Such interactions shape communities, the appearance of whole habitats and affect vital ecosystem processes (Kumar and Mina, 2018). Ants and termites occur in high abundances and their biodiversity hotspots and preferred habitats overlap, thus they are likely to encounter each other in many natural situations (Hölldobler and Wilson, 1990; Tuma et al., 2019a). Although their food sources differ substantially, the two groups forage in, or inhabit (thus compete for) similar microhabitats such as litter, deadwood or soil (Kimber and Eggleton, 2018). Ants often cohabit the same nest as termites (usually a termite mound) either completely separated from them or with occasional conflicts, where ants predate termites (Holt and Greenslade, 1980; Jaffe et al., 1995). This situation can turn into mutualism when ants protect the common nest against predators and termites consume remnants of ants as nitrogen source (Higashi and Ito, 1989; Jaffe et al., 1995). Nevertheless, probably the most common interaction is predation in which ants predate termites either opportunistically, in the case of many generalists ants, or almost exclusively in termite-eating specialists (Tuma et al., 2019a; chapter I, this thesis). However, all these interactions, despite their potential ecological significance, are largely understudied and – are yet to be quantified.

Soil-living ants and termites: the need for further research

All the effects ants and termites have on the environment are likely to be altered by habitat change because ant and termite communities are predicted to shift when the habitat is altered. Previous work has revealed pronounced changes in canopy or litter-dwelling ant and termite communities in logged forests or plantations (Dambros et al., 2013; Eggleton, 1996; Jones et al., 2003; Mezger and Pfeiffer, 2011; Philpott and Armbrecht, 2006; Solar et al., 2016). However, the response of soil-dwelling ants and termites to habitat change is largely understudied (but see Luke et al., 2014). This is important since soil invertebrates are considered as good indicators of soil quality (Stork and Eggleton, 1992) while ants and termites can be used as indicators of habitat degradation (Osborn et al., 1999). Similarly to the regulation of herbivores by their predators, mutualism of ruminal prokaryotes with large herbivores or pollinators with plants, we predict that ant-termite interactions (mainly predation) significantly affect the environment through influences on decomposition processes. Nevertheless, the literature exploring the interaction between ants and termites is not well synthesised, and the importance of this interaction remains unclear. Thus studies investigating ant and termite communities and interactions in soil, along with the ecosystem processes they affect in disturbed habitats, are essential for understanding how such changes will impact soil processes and consequently production, sustainability and resilience of human-modified environments (Coleman et al., 2017).

Figure 3. Gradient of forest degradation in Borneo. **Primary forest** is characterised by closed, multistorey canopy, and the presence of large trees, lianas and sparse undergrowth. **Logged forest** lacks larger trees; instead fast growing pioneer tree species (e.g. *Macaranga* sp.) thrive here. There is usually dense undergrowth of herbaceous vegetation, vines and scrub due to the more open canopy. **Oil palm** plantation consists of palm oil (*Elaeis guineensis*) trees planted in rows on artificially levelled terraces (if grown in hilly areas). The litter consists mainly of fronds – palm leaves stacked in rows. The soil is either bare, covered by mosses, or covered with leguminous vines. There is a semi-open, one storey canopy, typically with low humidity and high temperatures. These types of habitats were surveyed in the work described in the second and third chapter of this dissertation. Photos copyright Jiří Tůma.

The content of dissertation chapters:

In the **first chapter,** I present a literature review exploring the prevalence and importance of interactions between ants and termites. First, I present evidence of the importance of ants and termites for the environment with their high abundances and wide distributions. I show the main interactions that ants and termites are involved in with other organisms and then focus on all of the ways ants interact with termites. I infer that ant predation on termites is the most important, most widespread, and most studied type of interaction between these two groups. This predation affects populations of termites and as a consequence, it can limit the decomposition rate of dead plant organic matter. There is probably a high number of opportunistic ant predators of termites, but compared to specialised ants, these opportunists are understudied. However, they may also be potentially important for limiting termite populations. I present the most useful methods for exploring ant-termite predation and how those can be applied in revealing the consequences of this interaction for ecological processes. This will be necessary for evaluating the effect of specific ant species and also of whole ant communities in regulating termite populations in different biomes. I propose that combining methods including DNA barcoding, exclusion experiments and field observations are necessary for assessing the effect of this interaction on entire ecosystems.

In the **second chapter**, I present new data on the distribution of tropical soil-dwelling ant and termite communities in differently degraded habitats (Figure 3) and explore the predation of ants on termites using DNA barcoding of ants. I collected ants and termites using soil pit excavation in primary forest, selectively logged forest and oil palm plantation. I also measured basic environmental variables. Ants and termites were identified to the species level. The abundance of ants was highest in logged forest while termite abundance showed no clear differences between habitats. The species richness and Shannon diversity index of ants was comparable between primary and logged forest but was much lower in oil palm plantation. Termites had more species in the logged forest than in primary or oil palm plantation. Furthermore, the oil palm was predominantly occupied by the invasive ant *Anoplolepis gracilipes*, and there was only one termite species - *Macrotermes gilvus*. Soil temperature was the strongest factor in shaping ant communities across different habitats while the amount of leaf litter was most important for termite communities. These results emphasize the value of the logged forest for supporting species diversity while oil palm plantations showed a lower number of species and susceptibility to invasive species. Randomly selected ant individuals (from 12 genera) from soil pits were analysed for termite DNA in their bodies using DNA barcoding. I found that from 124 ant individuals, 32% of them contained termite DNA and this percentage was similar across habitats. However, termite predation rates differed across ant genera. This means that overall ant predation on termites is similar even in the most degraded habitats. Hence I speculate that the predatory pressure of ants on termite populations and the influence of this pressure on the ecosystem functions termites provide is resilient to habitat change.

Since I found that ant and termite communities vary across the gradient of anthropogenic change I predicted that this would affect ecosystem processes. In the **third chapter**, I target the process of bioturbation: the turnover of soil material by soil-dwelling organisms, which is one of the most important ecosystem functions soil-dwelling ants and termites provide. I developed a protocol (available as a Supplementary material 2) to identify the main bioturbators and estimate aboveground animal-driven bioturbation. I assess how bioturbation rates and amount of standing bioturbated soil differs across a habitat degradation gradient in Borneo. I found that termites were responsible for 97.0% of standing bioturbated soil across all habitats, while short-term small-scale bioturbation was mainly driven by earthworms (87.3%). The total standing bioturbated soil and the bioturbation rate was highly variable and did not differ between habitats. However, the species richness of ants and termites involved in bioturbation was higher in the primary forest than in either logged forest or oil palm plantation. This work also indicates that tropical bioturbation may be maintained by a group of previously underestimated "hidden bioturbators" i.e. earthworms, producing smaller soil structures that are rapidly broken down, rather than by groups producing larger, long-lasting and well visible soil structures. Furthermore, the standing bioturbated soil in oil palm was almost exclusively generated by a single species of termite – *Macrotermes gilvus*, while bioturbation in primary forest and logged forest was maintained by a high diversity of animal groups. In conjunction with our findings in the second chapter, this termite species is not the only one found in soil, but it maintains vital ecosystem processes in disturbed habitats. Conversely, the reliance on a single bioturbator species in oil palm plantation over larger scales is of concern because it leaves this important ecosystem process vulnerable to future extinction events.

Taken together, this work emphasizes the role of soil-dwelling ants and termites and their interaction in essential ecosystem processes in Borneo. It shows the decline of ant and termite species diversity and also functional diversity in oil palm plantations compared to primary and logged forests. The logged forest proved to still be a valuable habitat maintaining not only ant and termite species diversity but also bioturbation levels and diversity of bioturbator groups. These findings thus support the policy of maintaining logged forests for their high conservation value. This also raises concerns for the future sustainability of expanding oil palm plantations, especially in the face of current global change, along with anticipated species extinctions and potential loss of the vital ecosystem processes that ants and termites provide.

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CHAPTER I

Ant-termite interactions: an important but under-explored ecological linkage

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Ant-termite interactions: an important but under-explored ecological linkage

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ABSTRACT

Animal interactions play an important role in understanding ecological processes. The nature and intensity of these interactions can shape the impacts of organisms on their environment. Because ants and termites, with their high biomass and range of ecological functions, have considerable effects on their environment, the interaction between them is important for ecosystem processes. Although the manner in which ants and termites interact is becoming increasingly well studied, there has been no synthesis to date of the available literature. Here we review and synthesise all existing literature on ant–termite interactions. We infer that ant predation on termites is the most important, most widespread, and most studied type of interaction. Predatory ant species can regulate termite populations and subsequently slow down the decomposition of wood, litter and soil organic matter. As a consequence they also affect plant growth and distribution, nutrient cycling and nutrient availability. Although some ant species are specialised termite predators, there is probably a high level of opportunistic predation by generalist ant species, and hence their impact on ecosystem processes that termites are known to provide varies at the species level. The most fruitful future research direction will be to evaluate the impact of ant–termite predation on broader ecosystem processes. To do this it will be necessary to quantify the efficacy both of particular ant species and of ant communities as a whole in regulating termite populations in different biomes. We envisage that this work will require a combination of methods, including DNA barcoding of ant gut contents along with field observations and exclusion experiments. Such a combined approach is necessary for assessing how this interaction influences entire ecosystems.

Key words: ants, termites, predation, Formicidae, Termitoidae, ecosystem engineer, food web, interaction network

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I. Introduction

Quantification of species interactions is fundamental for understanding ecosystems, since interactions structure communities and influence the abiotic environment. Species interactions are usually difficult to measure as they vary with scale and context (Harrison & Cornell, 2008). Nevertheless, studying species interactions allows us to describe naturally occurring processes and tackle urgent environmental problems such as predicting how ongoing anthropogenic habitat change will affect natural communities and their functional roles, and its consequences for ecosystem processes and properties (Chalcraft & Resetarits, 2003; Agarwal, 2007).

Ants and termites are involved in numerous ecological interactions and play important roles in many ecosystem processes (Hölldobler & Wilson, 1990; Bignell & Eggleton, 2000; Philpott & Armbrecht, 2006; Del Toro & Pelini, 2012). These two groups of social insects are considered to be ecosystem engineers because of their complex effects on biotic and abiotic aspects of ecosystems (Jouquet *et al.*, 2006). Such effects are mediated *via* predation, scavenging, mutualistic interactions or secondary herbivory in the case of ants, and mainly *via* plant organic matter decomposition and bioturbation in the case of termites (Lavelle & Spain, 2001). Ants and termites also reach high biomass, abundance and species richness in the same tropical and subtropical ecosystems and hence are likely to encounter each other frequently (Dial *et al.*, 2006). Despite this, their interactions are poorly known, and the existing literature has not yet been synthesised. This is of particular concern, because this interaction probably affects essential ecological processes such as organic matter decomposition, nutrient fluxes and greenhouse gas emissions, which are likely to be altered by ongoing anthropogenic change.

Here, we first evaluate the ecological importance of ants and termites, since this provides the background rationale for our review and also informs the later discussion of how their interactions affect ecosystems. We then bring together studies from various regions and habitats describing ant–termite interactions, the majority of which involve ants eating termites. We also review the methods that have been used to study this interaction. We synthesise the current knowledge regarding this interaction not only in terms of its effect on ant and termite populations, but also, most importantly, in terms of ecosystem processes. Finally, we highlight knowledge gaps and possible approaches to address them in future research.

II. The ecological importance of ants

Ants are an important functional component of most terrestrial ecosystems. They reach high abundances and occupy numerous niches both above and below ground. Because of their high biomass density they dominate many ecosystems, comprising between 20 and 52% of animal biomass in the tropics (Stork, 1996; Dial *et al.*, 2006). For example, there are estimated to be 8.6 million ants per hectare in Amazonian rainforest (Beck, 1971). High densities of ants have also been recorded in temperate regions with ants surpassing other macroinvertebrate groups in biomass (King, Warren & Bradford, 2013) (Fig. 1). Some ant species create extremely large colonies, which can be interconnected and cooperate in a phenomenon known as a supercolony. This can allow ants to reach even higher densities: Japanese grasslands can support 1.13 million ants per hectare of a single species, *Formica yessensis* (Higashi & Yamauchi, 1979).

Ants interact with many organisms in diverse roles. They are effective predators of a wide range of animals (Hölldobler & Wilson, 1990). The predation pressure ants exert on arthropod communities is of great importance, and they can shape entire insect communities (Floren, Biun & Linsenmair, 2002), and increase plant growth by reducing herbivore numbers (Schmitz, Hambäck & Beckerman, 2017). Many ants are involved in mutualisms. Ants tend honeydew-producing insects on plants, protecting them against predators and feeding on their carbohydrate-rich excretions (Styrsky & Eubanks, 2007). Many ants also form mutualisms directly with plants, trading protection against herbivores and plant competitors for housing space inside the plant, and consuming plant-provided food (Rico-Gray & Oliveira, 2010). Through mutualisms with cellulose-decomposing fungi (Agaricales: *Leucocoprinus*), leafcutter ants (tribe Attini) are also able to use plant materials as a food source, thus acting locally as effective and often selective herbivores that consume up to 17% of annual tree leaf production in Neotropical forests (Vasconcelos & Cherrett, 1997). Ants are also important seed dispersers for an estimated 4.5% of angiosperm plant species globally (Lengyel *et al.*, 2009).

Because of their high abundances, ants may have important effects on the environment. Recent studies show support for ants being the main scavengers in some ecosystems, particularly in the tropics (Fayle *et al.*, 2011; Tan & Corlett, 2012) with ants being responsible for 61% of all invertebrate-removed food items on the rainforest floor (Griffiths *et al.*, 2018). As a result of this, ants indirectly

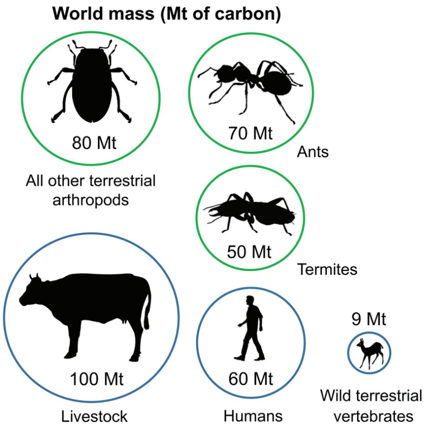

Fig. 1. Global dry biomass of selected animal groups in comparison with that of ants and termites. Values are in megatonnes of carbon. Biomass of ants was assessed by first estimating the average proportion of arthropod biomass that is ant biomass from Dial *et al.* (2006) and Stork (1996) [(0.52 + 0.20)/2 = 0.36]. This value was then multiplied by the biomass of all terrestrial arthropods taken from Bar-On, Phillips & Milo (2018) [0.36 × 200 Mt = 70 Mt]. For termites, a total global wet biomass of 440 Mt was calculated by multiplying by area and summing the values for different biomes from Table 3 of Sanderson (1996), and then converting to dry biomass using the average proportion of wet biomass as dry biomass for the two termite species measured in Cooper & Withers (2004) [440 Mt × (0.220 + 0.233)/2 = 100 Mt dry biomass]. Finally, conversion to dry carbon biomass assumed that carbon comprises 50% of total dry biomass following Bar-On, Phillips & Milo (2018) [100 Mt × 0.5 = 50 Mt dry carbon biomass]. Biomass of all other terrestrial arthropods was calculated by subtracting our calculated values for ants and termites from the total terrestrial arthropod biomass from Bar-On, Phillips & Milo (2018) [200 − (70 + 50) = 80 Mt]. Biomasses of humans, livestock and wild terrestrial vertebrates were taken directly from Bar-On, Phillips & Milo (2018). As stated previously by Hölldobler & Wilson (1994, p.1): "When combined, all ants in the world taken together weigh about as much as all human beings." Note that all calculations were carried out on unrounded numbers.

accelerate the decomposition of dead organic matter and the redistribution of nutrients (Frouz, Santruckova & Kalcik, 1997; Frouz & Jilková, 2008). Ants build large, mainly underground nests. During the building process they turn over vast quantities of soil – a process called soil bioturbation. The amount of soil moved is estimated at 1–5 tons per hectare per year, but could reach 5–50 tons per hectare per year (Wilkinson, Richards & Humphreys, 2009). Ant bioturbation affects the distribution of soil colloids and soil organic matter, stimulates microbial activity, and creates soil pores, which increases aeration and water infiltration, thus influencing overall soil health (Gabet, Reichman & Seabloom, 2003; Meysman, Middelburg & Heip, 2006). As a result, ants have positive impacts on plant growth in both natural ecosystems and in agricultural areas (Evans *et al.*, 2011).

III. The ecological importance of termites

Like ants, termites reach their highest abundances in tropical forests. However, termites are restricted mainly to the tropics and subtropics with the highest densities being found in African rain forest (Bignell & Eggleton, 2000). Termite biomass can comprise 40–60% of total soil macrofaunal biomass, with up to 12 million individuals per hectare (Dahlsjö *et al.*, 2014), although older studies estimate 20–70 million individuals per hectare in some biotopes (Wood & Sands, 1978; Jouquet *et al.*, 2011).

Termites differ from ants in the food they consume. Termites are decomposers, with the main source of food being dead plant material in various stages of decay – i.e. dead wood, leaf litter, dry grass, and, soil with varying amounts of minerals (Donovan, Eggleton & Bignell, 2001). Additionally, they may be responsible for a large proportion of herbivore dung decomposition (Freymann *et al.*, 2008; Noble *et al.*, 2009). Termites are able to digest a significant part of the cellulose present in ingested food with the help of their powerful mandibles and gizzard, their own enzymes, their complex digestive system with steep pH gradients and oxic and anoxic compartments, and with the help of a diverse community of endosymbiotic flagellate eukaryotes, bacteria and archaea. Additionally, termite species belonging to the subfamily Macrotermitinae cultivate and feed on an exo-mutualistic fungus (*Termitomyces* spp.) that lives in their nests. These fungi are fed on pre-digested leaf litter and wood by the termites (Radek, 1999; Li *et al.*, 2018; da Costa *et al.*, 2019).

With their complex and effective gut biota, termites are one of the most important animal decomposer groups at a global scale. Termites are able to process 3–60% of annual litter production in tropical ecosystems and up to 60% of annual wood-fall (Wood & Sands, 1978; Collins, 1981). Similarly, in Malaysian rainforests, termites can be responsible for 54–68% of total decomposition of experimentally placed wood blocks (Ashton *et al.*, 2019) and a single species of termite can consume 2–32% of daily litterfall (Abe & Matsumoto, 1979). On pastures in Kenya, termites and grazing mammals were responsible for the same amount of herbage consumption: 1 ton per hectare per year (Lepage, 1981). The most efficient removers and decomposers of dead plant organic matter are termites from the subfamily Macrotermitinae (fungus-growing termites; Aanen & Eggleton, 2005). Nevertheless, it has been suggested that in some dry areas termites can have a negative effect on the ecosystem, where they exacerbate overgrazing of natural vegetation by livestock, competing with native and farmed mammals, and leaving the soil bare and prone to erosion (Lavelle & Spain, 2001).

With high abundances and effective utilisation of ingested cellulose, termites contribute to global gas fluxes through the gases they produce. Termites are expected to be an important source of methane emissions and carbon dioxide emissions globally (Sanderson, 1996). However, recent studies report that 20–80% of produced methane is in fact oxidised by methanotrophic bacteria living in the termite mound wall, so the total net emissions to the atmosphere should be revised (Nauer, Hutley & Arndt, 2018). They also produce a substantial amount of hydrogen (Sugimoto *et al.*, 1998), nitrous oxide (Brauman *et al.*, 2015) and some termites contribute to nitrogen fixation in tropical habitats through the action of their endosymbiotic bacteria (Yamada *et al.*, 2006).

Termites produce enzyme- and microbial-rich faeces and hence contribute to the soil microbial pool and to nutrient redistribution (Jouquet *et al.*, 2011). The nutrients in ingested matter that are not used by the termites are deposited within the mound, with these mounds consequently becoming nutrient rich relative to the surrounding area (Brauman, 2000; Sarcinelli *et al.*, 2013). As a result, these fertile mounds are characterised by vegetation that differs from that found in the rest of the habitat (Muvengwi *et al.*, 2017). Termites can therefore effectively shape plant community patterns and even stabilise ecosystems in the face of global climate change (Traoré *et al.*, 2008; Bonachela *et al.*, 2015; Ashton *et al.*, 2019). Termites also affect the physical soil profile by excavatation of large amounts of soil during the building and maintenance of mounds and protective sheeting. Termites construct this sheeting from a mixture of soil particles and faeces. The sheeting is built over the surface of food items and exit holes as a protection against predators and desiccation (Harit *et al.*, 2017). Rates of bioturbation have been measured at 1–11 tons per hectare per year (Jouquet *et al.*, 2015), although the real value is likely to be even higher as these measurements account only for mound material, not for soil sheeting (Lee & Wood, 1971; Kooyman & Onck, 1987). There is also turnover of bioturbating termite species when the habitat is degraded (Tuma *et al.*, 2019). Consequently, termite bioturbation leads to physical changes in the soil, such as increased aeration and infiltration of water, higher levels of clay compared to adjacent soil, or redistribution of nutrients throughout the soil profile (Donovan *et al.*, 2001; Ashton *et al.*, 2019). Termites thus contribute significantly to soil creation and can support plant growth *via* incorporation of organic matter into the soil profile (Mando, Brussaard & Stroosnijder, 1999). These processes have been best studied in mound-building species, while the impacts of species that do not build soil termitaria (mounds) (either nesting directly in soil or wood, or building carton termitaria) on soil properties remain poorly explored.

IV. Types of interaction between ants and termites

Because of their ecological significance, numerous interactions with other organisms, relative ubiquity and common co-occurence, understanding the relationships between ants and termites is important. However, these interactions are still very poorly documented (see online supporting information, Fig. S1). This is despite the two groups being estimated as each having as much global biomass as all other terrestrial arthropods, and nearly an order of magnitude more biomass than all wild vertebrates (Fig. 1). Ants and termites interact in a number of ways, including living together commensally, mutualistically, competing for nesting space, and probably most importantly as predators/prey (see Table S1; Hölldobler & Wilson, 1990).

Co-habitation involves ants living inside a termite nest taking advantage of termitarium structures. This arrangement is usually beneficial for ants, when cleptobiosis (theft of food or another item of value from another animal) or lestobiosis (cleptobiosis but with the thieving species nesting in or near the chambers of the host species) is involved, and can range from detrimental to beneficial for termites. Co-habitation has been best studied for the minority of termite species that build externally visible mound structures. These structures represent protected spatial and functional niches in the environment and consequently, the termite mound is often used as a nesting site by numerous ant species (Holt & Greenslade, 1980), even while still inhabited by termites. Wheeler (1936) recorded 198 ant species inhabiting termite nests. Although these inquiline ants interact with host termites in various ways, there is little information on the nature of these interactions. Ants can either inhabit the parts of termite nest where termites do not occur, or ants can exclude termites from a certain part of the nest (Lubin & Montgomery, 1981). It is likely that inquiline ants living in termite nests feed opportunistically on termite brood or adults (Jaffe, Ramos & Issa, 1995), as well as on other inquiline arthropods present in the termitaria (Gallego Ropero & Feitosa, 2014). The relationship between inquiline ants and termites can also shift from commensal, in which only the ants benefit and the fitness impacts on termites are minimal, to more mutualistically beneficial interactions (Jaffe, Ramos & Issa, 1995).

Where the relationship is mutualistic, ants can benefit from the use of a nesting site in the termite nest, while termites can consume ant food remnants, which are rich in nitrogen, and even benefit from ant protection (Hölldobler & Wilson, 1990; Diehl, Junqueira & Berti-Filho, 2005). Jaffe, Ramos & Issa (1995) observed a common protective reaction of ants and termites living in the same nest against other attacking ant species. In this case, ants and termites were not physically separated in the nest. Sometimes the protective burden falls on the ant partner, with the ant *Camponotus* sp. effectively protecting nests shared with termites against intrusion of the regular termite predator ant *Iridomyrmex sanguineus* (Higashi & Ito, 1989). Similarly, nesting in the base of the mound of the termite *Odontotermes latericius*, the ant *Pheidole megacephala* was observed to attack predatory *Megaponera analis* workers when they attempted to raid the termite colony in African savanna (Sheppe, 1970). Note that *P. megacephala* is globally invasive, although this behaviour was observed in Zambia, which might be part of its native range [www.antmaps.org (Economo & Guénard, 2016)]. However all these instances of 'defence' could be by-products of ants protecting their own nest or territory. It is unclear whether any of these ant–termite interactions have progressed beyond being 'by-product' mutualisms (De Jaegher, 2017) to a stage where there is reciprocal altruism between partners. Furthermore, the degree to which termites benefit from co-habiting with ants appears to vary among both ant and termite species.

Ants can also inhabit the same niche as termites and hence potentially compete for nesting space. Deadwood is an important nesting site for both ants and termites and they compete for this resource (Kimber & Eggleton, 2018). Termites furthermore not only inhabit (and defend) pieces and logs of deadwood, but they also consume wood and thus remove this nesting site from the environment. Another example comes from standing, living trees. Colonies of the two groups inhabit the tree *Cecropia pachystachya* in Brazil, being spatially and mechanically (termites build protected foraging galleries from fibrous material) segregated from each other, without any apparent direct antagonistic interactions (Neves, Bernardo & Santos, 2014). Similarly, ants build physical barriers from fibrous material at territory boundaries in this system (Quinet, Tekule & de Biseau, 2005). Termites can also use vibrations to detect or avoid ants, or even mimic ant vibrational signals to prevent direct confrontation (Oberst *et al.*, 2017). Something similar is observed in epiphytic bird's nest ferns (*Asplenium* spp.), in which ant colonies and termite colonies are able to co-exist in the root mass of larger ferns, but smaller ferns support colonies of either ants or termites with the two groups not co-occurring (Ellwood, Jones & Foster, 2002). Presumably, ants and termites compete for nesting space in the ferns. The behaviour and feeding nature of ants is also of importance. Ants predating arthropods can lower the activity of foraging arboreal termites, while non-predatory ants had no such effect in Brazilian rainforest (Conçalves *et al.*, 2005). This suggests that predation but not competition (for space) is a limiting factor for termite activity.

Because termites represent an abundant food source, and many ant species are at least partly predatory, predation of termites by ants is probably the most common type of interaction (Table S1) and this forms the focus of the remainder of this review. Ants have been described as being the most significant and regular predators of termites (Deligne, Quennedey & Blum, 1981; Abe & Darlington, 1985; Hölldobler & Wilson, 1990). Since the global-scale distributions of ants and termites overlap (Fig. 2), the two groups are often found in the same habitat, and many ants are often predate a broad range of insects, it is expected that predation of ants on termites should also be widespread. Since termites are mainly detritivores, predation of ants by termites is unlikely to occur. The only evidence for any consumption of animal-derived food by termites is keratophagy (consumption of skin) on mammal carcasses in the African savannah (Freymann *et al.*, 2007), feeding on vertebrate carcasses by *Nasutitermes* termites in Panama (Thorne & Kimsey, 1983) and feeding on rat carrion by *Rynchotermes nasutissimus* in Brazil (Prestes *et al.*, 2014). An anecdotal case of termites foraging for ant bodies was recorded when the termite *Nasutitermes corniger* harvested *Azteca* sp. ants, freshly killed during defence of their nest (Jaffe, Ramos & Issa, 1995). However, the latter might be a case of hygienic behaviour, as termites often clean up dead nestmates, or consume them as they are rich in nitrogen, which is a scarce nutrient in wood-feeding termites (Shelton & Grace, 1996; Neoh *et al.*, 2012; Sun, Haynes & Zhou, 2013). Since there is no evidence of termite predation on ants, we here discuss only cases in which ants directly predate termites.

V. Methods for studying ant–termite interactions

1. Field observations

The first approach that was applied (Wheeler, 1900) involves direct observations of ant species interacting with termites in natural conditions. This method is highly time-consuming in the field and almost all published reports are anecdotal (for examples see Table S1), and hence do not result from standardised surveys, making generalisation challenging. However, these reports are useful for identifying possible termite specialists, and guiding further research, such as species-targeted observations where specific colonies are observed for longer periods in order to describe temporal changes in behaviour (Leal & Oliveira, 1995).

2. Field experiments

Field manipulations allow us to create and manipulate natural events in real time. One use of such manipulations is to create artificially a natural situation that is otherwise rare or difficult to observe. For example, a termite mound can be artificially broken to mimic vertebrate damage and to expose the termites to ant predation (Hasan, 2015). In some recent studies, ants were artificially excluded or poisoned, resulting in increases in consumption rates of cellulose baits, plausibly because of an increase in termite abundance (Parr *et al.*, 2016). Another common experimental approach is using termites as bait to observe ant behaviour and food preferences (Campos & Camacho, 2014; Neves, Bernardo & Santos, 2014). However, caution must be used when interpreting the results from facilitated predation experiments, as they may involve the problems discussed below for laboratory experiments.

3. Laboratory experiments

Laboratory predation tests of specific ant species on specific termite species can show us whether that ant is likely to eat that termite, and whether it can cope with the termite's defences (see Section VII.2). Such tests are likely to fail to describe the real interactions of ant and termite species under natural conditions and are also unlikely to reveal the potential effects of ants on termite populations for two reasons. First, the defence mechanisms of termites can work with

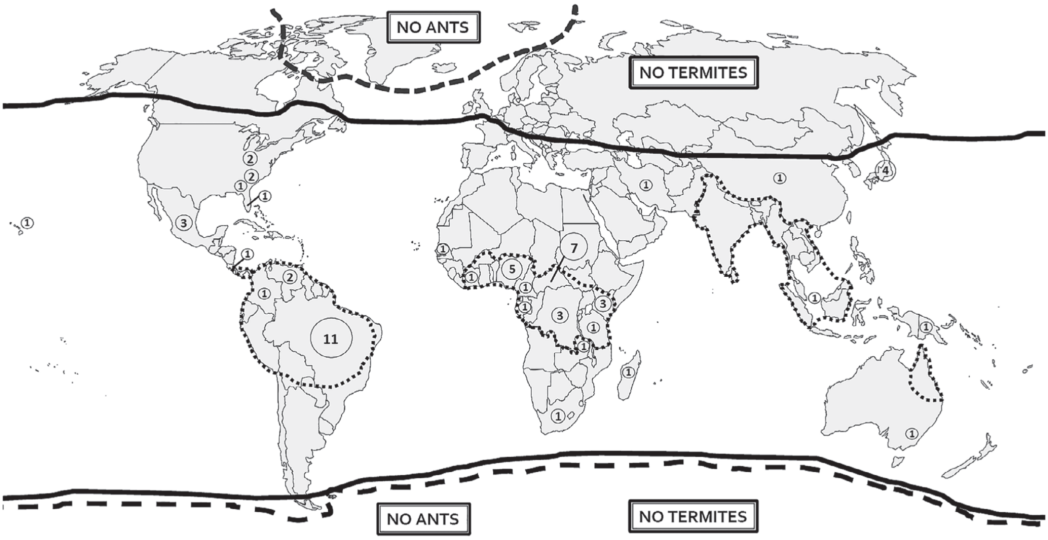

Fig. 2. Global geographical co-occurrence of ants and termites, joint diversity hotspots and number of studies describing ant and termite interactions. Dotted lines mark the areas where ant and termite biodiversity hotspots overlap [data on termite generic diversity from Eggleton, 2000; ant species diversity from Guénard, Weiser & Dunn, 2012]. Solid lines define the area where at least one termite species occurs. Dashed lines define the area where at least one ant species occurs. Numbers in circles denote number of studies describing ant and termite interactions (see Table S1) and are positioned approximately in the centre of country or state in which the study was conducted. Note that there are isolated islands with no termite or ant species that are not marked here. World map source: https://simplemaps.com/resources/svg-world.

much lower efficiency in an artificial laboratory environment, where test arenas usually do not mimic natural conditions. For example termites with wide mandibles cannot open their mandibles fully in confined spaces, while the strike attack of snapping termites is most effective in narrow tunnels (Deligne, Quennedey & Blum, 1981). Second, we can speculate that termites and their developmental stages are likely to represent suitable prey for a majority of ant species, even if they never meet in nature because of geographical barriers, physical barriers (termite mounds and sheetings), or microhabitat partitioning. As one example, in Bornean rainforest, wood/soil-feeding termites (e.g. *Dicuspiditermes nemorosus*) forage for substrates rich in organic matter underground, while canopy ants (e.g. *Polyrhachis ypsilon*) forage and nest in the forest canopy. These two species would probably never meet under natural conditions, and hence any predation observed in the laboratory would not be representative of any real-world interaction. It is even likely that termites would be predated in laboratory experiments by many ant species from geographical areas in which termites do not occur. Note that because of this limitation, we have not included in this review studies in which termites were used only as bait for ants, since such observations provide minimal information about real-world ant–termite predation.

4. Molecular gut content analyses

Termite-specific DNA primers can be used to amplify and detect termite genetic material in ant guts. Termite DNA sequences are then compared with online databases (e.g. GenBank) of known termite DNA to identify the termite genera or species involved (Fayle *et al.*, 2015). This technique returns only a binary outcome of ant predation on termites, i.e. whether the termite was or was not consumed. Hence, this method cannot describe behavioural patterns and cannot quantify the possible effect of ants on termite colonies. Furthermore, while a positive result indicates ant predation, a negative result might relate only to the failure of primers to amplify termite sequences, rapid breakdown of termite DNA in ant guts, or a lengthy period since predation (making episodic predation events hard to detect). The manner in which these factors vary among both ant and termite species is not known. However, this method can reveal, without the need for field observations, which species of ants feed on which species of termites, even when predation takes place cryptically, for example in strictly soil-dwelling ants. It can also shed light on the true nature of the interactions between cohabiting ants and termites (although note that contamination may be more challenging to address in this case). This method can be used for the screening of entire ant communities and hence to identify potentially important ant–termite predation that could then be studied in greater detail. Summarising information from studies using the methods described above, we will now speculate on how important termites might be as prey for ant populations, and also to what extent ant predation might control termite communities.

VI. The importance of termites as prey for ants

Termites represent a rich source of lipids, proteins, minerals, sugars and micronutrients (Wood & Sands, 1978; Sogbesan & Ugwumba, 2008). This is likely to vary among castes and developmental stages, because alates have comparatively higher lipid content than workers, which contain higher levels of indigestible inorganic ash, especially in soil-feeding species where the gut is usually filled with soil (Redford & Dorea, 1984). The importance of termites as a food source may rather be associated with their high density (in the nest) than with their individual nutritional value. Termites have relatively stable occurrence in space with high abundances across various habitats and the highest densities being in the tropics (Eggleton, Williams & Gaston, 1994). In addition, termite bodies, particularly those of workers, are not strongly chitinised, and so despite their defence mechanisms, they constitute a suitable, relatively low-cost food for a wide range of animals, including ants.

It is likely that termites represent an important food source for ants, although the proportion of overall ant diets that termites account for is poorly known, even in well-studied termite predators. However, we can speculate that this proportion is likely to vary in several ways. (i) There is likely to be large-scale geographical variation, because areas of high ant and termite genus richness overlap mainly in warmer environments (Figs 2 and 3). For example, there is a greater diversity of potential termite prey available in Africa than elsewhere (at the genus level), while there is a greater diversity of ant genera in SE Asia. Simplistically, we might expect this to lead to greater numbers of termite-specialist ant genera in Africa, where the number of termite genera per ant genus is greatest. Conversely, fewer termite-specialist ants are expected in SE Asia, where ant diversity is high and termite diversity is low relative to other tropical areas (Fig. 3). Although species richness distribution patterns are not currently available at global scales for either taxon, note that genus-level diversity correlates with species-level diversity in both ants (Andersen, 1995) and termites (Eggleton, Williams & Gaston, 1994), so the genus-level patterns could well hold for species richness. Such predictions do not account for variation in the density of ants and termites either in terms of individual insects or entire colonies, which may not have the same global distributions as that of diversity for the two groups, and will also drive proportion of termites in ant diets. (ii) Between habitats at a geographic location there is likely to be variation in both termite and ant density, and hence variation in the consumption of termites by ants. For example, logging primary tropical forest and conversion to oil palm plantations results in increased soil ant densities but decreased termite densities (Luke *et al.*, 2014). In this case we would expect reductions in termite-specialist ants with increasing anthropogenic habitat disturbance. (iii) In a similar manner, within a habitat there is also likely to be variation in the abundance of both termites and ants, for example in relation to soil conditions, abundance of dead wood, and in relation to vertical stratification within forested habitats. (iv) Finally, there is likely to be variation among species of ants even at the same location. For example, ants that feed mainly on carbohydrate resources (e.g. *Acropyga* spp.), symbiotic fungi (e.g. *Atta* spp.), plant-provided food bodies (e.g. *Pseudomyrmex* spp.), or have highly specialised diets (e.g. *Euprenolepis procera* specialise on macromycete fungi), are relatively unlikely to feed on termites. Generalist predators and scavengers (e.g. *Pheidole* spp., *Odontomachus* spp.), are more likely to feed opportunistically on termites when they are available, for example if nest structures are damaged. However these species probably lack adaptations for coordinated raids on termite nests. Finally, there are some species that are thought to be almost exclusively termitophagous (e.g. *Neoponera marginata*). This variation among ant species is supported by a study in which the presence of *Crematogaster irritabilis* caused a decrease of up to 50% in termite abundance in comparison with a *Camponotus* species that inhabited termite nests but did not show significant predation (Leponce, Roisin & Pasteels, 1999).

Opportunistic predation on termites is likely to occur in ant species that are generalised arthropod predators. Many ant species might prey on exposed termites given the opportunity, for example when they encounter termite individuals while foraging. Consequently, many ant species with various feeding habits are likely to prey at least sometimes on termites (Carroll & Janzen, 1973; Hölldobler & Wilson, 1990). The best known and widely reported ant groups that feed on termites are the generalists *Pheidole* spp. and *Camponotus* spp. (Hölldobler & Wilson, 1990).

In addition to opportunistic predators, there are also ants that specialise in termite predation (Table S1). These belong mainly to the subfamilies Ponerinae and Myrmicinae and the genus *Dorylus* (Culliney & Grace, 2000). There are known cases of regular raids on termite mounds. For example, the ant *Megaponera analis* (the Metabele ant) repeatedly raids fungus-growing termites *Odontotermes latericius* (Macrotermitinae) in sub-Saharan Africa and can eventually cause the death of the whole colony. These ants collectively use a pheromone attractant to locate where to dig into the nest (Sheppe, 1970; Longhurst & Howse, 1978); chemicals embedded in the termite tunnels and chamber walls are perceived as a kairomone by *M. analis.* These ants create regular foraging trails leading to the termitaria, which they explore and dig into in order to prey on termites at sites of termite feeding, e.g. inside fallen dead wood (Longhurst & Howse, 1978) using their sting and mandibles to kill and transport the seized termites (Yusuf, Crewe & Pirk, 2014). *M. analis* workers help nestmates wounded during the raid by carrying them back to the nest

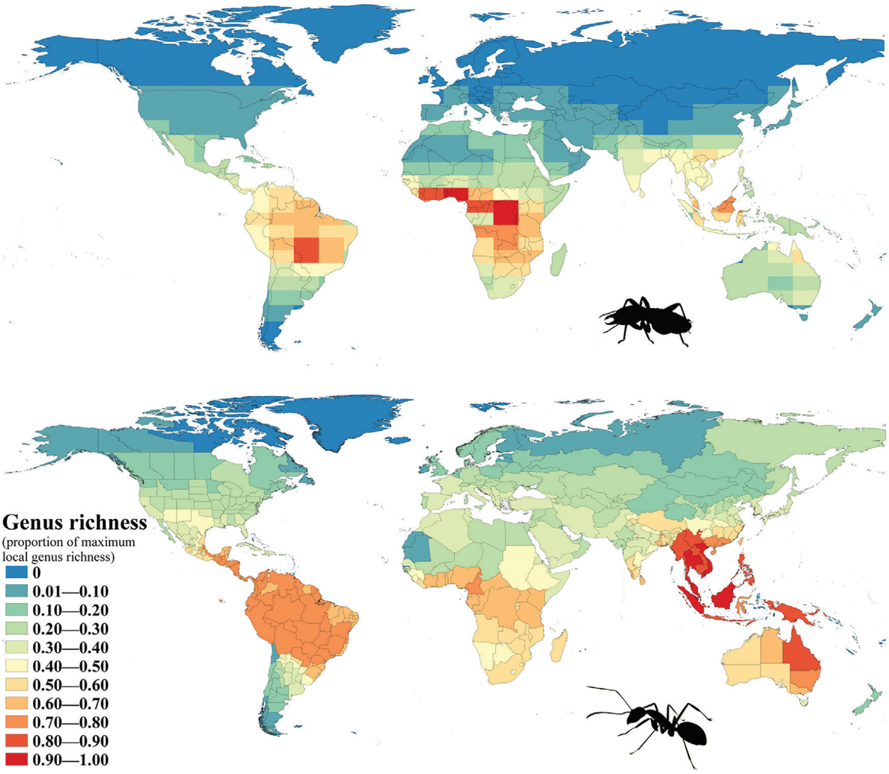

Fig. 3. Global genus richness patterns for termites (top) and ants (bottom). The colour fill is scaled relative to the maximum local richness for each of the groups (termites = 65, ants = 116). For termites, genus counts are taken from an updated version of the map in Eggleton, Williams & Gaston (1994), using grid cells of 10 degrees longitude and an area of approximately 611000 km^2 (hence latitudinal divisions are smaller closer to the equator). For ants, genus counts for political divisions are from the Global Ant Biodiversity Informatics (GABI) database (Guénard *et al.*, 2017), with the map provided courtesy of Benoit Guénard. Note the contrasting diversity patterns in the tropics, with ant diversity being greatest in SE Asia (where termite diversity is low relative to other tropical areas), and termite diversity being greatest in Africa (where ant diversity is low relative to other tropical areas). The Neotropics are of intermediate diversity for both groups.

and licking their wounds (allogrooming), improving their survival chances by up to 80% and thus enabling them to be involved in the next raid (Frank, Wehrhahn & Linsenmair, 2018). A subterranean *Dorylus* ant species is an effective predator of termites, performing regular raids on termite colonies in Africa (Bodot, 1961; Abe & Darlington, 1985). Similarly, *Odontoponera transversa* follows the pheromones produced by termites to track and hunt them (Wen *et al.*, 2017). A particular adaptation occurs in *Neoponera marginata*: worker ants sting termites during raids to paralyse them, and the immobilised termites are then stored in the ant nest as a living food reserve (Leal & Oliveira, 1995).

Feeding specialisation also involves higher tolerance of termite defence mechanisms. Small opportunistic predators of termites from the ant genera *Solenopsis*, *Pheidole*, *Wasmannia* and *Paratrechina* (which are dietary generalists) show higher mortality and debilitation following attacks from termite soldiers compared with species from the subfamily Ponerinae that are mainly predatory (Traniello, 1981) (note that *Paratrechina* were only identified to genus level in that study, and so these findings are unaffected by subsequent taxonomic splitting of the genus). The African ant *Centromyrmex bequaerti* nests directly in termite nests and regularly preys on their inhabitants. This species is able easily to overcome termite soldiers and performs a specialised, highly effective predator behaviour. It makes temporary stockpiles of killed termites before they are transported back to the ant nest, increasing its attack efficiency on the colony (Dejean & Fénéron, 1999). However, overall the absolute number of ant species specialising on termites is relatively small, and we speculate that much

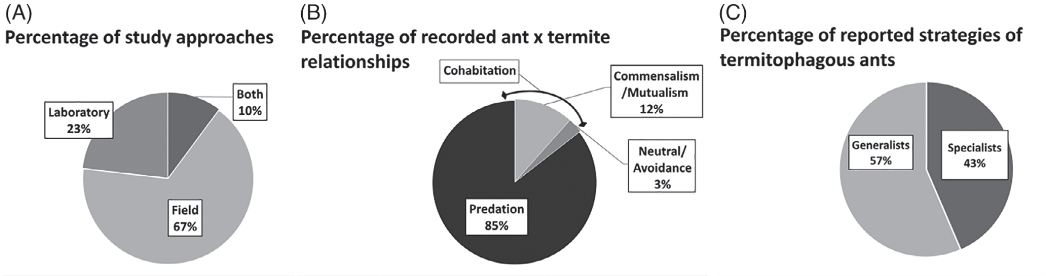

Fig. 4. A summary of published studies describing ant–termite interactions (see Table S1 for full list). (A) Different study approaches. The 'both' category involves studies that combined laboratory experiments with observations or experiments in the field. (B) Percentage of different kinds of interactions recorded between ants and termites. (C) Recorded degree of predatory specialisation in studies for which ants were observed directly predating termites. Generalist ants are defined as those preying on a wider spectrum of prey, including termites. Specialists are defined as those known to prey exclusively or almost exclusively on termites [data extracted from AntWiki, 2019 for each ant species; individual termite-preying specialists were confirmed in literature cited therein]. Note that the percentages in B and C may reflect a tendency for research to focus more on ant species that are termite specialists. Cases where the nature of interaction or ant species was unclear are omitted from the figures. The categories in B are necessarily simplified and do not reflect all kinds of interactions described in the main text as the categories in the pie chart are derived solely from Table S1.

predation of termites by ants is opportunistic, although this phenomenon has not been thoroughly investigated (Hasan, 2015; Fig. 4).

If termites are an important prey group for ants, then we would expect correlations at the community level in terms of numbers of species of the two groups. In support of this, Mertl *et al.* (2012) found that ant species richness correlated positively both with overall termite species richness and with species richness of soldierless termites in Amazonia. However, in a study from Gabon, termite species richness and abundance correlated negatively with the density of predatory ants, but not with non-predatory ones (Scholtz, 2010; Dambros *et al.*, 2016). Such correlations might not be driven by direct ant–termite interactions but rather by a third unknown driver that affects both groups, and hence we recommend caution when interpreting such results. The drivers of these patterns could be revealed by experimental manipulations, with correlational studies serving to generate hypotheses for such research.

VII. Ant predation as a top-down controller of termite communities

1. Ant predation in the context of other termite predators

In order to explore whether ants are a possible controller of termite populations, it is necessary to determine the relative proportion of termite predation that is due to ants as opposed to other animal groups. As with predation by ants, the most obvious predation on termites by other groups occurs during mating flights, when large numbers of winged individuals are susceptible to predation, mainly by birds. After landing on the ground or falling into water they are eaten by fish, frogs, lizards, mammals and a variety of insects (Deligne, Quennedey & Blum, 1981). Although predation on alates often involves large numbers of termite individuals, it affects only dispersal, not the viability of established colonies. This can be compared to seed predation, which does not affect the survival of the adult plant (in contrast to direct herbivory of the plant). The effects of such predation on persistence of termite populations remains unexplored, although with their high production of alates, it seems unlikely that this could be a limiting factor.

Apart from ants, vertebrates, and specifically mammals, represent probably the most important group of termite feeders (Deligne, Quennedey & Blum, 1981). Pangolins, echidnas, armadillos, sun bears, sloth bears and aardvarks all forage for termites on open ground, but also by digging into their nests to search for all developmental stages (Abensberg-Traun, 1991; McNab, 1992; Swart, Richardson & Ferguson, 1999; Taylor, Lindsey & Skinner, 2002; Te Wong, Servheen & Ambu, 2002). It should be noted that many of these animals also feed on ants in a similar manner, and so their presence is likely to have both negative impacts on termites (*via* direct predation) and positive impacts *via* release from ant predation pressure. Specialised mammals and ants are known use different attack strategies. Mammals break open the mounds in one place and therefore are vulnerable to termites recruiting to that entry point (Redford, 1984). By contrast, ants attack in numbers and each ant must be dealt with separately. This, together with the much higher density of ants than of termite-eating mammals potentially makes ants more of a threat to colony survival. Lizards are also efficient termite predators. Pianka (1986) states that termites constitute up to 90% of lizard diets in African and Australian arid zones. However lizards probably feed on termites rather opportunistically as they do not usually invade termite mounds (Costa *et al.*, 2008).

Predation on termites from other arthropods is taxonomically variable, although numerous insect species either opportunistically or specifically feed on termites. The most common arthropod predators of termites are groups that also act as predators of other insects. Termite predators are found among spiders (Araneae; especially from the families Theridiidae and Ammoxenidae), rove beatles (Staphylinidae), centipedes (Chilopoda), larvae of carabid beetles (Carabidae), mites (Acarina) and a range of other groups (Deligne, Quennedey & Blum, 1981). A highly specialised predatory behaviour is known from an African genus of soil-dwelling spiders (*Ammoxenus*). These spiders can recognise the surface vibrations caused by foraging *Hodotermes mossambicus* termites. The spider then emerges from the soil, bites the termite with its mandibles and drags it under the soil surface, either in order to suck its body fluids directly or to store it as a food reserve (Dippenaar-Schoeman & Harris, 2005). *Ammoxenus aphalodes* is known to be strictly monophagous – feeding only on *H. mossambicus* (Petráková *et al.*, 2015). Other apparent termite specialists are assassin bugs (Gordon & Weirauch, 2016), especially *Tegea atropicta* (Reduviidae). This bug preys on *Nasutitermes exitiosus* termites by piercing the protective foraging carton barriers using its rostrum. When termites attempt to bite the rostrum, the bug pierces the termite body and sucks up its body fluids (Casimir, 1960). Another assassin bug species (*Salyavata variegata*) places carcases of dead termites onto its body as a bait to attract other termites (McMahan, 1983). This is the only known example of a predator of termites being considered as a potential biocontrol agent to regulate termite populations in plantations (Ambrose, 2003; Ambrose, Raja & Rajan, 2008). Apart from these specialists, it is likely that most predatory insects of appropriate size will prey on termites given the opportunity. For a detailed summary of arthropod termite predators see Deligne, Quennedey & Blum (1981).

2. Termite defence mechanisms as evidence for widespread ant predation pressure

Termites have developed various strategies to repel predators and competitors and to prevent access to the termitarium. Although termites do defend their nests against other termite species, their aggressive response depends on many factors, such as intruder species or even seasonality (Shelton & Grace, 1996). The presence of widespread ant-specific defence mechanisms would provide indirect evidence for a significant impact of ant predation, since it would imply that ant predation has been a selective pressure on termites in the past.

The first line of defence is the physical structure of the termite nest itself. The outer wall of the mound and the maze of inner tunnels and chambers serve as a physical barrier to keep termites separate from potential predators (Noirot & Darlington, 2000). The main strategy is to prevent or minimise colony damage, and particularly to protect the queen. Developing ideas from Eggleton (2011) we recognise three types of colony defence strategies: counterattack, strong point and maze.

The 'counterattack' strategy involves rapid co-ordination of movement and adaptations that appear to function to fight individual ants (Lubin & Montgomery, 1981). These include the squirting of toxic chemicals, the daubing of toxins directly onto intruders, and mandibles designed to slash or pierce predators. Soldiers, presoldiers and some workers develop specific exocrine glands which produce defensive substances such as sticky secretions, irritants, anti-healing substances, repellents, or toxins (Sobotnik, Jirosova & Hanus, 2010). Counterattacking is more efficient when greater numbers of defenders are involved. They can be recruited through vibration of the termite body in order to spread an alarm signal to other colony members (Deligne, Quennedey & Blum, 1981; Prestwich, 1984; Sobotnik *et al.*, 2010c), or by the use of alarm pheromones. In some cases, alarm pheromones have a dual function: when the colony is attacked, the alarm pheromones attract soldiers to the site of the strike, but also repel the more vulnerable workers (Sobotnik, Jirosova & Hanus, 2010). However, workers also sometimes participate in colony defence. They will bite invading ants readily, although this does not appear to be a very effective strategy (Sheppe, 1970). Nevertheless, biting workers can hold an ant's legs, slowing it down so that other termite workers have time to plug passageways leading further into the nest. Species exhibiting this tactic tend to have low soldier to worker ratios, and their low densities of soldiers may necessitate worker involvment in colony defence (Eisner, Kriston & Aneshansley, 1976; Ishikawa & Miura, 2012).

The 'strong-point' approach involves individual termites that stand their ground creating a barrier in an easily defensible position. This is commonly achieved by having a large head that can block a tunnel ('phragmosis') and/or large crushing mandibles. One example of this is the drywood termite (*Cryptotermes*) that has a plug-shaped, strongly chitinised and wrinkled head that fills the width of the galleries. Other examples include species with symmetrical and asymmetrical snapping mandibles that require anchoring to the mound wall to be effective (Scholtz, Macleod & Eggleton, 2008). These adaptations have been shown to be extremely effective against ant invaders (Seid, Scheffrahn & Niven, 2008). Older soldiers tend to engage in such risky tasks more often than young soldiers, which are involved more in defence inside the nest (Yanagihara *et al.*, 2018). In some termite species (e.g. *Neocapritermes taracua*) the workers have abdomens that can rupture, smearing ants with a sticky, toxic substance from specialised glands in a process called autothysic ('self-sacrificial') rupturing. Rupturing can also cause the internal organs to burst out, in this case without toxic secretions, in a process called dehiscence that mostly occurs in soldierless termite workers (Sands, 1982), although it has been found in soldiers of the genera *Glossotermes*, *Serritermes* and *Apilitermes* (Deligne & DeConinck, 2006; Sobotnik *et al.*, 2010a). This tactic differs from others described here, as it is a single-use behaviour, because the worker invariably dies (Sobotnik *et al.*, 2012; Bourguignon *et al.*, 2016).

As an extension of the strong-point strategy, 'covering' refers to the defence of foraging parties outside the nest by using a substrate to build a short-lived, protective cover or 'sheeting' (Jouquet, Lepage & Velde, 2002; Harit *et al.*, 2017). Termites mix their saliva, faeces and soil particles to build such sheeting over their exit holes, paths and food sources (Holt & Lepage, 2000; Harit *et al.*, 2017). Sheetings protect termites from predation and desiccation and their food sources from competitors. Typical items covered by sheeting are dead leaves, dead twigs, wood logs and standing dead trees or dung. Foraging parties are protected by tunnel-like vertical covers on the tree trunks or on vegetation (Jouquet *et al.*, 2015). Termites also stabilise standing wood by filling up spaces with clay-rich materials to prevent collapse, allowing the termites to feed on it for longer (Oberst, Lai & Evans, 2016).

The 'maze' [erroneously called a 'labyrinth' in Eggleton, 2011, as labyrinths strictly speaking have a single route, while mazes are branching and have dead ends] strategy has not been studied in detail. It is found particularly in the African wood-feeding genus *Cephalotermes* that builds large carton nests/mounds in west and central African rain forest. In this genus the density of individuals in the nest is extremely low. The nest is full of anastomosing tunnels, and most of it is empty. It is possible that this is a defence against ants; the extended searching time that an ant would need to find a prey item may be too great to make it energetically feasible to attack the nest (Eggleton, 2011). Experimental evidence regarding this strategy still needs to be obtained.

The counterattack and strong-point tactics are most relevant to termite soldier castes, whose primary job is to defend the colony, and to combat predators at close quarters. Production of the soldier caste is costly (Oster & Wilson, 1978), but it represents a highly effective defensive weapon for the colony. Usually soldiers comprise only about 6% of the total termite individuals in a colony (average calculated for 102 termite species; minimum 0%, maximum 34%) ranging from 0.4% in Apicotermitinae to 16% in Nasutitermitinae across species within a subfamily (data from Haverty, 1977). Because of the extreme body modifications of termite soldiers, they are often unable to feed themselves and need to be fed by workers (Su & La Fage, 1988). Deligne, Quennedey & Blum (1981), Prestwich (1984), and Scholtz, Macleod & Eggleton (2008) provide descriptions of the range of morphology in defensive structures on the heads of termite soldiers. Table 1 provides a summary of morphological and behavioural defensive tactics used by termites.

Most termite species have a single soldier morph. However, some species have multiple soldier morphs. The most extreme example is the desert termite *Psammotermes hybostoma* that probably has at least 11 soldier morphs (Bourguignon *et al.*, 2012), although only two of these are common. Across other genera with a polymorphic soldier caste the usual number of morphs is two, but some (e.g. *Velocitermes* and *Acanthotermes*) have three. These different soldier morphs probably exist to counter different predator types. The clearest example of this is in *Macrotermes* spp., where the major morph is large and able to break human skin with its mandibles. In this case, it is plausible that major soldiers are specialised to counterattack large specialist mammals (or the largest ants) and minor soldiers to fight smaller ants.

Table 1. Strategies used by termites to defend termitaria or foraging parties

Overall strategy	Soldier tactics	Termitarium type
Counter attack	Slashing/piercing mandibles Glue squirting Daubing brush Faecal daubing Biting (also in workers)	High surface:area
Strong point	Phragmotic heads Crushing mandibles Asymmetrical snapping Symmetrical snapping Autothysic rupturing Dehiscence	Low surface:area
Maze	Avoidance	Multicursal tunnels

3. Impacts of ant predation on termite communities

Ant predation and some specialised mammalian predators (see Section VII.1) can have severe outcomes for termite populations. Nevertheless, there are insufficient data to compare the impact of ant predation relative to that of other termite predators. The evidence for ants being able to kill entire termite colonies is scarce (see Sheppe, 1970; Longhurst & Howse, 1978). However, the loss of a large number of individuals could have serious outcomes for colony fitness. It has been estimated that *Neoponera commutata*, preying on termite foraging parties, can consume up to three times the standing population of workers and soldiers of the termite *Syntermes* spp. in Amazonian rainforest per year (Mill, 1984a), meaning that each colony of this termite species needs to produce three colonies' worth of individuals each year in order to compensate for ant predation. In a study from Nigeria, the ant *Tetramorium uelense* consumed approximately 70% of the annual production of individuals of the termite *Microtermes* spp. per year (Longhurst, Johnson & Wood, 1979). Most studies state only the numbers of termites killed by ants, not the colony size, so the impact on whole termite colonies and subsequently on termite populations cannot be assessed easily. However, such studies are a valuable source of information as they describe the natural behaviour of ants and the numbers may indicate the real predation pressure experienced by some termite species. For example, 1600 individuals of *Neocapritermes opacus* were captured per raid of *Neoponera marginata* in secondary forest in Brazil (Leal & Oliveira, 1995), and 100,000 individuals of *Macrotermes subhyalinus* termites were captured by the ant *Dorylus nigricans rubellus* in a single raid in Nigeria (Schöning & Moffett, 2007). Futhermore, winged termite individuals are preyed on by various ants (e.g. Chouvenc *et al.*, 2015) when they are attempting to found new termite colonies. While such predation pressure would not directly affect existing termite colonies, it could impose patchiness on new colony foundation.

Despite a lack of suitable data, it is likely that much ant predation on termites is likely to be opportunistic, and that this opportunistic predation, which occurs mostly outside colonies, is unlikely to have major effects on the survival of termite populations. Perhaps this predation should be considered to be analogous to herbivory on trees in that it will limit the size of the termite colony without killing it. The smaller number of ant species that are specialised termite predators may be capable of killing entire colonies, and hence are likely to exert a top-down control on termite populations. In Section VIII we speculate on how these two effects of ant predation on termites (colony control and colony predation), could have ecosystem-wide impacts.

VIII. The broader role of ant–termite interactions in ecosystems

Inferring the importance of ant–termite interactions to ecosystems is challenging without experimental manipulations. One demonstration consists of a ‘natural experiment’ in which natural communities and ecosystem functions were disrupted by the arrival of a non-native species. The termite-specialist ant *Brachyponera chinensis* was introduced into southeast USA sometime before 1932 (Smith, 1934; Guénard & Dunn, 2010). The species disrupted native ant communities and affected ant-mediated seed dispersal (Warren *et al.*, 2015) and mutualistic relationships with hemipteran insects. Furthermore, *B. chinensis* also proved to be an important predator of native *Reticulitermes virginicus* termites. It has been suggested that termite availability could act as a ‘springboard’ for the invasive success of this ant (Bednar & Silverman, 2011) with unknown effects on decomposition rates and other services that termites provide. On the other hand, in cases where termites are perceived as a serious pest either on crops or in wooden buildings, ant predation, even that from invasive ants, could be beneficial as a form of biocontrol. Termite-mediated increases in ant populations may have far-reaching effects, and not just for invasive ant species. We can speculate that if termites are an important and possibly an essential food source for predatory ants, these termite-mediated increases in ant populations could result in an increased predation pressure on other invertebrates (apparent competition between termites and other invertebrates). Hence in theory, the availability of termites could mediate many of the ecosystem functions that ants are known to perform, such as mutualistic interactions with sap-sucking insects or the control of invertebrate herbivores (Hölldobler & Wilson, 1990; Frouz *et al.*, 2008). This could be particularly important in non-specialist ants that predate termites and perform other ecosystem functions.

In addition to impacts on the biotic environment, ant–termite interactions can alter the abiotic environment. Both specialised predatory ants and ants that are opportunistic termite predators could potentially disrupt the ecosystem functions performed by termites. Lower termite abundance could consequently reduce dead plant material decomposition and thus nutrient cycling (Korb & Linsenmair, 2002). For example, in the presence of ants from the genus *Azteca*, the termite *Nasutitermes braziliensis* was not able to nest and exploit the tree occupied by these ants, probably due to predation (Lima Pequeno & Pantoja, 2012). This was supported by exclusion experiments: termite activity and abundance were greater on cellulose baits when ants were poisoned (Parr *et al.*, 2016; Ashton *et al.*, 2019). However, it is not clear if other decomposer organisms would replace termites in performing this function over time. It is likely that ant predation will be an important factor, since termites are ecosystem engineers that affect not only decomposition rates, but also nutrient cycling, soil quality, plant communities and the whole appearance of certain habitats (Holt & Lepage, 2000; Jouquet *et al.*, 2011; Ashton *et al.*, 2019).

IX. Synthesis and future research directions

1. Synthesis of current state of knowledge

It is clear that both ants and termites with their high abundance and biomass in the majority of terrestrial habitats, are an important component of terrestrial ecosystems. Furthermore, the diversity and abundance of ants and termites largely overlap geographically (Fig. 2) and the two groups also nest and forage in the same microhabitats (soil, litter, dead wood or in trees) where they must meet. To date, studies have found that their interactions (Fig. 4) include mutualistic/commensal, neutral/avoidant (when termites are physically separated from ants in space or have effective defences), competition for nesting or foraging space, and predation (when ants hunt for termites opportunistically or specifically, with some species being almost exclusively termitophagous). Ant–termite predation depends on the identity of interacting species, season, humidity, habitat degradation and on stochastic events in the environment (e.g. nest/mound disturbance by other animals). Because ant predation on termites is a widespread, yet understudied, phenomenon with wide-ranging consequences for ecosystem functioning, there are a range of potentially fruitful future research directions.

2. Future research directions

Because predation is almost certainly the ant–termite interaction with the widest ecological implications, future studies should assess the impact of ant predation on the fitness and survival of termite colonies and populations. Direct, long-term field observations of the abundance (number of colonies) of key species of both ants and termites would allow predator–prey models of pairwise interactions to be constructed and tested. Further specifically targeted field experiments, such as artificial suppression of ants or termites (e.g. Ashton *et al.*, 2019), would allow causal inferences about the impacts of these two groups on each other. Finally, identification of termite DNA in ant guts and quantification of its relative frequency of occurrence compared with DNA from other prey sources will allow the specificity of ant predators to be explored. Next-generation sequencing, in which large numbers of prey sequences from a single ant gut can be recovered, offers the possibility to place predation of termites within the broader context of ant diets. Despite their limitations, laboratory feeding-preference tests or arena-based predation studies can be a valuable source of information about behavioural adaptations and to suggest suitable field experiments.

To understand the importance of ant–termite interactions at a global scale, better estimates of ant and termite standing biomass are needed, along with improved knowledge about differences in ant–termite predation in relation to global environmental gradients across different biomes. This could then be compared with the performance of other predators in the same biome. In this way, predator redundancy, ant predatory pressure and the significance of termites as a food source could be estimated for different biomes. Such world-scale estimations of predation mass are rare, but have been made for spiders, with an estimated 400–800 million tons of prey consumed annually at a global scale (Nyffeler & Birkhofer, 2017). Such information can then be incorporated into global ecosystem models (e.g. Harfoot *et al.*, 2014).

Understanding how ants control termite communities may contibute to an open question in soil ecology: why is there abundant soil organic matter (SOM) in the soil? Are there enough decomposers to break it down, and if so, why is it not broken down as soon as it is created? This is known as the ‘brown ground’ question (Allison, 2006) and is conceptually similar to attempts to explain the wide availability of plant biomass in the face of abundant animal and microbial consumers (the ‘green world’ question; Hairston, Smith & Slobodkin, 1960). In the latter case, the proposed answer involves control of herbivore populations through predators or plant defences. Answering the ‘brown ground’ question in a parallel manner, it is likely that the predators and pathogens of decomposers such as bacteria, fungi and arthropods restrict their ability to break down SOM. Because termites are exceptionally effective in the decomposition of SOM in tropical and subtropical habitats and ant diversity and biomass is high in those regions as well, it is possible that ants are a significant restrictor of termite-induced SOM decomposition (DeSouza, Araújo & Reis-Jr, 2009). If so, ant–termite predation will have direct broad-scale impacts on nutrient cycling and availability, and on the availability of habitats/niches such as dead wood and litter (Fig. 5). Moreover, if termites are important emitters of animal-produced greenhouse gases, ant predation could

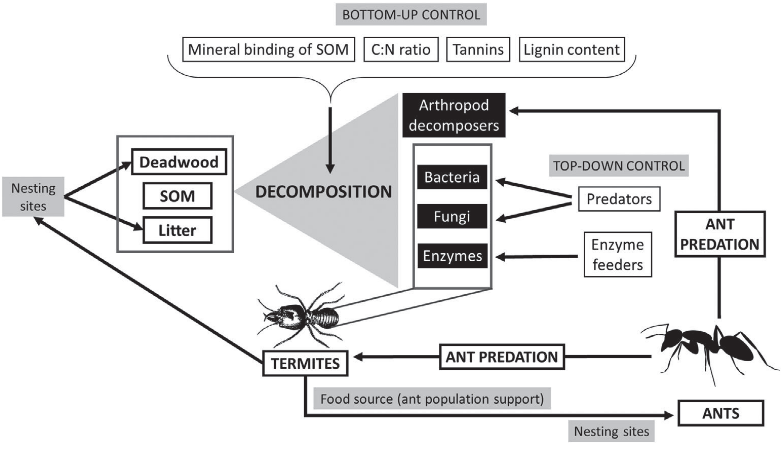

Fig. 5. Schematic outlining the role of ant predation of termites on the processes involved in soil organic matter (SOM) decomposition based on ideas from Allison (2006) and DeSouza, Araújo & Reis-Jr (2009). Ants are likely to be important predators of termites. This means that ants are likely to affect termite populations by predation but also that termite presence in the environment can support predatory ant populations. Termites host a variety of symbiotic organisms in their digestive system along with their own enzymes. This ‘gut bioreactor’ can decompose a significant portion of dead organic matter in the environment. Where predatory ants nest in litter or wood, termites cannot use these sources either as nesting sites or as food sources. Ants can nest in termitaria, and termites can feed on potential nesting sites for other termites. Hence, ants have the potential to restrict the decomposition of plant organic matter *via* predation on termites, and also *via* predation of other arthropod decomposers. In a similar manner, other predators of arthropod decomposers, enzyme feeders, and predators of bacteria and fungi might control decomposition rates. In addition to this, decomposition is also limited by a range of bottom-up factors.

regulate these emissions and thus might play a significant role in the control of global gas fluxes. Addressing these questions could be done in parallel with experiments exploring impacts of ants on termite populations, with rates of SOM breakdown and greenhouse gas emissions being measured as part of such projects.

Global databases of ant distributions have expanded rapidly [e.g. antweb.org (AntWeb, 2019); antmaps.org (Economo & Guénard, 2016); antwiki.org (AntWiki, 2019)] with steadily improving taxonomic resolution. Once the natural history of these ant species in terms of termite predation is fully documented, and similar databases become available for termites, we will achieve a better understanding of the global importance of this interaction. This could also enable us to predict how food webs will be affected by global change. With increasing temperatures due to global warming, termites are likely to shift their habitat ranges towards temperate regions, because temperature is an important limiting factor for termites (Dibog, Eggleton & Forzi, 1998; Joseph *et al.*, 2018; Ashton *et al.*, 2019). It would be useful to be able to predict the strength of predation pressure from ants that termites will face in their newly expanding ranges. These predictions can be made from the traits and phylogeny of ants and termites [see Pearse *et al.*, 2013 for a discussion of similar predictions for plant–herbivore interactions]. This would be valuable information for predicting the future spread of termites and for understanding the potential biological control provided by native ant communities (Kenne *et al.*, 2000).

Higher resolution phylogenies for both ants and termites are also becoming available (Ward, 2014; Bourguignon *et al.*, 2015), which should allow a better understanding of the evolution of interactions between these two groups. One approach could be to plot termite defensive traits onto dated termite phylogenies, and ant predation strategies and degree of specialisation onto dated ant phylogenies. This could reveal the timing of particular events in the 'arms race' between ants and termites and the degree to which termite defensive traits are a response to specialised or generalised ant predation, as opposed to competition with other termites or defence from non-ant predators. This will also allow testing for correlations between ant and termite diversity to investigate potentially causal relationships, with matching phylogenetic patterns for specialised ants and their termite prey supporting this hypothesis.

Anthropogenically modified habitats are potentially useful systems for studying ant–termite interactions because termite abundances are predicted to decline more rapidly in disturbed habitats than those of ants (Luke *et al.*, 2014). Anthropogenic disturbance gradients provide a 'natural experiment' that may allow us to study changes in ant and termite populations, changes in ways they interact, and eventually to link those changes with termite-driven ecosystem processes. Habitat change is a major ongoing driver of biodiversity loss, breaking down ecosystem stability and weakening ecosystem functions. Experimental ant and termite exclusions, coupled with molecular ant gut content analysis would allow us to explore shifts in this interaction in relation to anthropogenic habitat modification.

X. Conclusions

(1) Ant and termite world biomasses are high, with their maxima found in the tropics.

(2) Predation is the best-studied interaction, with ants likely to be important regulators of termite abundance.

(3) Ant predation on termites has apparently complex, but mostly unexplored effects for ecosystem processes.

(4) New techniques such as DNA barcoding of gut contents, large-scale experiments, and use of global ant/termite species distribution databases will allow further exploration of this interaction and its effects on ecosystems.

(5) We need to quantify the effects of ants on termite populations in different habitats and evaluate the consequences for ecosystem processes.

XI. Acknowledgements

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XII. REFERENCES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Published records of ant interactions with termites.

Fig. S1. Number of studies specifically studying or mentioning ant–termite interactions in relation to year of publication.

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Table S1. Published records of ant interactions with termites. Where studies involve laboratory experiments, the location and habitat are those from which field collections were made. Note that taxonomy follows that given in the articles. Some names may have subsequently changed. Country names have been updated where necessary to reflect current political boundaries. The studies were found using the *Web of Knowledge* website (https://www.webofknowledge.com) and *Google Scholar* (https://scholar.google.com) search engine with key words: "ant*s" AND "termite*s" with or without the words "interaction" and "predation" either in the title or in the abstract. *Web of Knowledge* records span the period 1945–2019 and Google Scholar 1800–2019. We also included references cited by the articles found using these search methods, but that did not appear in the original list of articles resulting from those searches (1800–2019). Studies where termites were used only as a helpless bait, typically only using workers or immobilised workers (e.g. Lange *et al.*, 2008), and/or where the aim of the study was not to explore ant–termite interactions, were not included in the table. Similarly studies were not included when the conditions of experiments were judged to be so artificial that they could not resemble any natural situation (e.g. Ishikawa & Miura, 2012). Studies describing only correlations between ant and termite communities (e.g. Mertl *et al.*, 2012), without any description of direct interactions, were also omitted, as well as field observations of vague nature with low informative value.

Ant species	**Termite species**	**Method**	**Location and habitat**	**Findings**	**Source**
Labidus sp.	*Cornitermes cumulans*	Direct observation of broken mound	Brazil, cerrado	Single anecdotal observation	Redford (1984)
No direct predation observations	No direct predation observations	Time to discovery of cellulose baits	Brazil, grassland	Baits took longer to be found by termites when ants were present	DeSouza *et al.* (2009)
Aphaenogaster rudis	*Reticulitermes flavipes*	Laboratory feeding experiments	N. America, oak-beech-hickory forest	Nesting in wood protects from ant predation	Buczkowski & Bennett (2008)
Crematogaster rochai	*Nasutitermes ephratae*, *Microcerotermes* cf. *indistinctus*	Laboratory predation experiments	Pentecoste, Brazil, caatinga	*Microcerotermes* much more vulnerable to predation	Quinet *et al.* (2005)
Dorylus nigricans rubellus	*Macrotermes subhyalinus*	Direct observation	Nigeria, savannah	Several 100,000 termites removed in a single raid	Schöning & Moffett (2007)
Paltothyreus tarsatus	*Cubitermes*, *Macrotermes*, *Nasutitermes*, *Trinervitermes*	Direct observation, search of nest refuse pile	Democratic Republic of Congo and Cameroon, forest and savannah	Always >50% prey items were termites in wild	Déjean *et al.* (1993)
Eurhopalothrix heliscata	*Bulbitermes* (2-3 species), *Havilanditermes*, *Odontotermes*, *Macrotermes*	Direct observation, search of nest refuse pile	Singapore, Malaysia, forest	This ant species is a generalist termite feeder	Wilson & Brown (1984)
Ectatomma tuberculatum, *E. ruidum*, *Odontomachus bauri*, *O. chelifer*, *Neoponera obscuricornis*, *N. apicalis*, *N. laevigata*, *Paltothyreus tarsatus*, *Rhytidoponera metallica*	*Nasutitermes costalis*	Laboratory predation experiments	Not reported	Only *Odontomachus* and *Paltothyreus* successfully predated exposed termites	Traniello (1981)
Crematogaster, *Camponotus*, *Wasmannia*, *Azteca*, *Pachycondyla* (s.l.), *Odontomachus*	*Nasutitermes*	Field observations	Not reported	Termites observed to be attacked by these ant species when covered trails exposed	Traniello (1981)
Tetramorium uelense	*Microtermes* spp., *Ancistrotermes cavithorax*, *Microcerotermes* spp.	Field observations	Nigeria, savannah	Mostly *Microtermes* spp. predated, with 74% of standing population removed annually	Longhurst *et al.* (1979)
Metapone madagascarica,	*Cryptotermes kirbyi*,	Laboratory	Madagascar	These ants are	Hölldobler *et*

Metapone sp.	*Schedorhinotermes lamanianus*	predation experiments		specialists on *C. kirbyi*, paralysing individuals in order to store them	*al.* (2002)
Myrmicaria opaciventris	*Microterotermes fuscotibialis*, *Macrotermes bellicosus*	Field predation experiments	Cameroon	Spatulate sting used to apply venom topically, both termite species were predated	Kenne *et al.* (2000)
Odontomachus bauri	*Nasutitermes*, *Amitermes*	Field observations	Panama, rain forest	32% of items brought to nest were termites	Ehmer & Holldobler (1995)
Odontomachus opaciventris	*Nasutitermes* sp.	Field predation experiments	Mexico	*O. opaciventris* will feed on a range of prey taxa. Effectively immobilises termite soldiers using a "mandible strike", but does not sting them	De la Mora *et al.* (2008)
Brachyponera chinensis	*Reticulitermes speratus*	Laboratory predation experiments	Japan, pine woodland	Homosexual tandem running by reproductive termites reduces predation risk through a dilution effect	Matsuura *et al.* (2002)
Neoponera marginata	*Neocapritermes opacus*	Field observations	Brazil, semi-deciduous forest	Raids only occurred on this termite species (*N* = 202), up to 1600 individuals captured per raid	Leal & Oliveira (1995)
Paltothyreus tarsata	*Odontotermes nilensis*	Laboratory predation experiments	Senegal	Termites are stung and then transferred from worker to worker	López *et al.* (2000)
Pheidole megacephala, *Anochetus emarginatus*, *Pachycondyla harpax*, *Pseudoponera stigma*, *Neoponera villosa*, *Ectatomma ruidum*, *Ectatomma tuberculatum*, *Eciton burchelli*, *Eciton hamatum*, *Labidus praedator*, *Solenopsis geminata*, *Dolichoderus bispinosus*, *Dorymyrmex pyramicus*, *Camponotus atriceps*	*Heterotermes* spp., *Microtermes* spp., *Nasutitermes mexicanus*	Field observations and field predation experiments	Mexico, mangrove	Density of *N. mexicanus* colonies was lower in the presence of invasive *P. megacephala*. Native ants were worse at predating termites than *P. megacephala*	Dejean *et al.* (2007)
Megaponera analis	*Macrotermes bellicosus*, *Odontotermes* spp., *Ancistrotermes cavithorax*, *Macrotermes subhyalinus*, *Microtermes* spp.	Field observations	Nigeria, savannah woodland	Feeds exclusively on Macrotermitinae. Mainly *Macrotermes bellicosus*, with smaller numbers of *Odontotermes* spp.	Longhurst & Howse (1978)
Megaponera analis	*Macrotermes bellicosus*, *Reticulitermes* spp.	Field observations and laboratory predation experiments	Nigeria, primary savannah woodland	*M. analis* workers are recruited using pheromones by scouts, and actively dig into termite nest chambers during raids	Longhurst & Howse (1978)
Pheidole megacephala	*Schedorhinotermes* sp., *Nasutitermes* sp., *Cubitermes fungifaber*, *Macrotermes bellicosus*	Field experiments	Cameroon, university campus	Ants are able to overcome soldiers many times their sizes (suggested use of offensive chemical compounds). Do	Dejean *et al.* (2007)

				not specialise on any one termite species	
Megaponera analis	*Macrotermes bellicosus*, *Coptotermes* sp., *Microtermes* sp., *Odontotermes pamper*, *Ancistrotermes cavithorax*	Field and laboratory experiments	Nigeria, primary savannah woodland	Ant scouts respond to kairomone in soil sheeting from *Macrotermes* and *Odontotermes*, by recruiting, but not to that from other species	Longhurst & Howse (1978)
Crematogaster sp. prox. *abstinens*, *C. distans*, *C. brevispinosa rochai*	*Nasutitermes ephratae*	Laboratory venom toxicity bioassays	Brazil, sandy/littoral areas, caatinga	Venom of all species was highly effective: mortality after 24 hours varied among species (48–96%)	Heredia *et al.* (2005)
Azteca sp., *Pheidole* sp., *Dolichoderus bispinosa*, *Camponotus abdominalis*	*Nasutitermes corniger*	Laboratory observations and experiments	Venezuela, savannah and secondary forest	Termite species able to defend nest from ants using cephalic chemical defence secretions. Ants co-habiting with termites are not aggressive. Termites may feed on dead ants and ant middens	Jaffe *et al.* (1995)
Centromyrmex sellaris, *Megaponera analis*	Not specified	Field observations	Ivory Coast	*C. sellaris* hunts under the soil, *M. analis* above the soil	Lévieux (1977)
Odontomachus assiniensis	Not specified	Field observations	"West Africa"	Termites captured using sting, while smaller insects using mandible strike	Brown (1976)
Odontomachus affinis	Not specified	Field experiments	South-eastern Brazil	*O. affinis* would not feed on termites. The author speculated that protective allomones repel the ants	Brown (1976)
Centromyrmex bequaerti	Termitinae and Macrotermitinae. Found in nests of *Amitermes*, *Coactotermes*, *Cubitermes*, *Furculitermes*, *Odontotermes*, *Trinervitermes* and *Tuberculitermes*	Museum collections	Cameroon, Gabon, Central African Republic, Democratic Republic of Congo, Angola, Malawai, Zambia	Species is an obligate predator of termites. Assumed to predate species with which it co-habits	Bolton & Fisher (2008)
Centromyrmex angolensis	Found in termitara of *Apilitermes* and *Protermes*	Museum collections	Liberia, Ivory Coast, Ghana, Cameroon, Gabon, Central African Republic, Democratic Republic of Congo, Angola	Probable range of prey genera is much larger. Assumed to predate species with which it co-habits	Bolton & Fisher (2008)
Centromyrmex sellaris	Found in termitaria of *Odontotermes*	Museum collections	Guinea, Ivory Coast, Ghana, Nigeria, Cameroon, Gabon, Democratic Republic of Congo, Uganda, Kenya, Mozambique, Zambia,	Probable range of prey genera is much larger. Assumed to predate species with which it co-habits	Bolton & Fisher (2008)

			Zimbabwe		
Oecophylla longinoda	Not specified	Observations	Democratic Republic of Congo, Cameroon	Predation on swarming termites, presumably alates	Dejean (1991)
Centromyrmex bequaerti	*Cubitermes subarquatus*, *Ophiotermes*, *Microtermes*, *Protermes*, *Cubiterms fungifaber*, *Nasutitermes*, *Odontotermes* sp., *Macrotermes* sp.	Observations of semi-consumed termites within ant nests	Cameroon	Shelters directly in the termitarium cavities. Predates guest termite species, and main residents	Dejean & Fénéron (1996)
Platythyrea conradti	*Macrotermes bellicosus*	Laboratory predation experiments	Cameroon	Ants probably use volatile secretions from mandibular glands to incapacitate termites remotely	Dejean (2011)
Dorylus nigricans molestus	*Odontotermes montanus*	Field observations	Kenya	Single observation of ants retrieving termite workers	Schöning *et al*. (2008)
Brachyponera chinensis	*Reticulitermes virginicus*	Laboratory feeding experiments	USA	*B. chinensis* readily feeds on *R. virginicus* workers, detecting them by their odours. Speculated that this ability to feed on termites has contributed to the invasion success of this species	Bednar & Silverman (2011)
Nomamyrmex esenbeckii	*Nasutitermes*	Field observations	Brazilian Amazon	*N. esenbeckii* is an army ant. It also feeds on other ants	Souza & Moura (2008)
"Ants" (*Crematogaster quadriformis* for laboratory experiments)	*Coartitermes fulviceps*	Field and laboratory experiments	S. America	Ants preferentially attack worker termites, rather than soldiers. Soldiers use a "frontal secretion" to defend against ant attack	Brandao *et al*. (2008)
Pheidole megacephala	*Coptotermes formosanus*	Laboratory and field experiments	Florida/USA	Termites can effectively defend themselves in the nest. Both species compete for nesting sites. Ants prey heavily on alates during swarming events	Chouvenc *et al.* (2015)
Aphaenogaster rudis, *Brachyponera chinensis*	*Reticulitermes virginicus*	Laboratory experiments	Raleigh, NC/ USA	*B. chinensis* displace *A. rudis* by killing the native ant and also compete for termites as prey. *B. chinensis* is effective predator of *R. virginicus*, intruding also into the termite nests	Bednar *et al.* (2013)
Pogonomyrmex naegelii	Not specified	Field observations	South-east Brazil	Of arthropod prey, ants and termites were most abundant, especially dead individuals on the ground after rain event	Belchior *et al.* (2012)

Aphaenogaster rudis	*Reticulitermes flavipes*	Field observations, laboratory experiments	Indiana, USA	Protein marking confirmed usage of termites as a prey. Termites were fed to all developmental stages in the ant colony after 24 h period	Buczkowski & Bennett (2007)
Azteca (2 sp.), *Dolichoderus* (4 sp.), *Ectatomma tuberculatum*, *Gnamptogenys* sp, *Camponotus sericeiventris* + 9 sp., *Cephalotes atratus*, *Cephalotes borgmeieri* + 1 sp., *Crematogaster* (4 sp.), *Leptothorax* (2 sp.), *Procryptocerus* (2 sp.), *Trachymyrmex* sp., *Neoponera magnifica* + 3 sp., *Pseudomyrmex* (6 sp.)	*Nasutitermes kemneri*, *Nasutitermes* spp. (2 spp.), *Microterotermes* cf. *exiguus*	Field observations and collections	Brazil, Atlantic coastal forest	Presence of only predatory ants, not non-predatory ants, suppressed termite activity. Termites did not competed for living space with the ants	Conçalves *et al.* (2005)
Pheidole megacephala, *Ochetellus glaber*, *Tetramorium simillimum*	*Coptotermes formosanus*	Laboratory experiments	Hawaii	*T. simillimum* caused more termite worker and soldier mortality than other two species. Mortality of *P. megacephala* was higher than in the other species	Cornelius & Grace (1995)
Neivamyrmex sp., *Azteca* sp.	*Nasutitermes* sp.	Amber from late Oligocene – middle Miocene period	Totolapa, State Chiapas, Mexico	*Neivamyrmex* is attacking *Nasutitermes* minor worker	Coty *et al.*, (2014)
Azteca sp.	*Nasutitermes ephratae*	Field observations/ experiments	Corumbá, Brazil	Termites inhabited the same tree of *Cecropia pachystachya* as *Azteca* ants, without antagonistic interactions. Termites were segregated in their own spaces by building protective sheetings from fibrous material.	Neves *et al.* (2014)
Lasius japonicus	*Reticulitermes speratus*	Field observations, laboratory experiments	Tsukuba, Ibaraki, Japan	The termite alarm pheromone acts as a kairomone for *L. japonicus*	Nguyen Trong & Akino (2012)
Dorylus nigricans rubellus	*Macrotermes subhyalinus*	Field observation	Eastern Nigeria, savannah and gallery forest	A massive raid (more than 2.4 kg dry termite mass retrieved) on *M. subhyalinus* was described	Schöning & Moffett (2007)
Megaponera analis	*Odontotermes* sp.	Laboratory experiments	Central Kenya	*M. analis* is semiochemically attracted to galleries, where termites are also present	Yusuf *et al.* (2014)
Azteca sp., *Monacis bispinosa*, *Camponotus abdominalis* +1 sp., *Hypoclinea* sp., *Wasmannia* sp., *Paratrechina* sp., *Pheidole* sp., *Pseudomyrmex* sp., *Crematogaster* sp., *Solenopsis* spp.	*Nasutitermes corniger*	Field observations and laboratory experiments	Venezuela, savannah, secondary forest	Ants associated with termites in their nests are more susceptible to termite defence and are unable to prey on live termites	Jaffe *et al.* (1995)

Brachyponera chinensis	*Reticulitermes speratus*	Laboratory experiments	Japan	Significantly more workers were killed by ants in the absence than in the presence of termite soldiers	Matsuura (2002)
Neoponera commutata	*Syntermes molestus*, *Syntermes calvus*, *Syntermes solidus*	Field observations	Brazil, semi-deciduous rain forest	The ant feeds exclusively on termite foraging parties. The ponerines consumed approximately three times the standing size of *Syntermes* population per annum	Mill (1984*b*)
Carebara vidua	*Macrotermes michaelseni*, *Macrotermes subhyalinus*	Field observations and laboratory experiments	Kenya Semi-arid grasslands	*C. vidua* ants nesting in *Macrotermes* spp. mounds. Termites ignore ant presence. *C. vidua* is able to kill and consume soldiers of *Macrotermes* spp.	Lepage & Darlington (1984)
Odontoponera transversa	*Odontotermes yunnanensis*, *Macrotermes yunnanensis*, *Ancistrotermes dimorphus*	Field observations and laboratory experiments	Xishuangbanna Tropical Botanical Garden (XTBG; Yunnan, China)	*O. transversa* preferred to hunt for *O. yunnanensis* above other species in the field. The ants perceived termite's trail pheromones as kairomones in laboratory	Wen *et al.* (2017)
Various ants (*Anonychomyrma* spp., *Crematogaste*r spp., Dolichoderinae, Formicinae, Myrmicinae, *Pheidole* spp.)	*Coptotermes* spp., *Nasutitermes exitiosus*	Field observations	Australia, grassy woodland	Termites lived together with ants under wood logs, separated by soil sheeting. When the sheeting was damaged, ants immediately attacked termites	Oberst *et al.* (2017)
Pheidole megacephala, *Megaponera analis*, *Myrmicaria eumenoides*	*Odontotermes lateritius*, *Pseudacanthotermes militaris*, *Microtermes* sp., *Macrotermes falciger*, *Hodotermes mossambicus*, *Macrotermes subhyalinus*	Field observations	Zambia, wooded savannah	*P. megacephala* was the most common ant attacking either foraging termites or underground chambers. Competition between *P. megacephala* and *M. analis* for termites observed	Sheppe (1970)
Megaponera analis	"termites"	Field observations	Tanzania, secondary coastal forest	*M. analis* raiding parties killed approx. 3000 termites per day	Bayliss & Fielding (2002)
Plagiolepis pallescens, *Polyrhachis lacteipennis*, *Pheidole teneriffana*, *Crematogaster antaris*, *Monomorium destructor*	*Microcerotermes diversus* (nymphs)	Laboratory experiments	Iran, date palm plantation	*P. lacteipennis* and *P. teneriffana* showed the highest attack rate and lower handling time. Some ant body traits correlated with effectiveness of termite predation	Latifian (2018)

Anochetus traegordhi	*Nasutitermes* sp.	Field observations	Democratic Republic of the Congo; Cameroon, tropical rainforest	*A. traegordhi* is an efficient predator of termites; ants prefer termites with which they share the same log	Schatz *et al.* (1999)
Linepithema humile	*Amitermes hastatus*	Field experiments	South Africa	Termites, topically treated with insecticide, were predated by *L. humile* hence poisoned the ant colony	Buczkowski *et al.* (2018)
Anoplolepis carinata, *Camponotus* sp., *Centromyrmex* sp., *Crematogaster* sp., *Dorylus* sp., *Euponera brunoi* sp., *Hypoponera* sp., *Leptogenys* sp., *Mesoponera caffraria*, *Mesoponera senegalensis*, *Odontomachus troglodytes*, *Odontomachus assiniensis*, *Pheidole pulchella*, *Ponera* sp., *Tetramorium* sp.	Rhinotermitidae, *Reticulitermes flavipes*, *Macrotermitinae*, *Anoplotermes-group* sp., *Termitinae*	Field collections	Gabon, primary rain forest	Termite DNA was detected in all ant species and in 17.2% of 215 tested specimens, but not in *Ponera* sp.	Fayle *et al.* (2015)
Megaponera analis	*Macrotermes ivorensis*, *Cubitermes* sp.	Field experiments	Cameroon, tropical forest	*M. analis* preyed on *M. ivorensis* when offered along the foraging trail, while rejected *Cubitermes* sp.	Patel *et al.* (2018)
Camponotus sp. "A" and "B", *Crematogaster irritabilis*, *Phillidris cordatus*, *Calomyrmex* sp., *Tapinoma* sp.	*Nasutitermes princeps*	Field observations and experiments	Independent State of Papua New Guinea, coconut plantation	*Camponotus* sp. A nested most frequently inside termite nests, causing no predation unless the nest was artificially opened. *C. irritabilis* attacked termite colonies. The presence of *C. irritabilis* on a tree prevented termites from establishing a colony there	Leponce *et al.* (1999)
Crematogaster sp., *Dolichoderus* sp.	"termite"	Field observations	The Republic of Colombia	*Crematogaster* and *Dolichoderus* ants found in mango tree inhabiting enclosed nests within termite nest structures	Wheeler (1901)
Brachyponera chinensis	*Reticulitermes speratus*	Laboratory experiments	Japan, secondary forest	Older soldiers were involved in fighting with ants when guarding the nest entrance more often that younger ones	Yanagihara *et al.* (2018)
Brachyponera chinensis, *Aphaenogaster rudis*	*Reticulitermes flavipes*	Field experiments	Georgia, USA, deciduous forest	Both ant species prevented termites from occupying artificial feeding/nesting sites. Both ant species attacked termites when protection sheetings were disturbed	Warren *et al.* (2015)

Fig. S1. Number of studies specifically studying or mentioning ant–termite interactions in relation to year of publication. Studies were found using the *Web of Knowledge* website (The Web of Knowledge, 2019) and *Google Scholar* (Google Scholar, 2019) with the key words: "ant*s" AND "termite*s" with or without the words "interaction" and "predation" either in the title or in the abstract. Note the gap between 1901 and 1970, where no such studies were published. The criteria for inclusion/exclusion of studies are as listed in the legend to Table S1.

CHAPTER II

How does rainforest logging and conversion to oil palm affect soil-living ants and termites and ant-termite predation rate?

Manuscript

How does rainforest logging and conversion to oil palm affect soil-living ants and termites and ant-termite predation rate?

Authors: Jiri Tuma, Sarah H. Luke, Richard G. Davies, Paul Eggleton, Petr Klimes, David T. Jones, Hana Konvickova, Pavel M. Maraví, Simon T. Segar, Tom M. Fayle.

Abstract

Habitat change is one of the main threats to biodiversity and stability of ecosystems worldwide. Southeast Asia is a global hotspot of biodiversity with a high degree of endemism. However, the region also has the fastest rates of deforestation. This deforestation is caused by expanding oil palm plantations throughout the region with serious impacts on biodiversity. Ants and termites dominate tropical ecosystems where they reach high abundance and diversity and are vital for maintaining key ecosystem processes. Furthermore, predation of ants on termites is also expected to play an important role in ecosystems.

We collected ants and termites using soil pit excavation in primary forest, selectively logged forest and oil palm plantation. We also measured environmental characteristics we expected to be important for ant and termite distributions. Ants and termites were identified to species level. Additionally, we randomly selected 124 ant individuals (from 12 genera) from soil pits and we analysed those for termite DNA in their bodies using DNA barcoding.

We found that the abundance of ants was highest in logged forest while termite abundance showed no clear differences between habitats. The diversity of ants was comparable between primary and logged forest but was much lower in oil palm plantation. Termites were more species rich in the logged forest than in primary forest or oil palm plantation. Furthermore, the oil palm was predominantly occupied by the invasive ant *Anoplolepis gracilipes*, and there was only one termite species - *Macrotermes gilvus*. These results emphasize the value of logged forests for supporting species diversity, while oil palm plantations showed a lower number of species and susceptibility to invasive species. Furthermore, 32% of analysed ants contained termite DNA and this rate differed between ant taxa, but was similar across habitats. Hence we speculate that the predatory pressure of ants on termite populations and the influence of this pressure on the ecosystem functions termites provide is resilient to habitat change.

Manuscript is ready for submission

CHAPTER III

Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation

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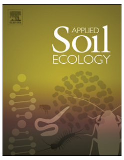

Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation

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ABSTRACT

Anthropogenic habitat change is a major driver of species extinctions and altered species communities worldwide. These changes are particularly rapid in the tropics, where logging of rainforests and conversion to agricultural habitats is widespread. Because species have varying effects on their abiotic environment, we expect shifts in species composition to drive changes in ecosystem processes. One important ecosystem process is animal-driven bioturbation: the turnover of soil material by soil-dwelling organisms. We developed a protocol for measuring aboveground bioturbation, and assessed how bioturbation rates and standing amounts of aboveground bioturbated soil change as primary tropical rainforests are logged and converted to oil palm plantation. By identifying the animals that created soil structures, we assigned bioturbation activity to different soil-dwelling groups. Across all habitats, most standing bioturbated soil was generated by termites (97.0%), while short-term, small-scale bioturbation was mainly generated by earthworms (87.3%). The species diversity of social insects (ants and termites) involved in bioturbation was higher in primary forest than in either logged forest or oil palm plantation. However, neither standing bioturbated soil, nor short-term bioturbation rate differed among habitats. Unexpectedly, in primary forest, high levels of bioturbation were associated with low bioturbator diversity. This was because two termite species, where present, conducted nearly all bioturbation. There was no relationship between levels of bioturbation and diversity in the other habitats. Our results emphasize the importance, across all habitats, of termites for generating standing aboveground soil structures, and earthworms for short-term soil turnover. In oil palm plantation, bioturbation relies on a smaller number of species, raising concerns about future environmental change and consequent species loss.

1. Introduction

Habitat change and habitat loss are the most important threats to biodiversity, ecosystem stability and nature conservation worldwide (McGarigal et al., 2005; Meffe and Carrol, 1997; Sala et al., 2000). The conversion of natural habitats, mainly to agricultural landscapes, leads to species loss and altered species composition due to modified abiotic conditions (Mack et al., 2000). The response of organisms and associated ecosystem functioning to disturbance are of particular importance in the tropics, which are experiencing rapid anthropogenic habitat change. Tropical forests are global biodiversity hotspots, yet are threatened by logging and conversion to agriculture (Basiron, 2007; Sodhi et al., 2004). In South East Asia, primary forests often undergo multiple rounds of logging before conversion to oil palm plantation (Woodcock et al., 2011). However, even severely logged forests still support numerous species (Fitzherbert et al., 2008) and some forest functions such as soil erosion protection can be restored within just five to ten years if the forest is left to regenerate naturally (Bruijnzeel, 2004; Douglas, 1999). In contrast, oil palm plantation supports a very low diversity of taxa compared to natural forests. According to a review 25

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of 27 studies concerning various animal taxa demonstrated a reduction of species richness in oil palm compared to other habitats (Turner et al., 2011). Taken together, logging of rainforest and consequent conversion to oil palm plantation cause various changes, many of which are predicted to influence the community of organisms and hence to affect ecosystem functions.

Soil modification and development is a key ecosystem process driven by animals and plants that is likely to be affected by habitat change in the tropics. Although soil organisms represent a small fraction of the total soil mass, they are a vital functional component of the ecosystem: they affect water quality, water supply, erosion, and are important for climate regulation, pollutant attenuation and degradation, and pest and disease control (Barrios, 2007; Brussaard, 1998; Decaëns et al., 2006). From a soil processes perspective, soil organisms are responsible for decomposition of litter, soil organic matter dynamics at different spatial and temporal scales, and maintenance of soil structure and aeration (Frouz, 2018). They also store nutrients in their living tissues and faeces and thus reduce nutrient leaching (Cunha et al., 2016; Doran and Safley, 1997). All these activities performed by soil organisms affect overall soil health and as a result plant growth, and thus they are crucial in both natural habitats and agroecosystems (Brussaard et al., 2007; Kohl et al., 2014; Usman et al., 2016).

One of the main ways in which living things modify soil is through bioturbation; the reworking and mixing of soil by organisms (Kristensen et al., 2012). This process is sometimes called 'mounding' when only production of aboveground soil structures is taken in account (Wilkinson et al., 2009). Bioturbation relates not only to physical movement of soil by organisms, but also to transport of soil particles to soil layers with different oxygen and water levels. This movement significantly affects the redistribution of soil organic matter and the creation of biopores, and it hence enhances microbial activity and consequent organic matter decomposition and nutrient release due to increased water infiltration and soil aeration (Lobry De Bruyn, 1997; Meysman et al., 2006; Wilkinson et al., 2009; Yair, 1995). As a result of this importance, the presence of bioturbating organisms correlates with production, health and fertility of soils (Wilkinson et al., 2009).

Despite the importance of terrestrial bioturbation, methods for measuring this process are not yet well developed. Usually a single organism is studied in detail and extrapolations of its bioturbation are then made (Meysman et al., 2006). The most common way to estimate bioturbation involves direct measurements or collections of the soil structures on the soil surface, e.g. termite mounds, earthworm casts or ant nests (Wilkinson et al., 2009). It is important to note that the soil deposited on the surface does not necessarily reflect total animal-driven bioturbation. A significant share of soil mixing occurs underground, performed mostly by endogeic species of ants, termites, earthworms and other animals (e.g. Minter et al., 2012; Whalen et al., 2004). Methods to estimate the underground volume that is excavated by ants or termites comprise pouring dental plaster or molten aluminum into underground nests to obtain a solid casting of the hollow spaces (e.g. Mikheyev and Tschinkel, 2004) or direct observation of the movement of soil material in artificial arenas during excavation of underground spaces (Halfen and Hasiotis, 2010; Minter et al., 2012). However, these methods are often used only to describe nest architecture and do not account for backfilled or collapsed spaces, which often occur in ant nests (Halfen and Hasiotis, 2010). All of these approaches usually result good estimations of bioturbation activity of a single species or faunal group at one location or under laboratory conditions. However, measurements of bioturbation at the level of entire communities with comparisons between habitats are rare. Additionally, to our knowledge, there is no information about how overall bioturbation in any habitat is partitioned between different faunal groups for the tropics.

The most important groups of bioturbating invertebrates worldwide are ants, earthworms and termites (Paton et al., 1995). There is also a range of other invertebrates and burrowing vertebrates that affect soils. The importance of these groups varies with the climatic conditions. For example, ants and termites tend to dominate in drier environments, where they replace earthworms, which are the main bioturbating group in moister environments (Jones et al., 1994; Wilkinson et al., 2009). Understanding which organisms are responsible for bioturbation is important because soil organisms differ in the ways they manipulate the soil during the bioturbation process (Meysman et al., 2006). For example, ants or rodents mainly translocate mineral soil within the soil profile, while earthworms and termites not only translocate the soil, but also ingest various soil materials, so their faeces are moistened and enriched by a diverse spectrum of microorganisms (Brauman, 2000; Lavelle et al., 2004). Conversely, the casts of earthworms are often compacted and bacterial cells can be coated by clay materials that stabilizes the cast and lowers microbial activity in the long term (Guéi and Tondoh, 2012; Hopkins et al., 1998). Through these mechanisms, variation in bioturbator community composition gives rise to variation in the functional importance of resulting soil structures, with consequences for soil processes such as soil organic matter dynamics, especially in habitats being affected by anthropogenic change (Frouz, 2018; Lobry de Bruyn and Conacher, 1994).

Because of their ecological importance, impacts of anthropogenic habitat change on bioturbating organisms are of great concern. The abundance and species richness of bioturbating soil macrofauna in ecosystems is usually reduced with habitat degradation, and species composition is altered. Lower diversity in human-disturbed habitats has been reported for soil and leaf litter ants (e.g. Hernández-Flores et al., 2016; Solar et al., 2016), termites (e.g. Dambros et al., 2013; Dosso et al., 2013), cicadas (e.g. Chiavacci et al., 2014; Karban, 2014) and earthworms (e.g. Guéi and Tondoh, 2012; Dey and Chaudhuri, 2014). For example, species richness of ants, termites and earthworms was lower in pasture or sugarcane plantation than in natural vegetation in Brazil (Franco et al., 2016). The same animal groups had lower abundance, biomass and diversity in logged lowland tropical forest, compared to primary forest in Malaysian Borneo (Ewers et al., 2015). This reduction in species richness compared to natural ecosystems is often attributed to lower habitat complexity with lack of niches and altered microclimatic conditions (Ewers et al., 2015; Foster et al., 2011). However, anthropogenic disturbance can also lead to higher abundances of certain taxa. For example, cicadas can increase in abundance in logged forest gaps (Karban, 2014) and along forest edges (Chiavacci et al., 2014), where there are more young saplings, which are vital for cicada nymph development. There can also be increases in the dominance of particular groups. For example, disturbed and converted habitats can be invaded and dominated by a single species of earthworm that contributes greatly to bioturbation (González et al., 2006). All of these compositional changes driven by human-induced habitat degradation result in changes in assemblages of bioturbating organisms. Animals that perform soil mixing differ in their efficiency, and hence disturbance is predicted to influence bioturbation rates via turnover of species.

Despite the plausibility of anthropogenic impacts on bioturbation, even comparisons of different faunal groups in terms of their contribution to bioturbation in a single habitat are rare, albeit called for by soil ecologists (Wilkinson et al., 2009). Similarly, studies of bioturbator groups or area-based bioturbation rates across contrasting habitats are uncommon. One study in Sweden found that earthworms performed the vast majority of bioturbation in most habitats (> 98%), with the exception of abandoned fields (12% ant-mediated bioturbation) and spruce forest (93% ant bioturbation) (Persson et al., 2007). In tropical regions, to the best of our knowledge only one study has assessed impacts of logging on bioturbation. This focused solely on dung beetles and their small-scale effects in an area surrounding experimentally placed dung (França et al., 2017), finding that even low intensities of logging led to reduced bioturbation by this group. However, no work has attempted to quantify the activity of entire bioturbating animal communities on the soil surface.

In this study we develop and apply a novel method to quantify the aboveground soil structures created by animal-driven bioturbation. We investigate how bioturbation rates and standing amounts of bioturbated soil are affected by logging and conversion to oil palm of primary lowland dipterocarp rain forest in Sabah, Malaysia. By identifying the groups and species that generate bioturbated aboveground soil, we were able to measure for the first time the individual contributions of different ecological groups to the bioturbation process in the tropics. Specifically, we test the following hypotheses:

1. Bioturbation rate will decrease and there will be less standing bioturbated soil in more disturbed habitats.
2. Bioturbator diversity will decrease in more disturbed habitats.
3. Bioturbation rates and amounts of standing bioturbated soil will be higher in plots with greater bioturbator diversity.

2. Materials and methods

2.1. Study sites

The study sites were part of the Stability of Altered Forest Ecosystems (SAFE) project in Sabah, Malaysian Borneo (Ewers et al., 2011). Six sampling points were surveyed in each of the three habitats (N = 18 plots in total): 1. Primary lowland rainforest at Maliau Basin Conservation Area (MBCA, SAFE Project site ‘OG2’). This forest has never been logged and is part of a large continuous forest block: the 58,840 ha of MBCA forest is surrounded by one million hectares of logged forest. 2. Continuous selectively logged forest in the SAFE Project experimental area, with two plots at each of the three SAFE Project sites: ‘LFE’ (Logged Forest Edge) and sites ‘B’ and ‘F’. All three sites have been at least twice logged (Struebig et al., 2013). Note that all sites were sampled before any SAFE project-related experimental fragmentation. 3. Oil palm plantations, with two plots at each of the SAFE Project sites ‘OP1’, ‘OP2’ and ‘OP3’. OP1 and OP2 were planted in 2006, and OP3 in 2000. These are managed by the company Benta Wawasan Sdn Bhd (see Ewers et al., 2011) and the SAFE Project (see www.safeproject.net for details). For sample site coordinates see Supplementary material 1. Data were collected from 22nd June to 18th August 2015 and 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.

2.2. Sample collection and measurements

2.2.1. Assessing aboveground bioturbation

We defined and measured bioturbation activity as the amount of soil material moved to the soil surface by the activity of various animals. We carried out three kinds of surveys in order to: 1. Assess the distribution of larger aboveground bioturbated structures across larger spatial scales (‘standing bioturbated soil’); 2. Assess turnover of smaller aboveground structures at a smaller spatial scale (‘bioturbation rate’); 3. Measure growth and turnover of aboveground termite mounds (‘termite mound dynamics’). For further details of the measurements, see Supplementary material 2.

2.2.2. Assessing standing bioturbated soil

For large-scale surveys, at each of the six sampling points in each habitat a 25 m × 25 m (625 m^2) plot was searched thoroughly for any aboveground biogenic soil structure that could be seen without moving leaf litter, not including scrapes (resulting from shallow excavations such as digging) or plant-generated mounds and hollows, such as that caused by tree uprooting. Structures that were smaller than 6 cm in height were omitted from the standing bioturbation measurements. This excluded mainly epigeic and small anecic earthworms, some ant mounds and other small burrowers. We were able to distinguish five categories of larger structure: Cicada turret - a hollow cylinder of clay material, which was sometimes capped (Fig. 1b); Earthworm cast – a pile of soil extruded as a long cylinder (Fig. 1f); Ant mound - a pile of soil particles at a nest entrance (Fig. 1e); ‘Burrow’ – a heap (with no typical shape) of excavated soil usually around a tunnel/nest entrance, perhaps caused by large insects such as beetles, solitary wasps, small mammals or lizards.

These structures were collected in their entirety from the level of the soil surface upwards, identified, dried in an oven at 80 °C for two days and weighed.

Termite mounds - All intact, standing termite mounds, fragments of mounds and dead (fallen) mounds were counted in each plot. Aboveground mounds built by the three species of termite present in the plots were identified based on mound morphology and species identification from voucher samples. *Dicuspiditermes nemorosus* (Haviland, 1898) made dark-coloured mounds with multiple turrets emerging from an aboveground basal plate (Fig. 1a) while *Dicuspiditermes minutus* (Akhtar and Riaz, 1992) made single standing turret-shaped mounds (Fig. 1c). *Macrotermes gilvus* (Hagen, 1858), made large, dense, mounds with clay that was generally yellow (Fig. 1d). However, species boundaries between *Dicuspiditermes* termites were not clear in all cases, and so for mound growth and turnover analyses the two species in the genus were pooled as *Dicuspiditermes* spp.

The mound height from the soil surface and the most representative diameter were measured for each mound structure. Where the base of the mound was elliptical rather than circular, the mean of two perpendicular measurements of diameter was used. In cases of multiple turrets within one mound, separate measurements were made for each turret and the values were summed. The mound volume was then calculated by approximating the mound shape to a cylinder, using a standard formula for cylinder volume $V = \pi r^2 h$ for *D. nemorosus* and *D. minutus*, while a standard formula for cone volume $V = \pi r^2 h/3$ was used for *M. gilvus* nests. This value was converted to soil mass using soil samples of a known volume of mound material from each species, which were dried in an oven for two days at 80 °C before weighing.

2.2.3. Assessing bioturbation rate

To assess bioturbation performed by smaller organisms at smaller scales, which was not recorded during large-scale surveys (those that fell below the threshold of 6 cm in height), we established two 1 m^2 plots per sampling point (N = 12 per habitat). This assessment was performed in the same time as standing bioturbation was measured, and in the same area. First, we cleared all litter and soil structures caused by bioturbation from the plot. This was necessary because distinguishing bioturbated soil from other soil within the leaf litter layer was not possible. After five days we collected all the soil structures that had appeared on the soil surface. The five day period was established on basis of the prior measurement trials. This period was long enough for new structures to emerge, but also not excessively long for the effect of repeated rain to break and wash away the bioturbated soil structures. Rain is the main limiting factor in this kind of measurement, as it restricts the maximal time between the setup and re-visit of the plot. The collected structures were dried in an oven at 80 °C for two days and weighed.

2.2.4. Assessing termite mound dynamics

In addition to small-scale bioturbation rate, it is important to consider turnover of larger aboveground structures. This was not feasible at the scale of whole plots and for all types of bioturbated structures. However, we observed that the majority of such translocated soil originated in termite mounds of the three mound-building species present in the plots, presumably accumulated over longer timescales. Hence we measured the growth and turnover of termite mounds of *M. gilvus* and *Dicuspiditermes* spp. in primary forest, logged forest and oil palm plantation. We marked and measured all the standing soil termite mounds in the 25 m by 25 m plots in which large-scale standing bioturbated soil was surveyed (N = 18, see above). We selected five of the *M. gilvus* and *Dicuspiditermes* spp. mounds in each habitat in which the species were present, and applied thin plastic sticks with a measuring scale,

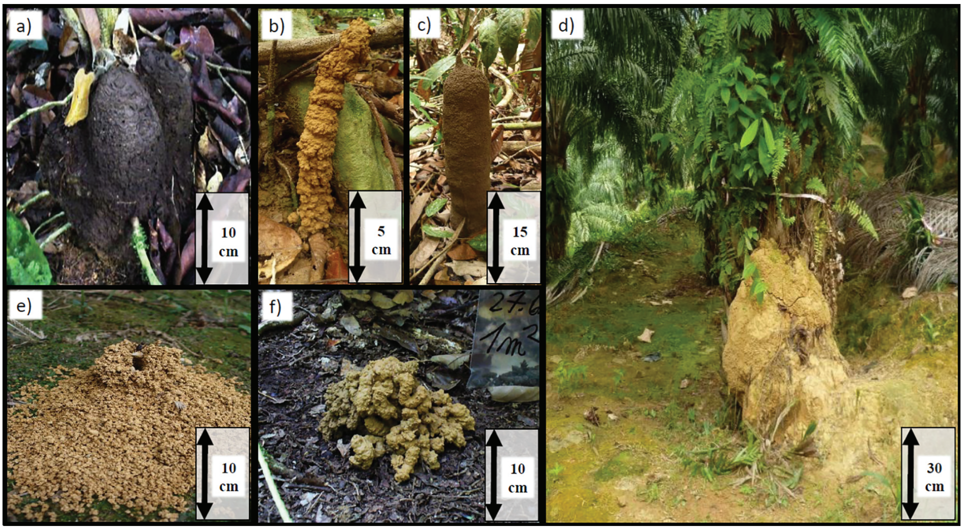

Fig. 1. Epigeous soil structures measured during surveys of standing bioturbated soil: (a) *Dicuspiditermes nemorosus* mound (note the two turrets emerging from the basal plate); (b) cicada turret; (c) *Dicuspiditermes minutus* mound; (d) *Macrotermes gilvus* mound at the base of an oil palm tree; (e) ant mound (*Odontoponera transversa*), at entrance to nest; (f) large earthworm cast. Scales vary between panels, and are indicated in the lower right corner of each panel.

vertically in the body of the mound. Termites did not preferentially cover the measuring sticks with mound material. After one year, we resurveyed all the plots and recorded the number and size of dead or newly-emerged mounds. Dead mounds were considered those that had fallen to the ground and newly-emerged ones those that were not present in the initial survey. For mound growth, the one-year increase of soil covering the measuring sticks was recorded (for further details of the measurements see the Supplementary material 2).

2.2.5. Limitations

Using these methods, we obtained a "snapshot" of aboveground bioturbation. We did not aim to evaluate the bioturbation activity of any particular animal in detail (apart from for termite mound dynamics). This method also necessarily underestimates total bioturbation values in the following ways:

1. The method measures only aboveground soil and it is known that underground soil mixing can account for a significant, but mostly unknown share of the overall bioturbation (Hasiotis and Halfen, 2010; Minter et al., 2012).
2. The method omits very small bioturbation conducted by certain meso- and micro-fauna, such as small earthworms and Enchytraeidae, dipterian larvae, nematodes etc.
3. In order to obtain a complete picture of aboveground bioturbation in certain habitat, multiple measurements during the year, both of standing structures and of mixing rate would have to be taken to record the creation and decay of more temporal structures (such as cicada turrets and earthworm casts). Nevertheless, we believe that our combined method for measuring aboveground bioturbation is of utility when the habitats are compared within the same region and over the same period.

2.3. Data analysis

The effects of habitat on standing bioturbated soil and bioturbation rate were tested using generalized linear models (GLM, family = Gaussian; link = log, log link used to account for non-normal distribution of errors). Chi-square tests of deviance were used to compare and simplify models. The contribution of various animal groups to the total bioturbation in different habitats was tested using ANOVAs (since data were normally distributed) with Tukey HSD post-hoc comparisons, where applicable. In order to assess the diversity of the animals contributing to soil bioturbation, a bioturbator diversity index was calculated based on Simpson's diversity index, D (Simpson, 1949). The sum of squared proportional contribution of individual bioturbator species to the total bioturbation within the plot was subtracted from 1, so $D = 1\text{-}\Sigma\,(n/N)^2$, where n denotes bioturbation performed by one type of bioturbator and N is the sum of measured bioturbation of all bioturbators within individual plot. This denotes the probability that two randomly chosen small particles of bioturbated soil were brought to the surface by different animal groups/species. The index was calculated for each plot, for both standing bioturbated soil and bioturbation rate measurements. Note that this index is based on relative amounts of soil uplifted, and not on numbers of individuals of different species. Differences between habitats in this index were tested using ANOVAs with Tukey HSD post-hoc comparisons, where applicable. The difference in growth rates of surviving *Dicuspiditermes* spp. nests in primary forest and logged forest (the two habitats in which they were present) was tested by standard unpaired *t*-test. The same test was used to compare the amount of soil brought up by new *Dicuspiditermes* spp. nests in primary forest and logged forest. The total amount of soil brought up by *Dicuspiditermes* spp. mounds was calculated as the mean number of live nests multiplied by their mean growth, and the mean amount of soil found in new *Dicuspiditermes* spp. mounds was added to this value. To test whether habitats with more diverse bioturbating soil fauna had higher levels of bioturbation we used generalized linear models (GLM, family = Gaussian; link = log) predicting mean standing bioturbated soil as a function of bioturbator diversity index. Statistical analyses were performed using R Statistical Software (version 3.6.0).

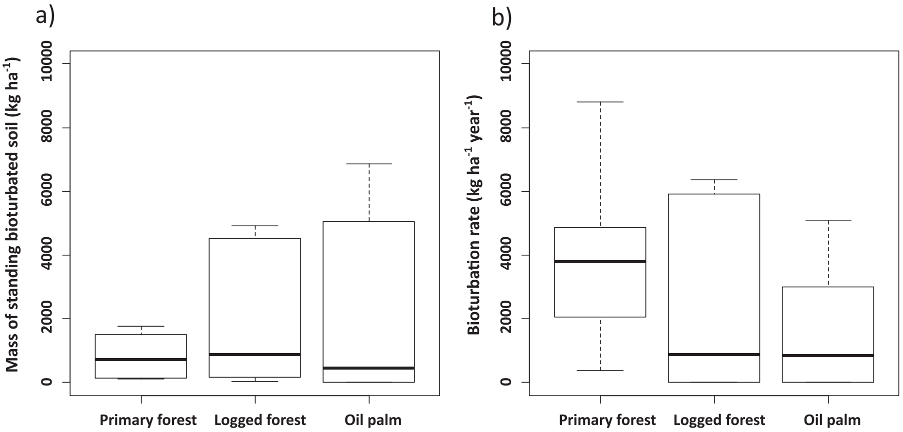

Fig. 2. (a) Mass of standing bioturbated soil across different land uses measured at large scale (25 m × 25 m). (b) Bioturbation rate at small scale (2 m × 2 m plots measured over five days). Medians are denoted by bold horizontal lines, the interquartile range box represents the middle 50% of the data, and the whiskers represent full data ranges.

3. Results

3.1. Standing bioturbated soil and bioturbation rate across different land uses

The mean mass of standing bioturbated soil at large scales (25 m × 25 m plots) was highly variable. Although mean values were lowest in primary forest (828 kg ha^{-1} ± 689; all numbers are presented as means with standard deviation), intermediate in logged forest (1900 kg ha^{-1} ± 2260) and highest in oil palm plantation (2140 kg ha^{-1} ± 3019, Fig. 2a), there was no significant difference between habitats in standing mass of bioturbated soil (GLM, $\chi^2_{15} = 5{,}848{,}485$, $p = 0.551$; note that χ^2 values are large as they are calculated using deviance, which is on the scale of kg ha^{-1}). The mean small-scale bioturbation rate was also highly variable, being highest in primary forest (3952 kg ha^{-1} year^{-1} ± 2665), intermediate in logged forest (2338 kg ha^{-1} year^{-1} ± 2760), and the lowest in oil palm (1643 kg ha^{-1} year^{-1} ± 1902, Fig. 1b). However, there was no significant difference in small-scale bioturbation rates between the habitats (GLM, $\chi^2_{15} = 16{,}842{,}008$ $p = 0.318$).

3.2. Contribution of different faunal groups to standing bioturbated soil and bioturbation rate across different land uses

The standing bioturbated soil across all habitats (Fig. 3a) was overwhelmingly generated by termites, comprising 97.0% of total bioturbation, with no significant difference in this total amount between habitats (ANOVA between habitats: $F_{2,\,15} = 0.10$, $p = 0.904$). A single termite species *Macrotermes gilvus* brought up on average 99.8% of all standing bioturbated soil in oil palm, 67.7% in logged forest and 1.1% in primary forest. Cicadas were responsible for 1.4% of the standing bioturbated soil across all habitats, also with no significant difference between primary and logged forest ($F_{1,\,10} = 0.627$, $p = 0.447$), while other unidentified bioturbators were responsible for 0.7% of bioturbation across all habitats, with higher bioturbation in primary forest than in both logged forest and oil palm (ANOVA: $F_{2,\,15} = 20.21$, $p < 0.001$, Tukey HSD: primary-logged $p = 0.012$, primary-oil palm $p < 0.001$). Earthworms (0.7%, with no difference between primary and logged, $F_{1,\,10} = 0.807$, $p = 0.390$) and ants (0.2%, with no difference between habitats, $F_{2,\,15} = 0.62$, $p = 0.549$) also made minor contributions to standing bioturbated soil. Note that there was no standing bioturbated soil > 6 cm generated by either earthworms or cicadas in oil palm.

The majority of contributions to small-scale bioturbation rate across all habitats (Fig. 3b) was from earthworms (87.3%), followed by ants (10.4%) and other unidentified animals (2.2%). Bioturbation rate across habitats did not differ significantly for ants between primary forest and oil palm (ANOVA, $F_{1,\,9} = 0.179$, $p = 0.682$) but it approached significance for earthworms (ANOVA, $F_{2,\,15} = 3.219$, $p = 0.069$).

There was no significant difference in bioturbator diversity for standing bioturbated soil between habitats (note the outlier in oil palm; Fig. 3c, ANOVA, $F_{2,\,15} = 2.0$, $p = 0.169$), or for bioturbation rate between primary forest and oil palm (Fig. 3d, ANOVA, $F_{2,\,15} = 1.54$, $p = 0.245$; note that logged forest was not tested as all values were zero).

3.3. Social insect bioturbator diversity across different land uses

When considering social insects that generated standing bioturbated soil (ants and termites) and which we were able to identify to species level (Fig. 4c), there was a significant difference in social insect bioturbator diversity index between habitats (Fig. 4a, ANOVA, $F_{2,\,15} = 17.43$, $p < 0.001$) with primary forest having higher values than logged forest and oil palm plantation (Tukey HSD, $p < 0.001$ and $p < 0.001$ respectively). For small-scale bioturbation rate, bioturbation was carried out solely by ants in primary forest and oil palm (Fig. 4b), and there was no social insect contribution in logged forest (see also above section). Although two species of ants performed bioturbation in oil palm (Fig. 4d), they never occurred in the same plot. Hence all values of the diversity index were zero in both disturbed habitats, making statistical comparisons with the primary forest impossible.

3.4. The relationship between diversity index of bioturbators and aboveground bioturbation

The bioturbator biodiversity index for broader taxonomical categories was significantly and negatively correlated with standing bioturbated soil in primary forest (GLM, $t_4 = -5.505$, $p = 0.005$) but not in logged forest (GLM, $t_4 = -0.889$, $p = 0.424$) or in oil palm (GLM, $t_4 = 1.128$, $p = 0.322$; Fig. 5). There was no significant correlation

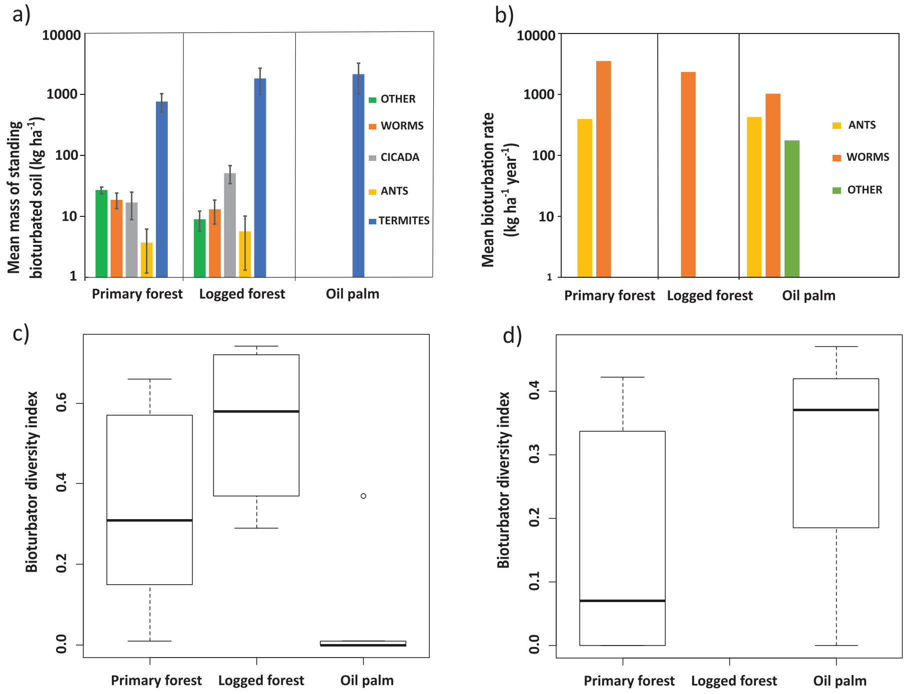

Fig. 3. The relative contribution of bioturbator groups to standing bioturbated soil and bioturbation rate across different land uses. (a) Large-scale standing bioturbated soil (note that the minimal values for 'ants' and 'other' groups are not visible in this graph for oil palm). (b) Small-scale bioturbation rate of different animal groups. Note the logarithmic y-axes in graphs (a) and (b). The error bars represent the standard error of mean. In graph (b) the SEM were removed for better data visualization and are available in Supplementary material 6. (c) The bioturbator diversity index for standing bioturbated soil. (d) The bioturbator diversity index for small-scale bioturbation rate. In both (c) and (d) broadly defined taxonomic groups were used for the index calculation (see methods for details). 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 open points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles.

between bioturbation rate and diversity of small-scale bioturbators across habitats (GLM, $t_4 = 0.135$, $p = 0.899$) for primary forest and (GLM, $t_1 = -5.402$, $p = 0.117$) for oil palm. There was no possible correlation for logged forest due to a lack of valid data points (see above), because only earthworms contributed to bioturbation rate.

3.5. Termite mound dynamics (the growth, turnover and densities of termite mounds)

Mounds of the termite *Dicuspiditermes* spp. grew by an average of 10.4 cm per mound per year, which accounted for 74.7 g of dry soil per mound per year (N = 5 measured in each habitat) across forested habitats. There was no significant difference in growth rate of individual *Dicuspiditermes* mounds between primary forest and logged forest (Fig. 6a, $t_8 = -0.586$, $p = 0.574$). We did not record any growth of the mounds of *M. gilvus* in one year across all habitats. The mean mass of soil brought up by new *Dicuspiditermes* spp. mounds was 2.6 kg ha^{-1} year^{-1} in primary forest, 1.5 kg ha^{-1} year^{-1} in logged forest and 0.0 kg ha^{-1} year^{-1} in oil palm, although with no significant difference between primary forest and logged forest (Fig. 6b, $t_{10} = -0.509$, $p = 0.615$). There was an average of 109.3 living *Dicuspiditermes* spp. mounds per hectare in primary forest (min. 0, max. 265), 69.3 mounds per hectare in logged forest (min. 0, max. 160) and no mounds in oil palm plantation (Fig. 6c). After one year, we recorded a reduction in density of living mounds (Fig. 6d) in primary forest by 26.8% (32.0 mounds built, 61.3 died per hectare) and in logged forest by 57.7% (5.3 mounds built, 45.3 died per hectare). Regarding *Macrotermes gilvus*, there were 2.7 living mounds per hectare in primary forest, 13.3 mounds per hectare in logged forest and 16.0 mounds per hectare in oil palm, with no recorded appearance, growth or death of mounds. Taking together growth of existing mounds and appearance of new mounds, the total amount of soil brought up by living termite mounds, which was entirely due to *Dicuspiditermes* spp., was 42.7 kg ha^{-1} year^{-1} in primary forest, 28.6 kg ha^{-1} year^{-1} in logged forest and 0.0 kg ha^{-1} year^{-1} in oil palm (the latter due to lack of any live growing nests).

4. Discussion

Our study represents the first assessment and quantification of the contributions of invertebrates to aboveground bioturbation in tropical forest ecosystems. Furthermore, we were able to compare their contributions across a gradient of anthropogenic habitat modification. Despite high variability in bioturbation values within and across habitats and hence lack of significant differences in bioturbation measures among the primary forests, logged forests and oil palm, we show the importance of changes in bioturbator community composition. Termites were the major generators of standing bioturbated soil across all habitats. However, mound growth was very slow, and hence turnover was dominated by non-termite groups carrying out soil uplift over

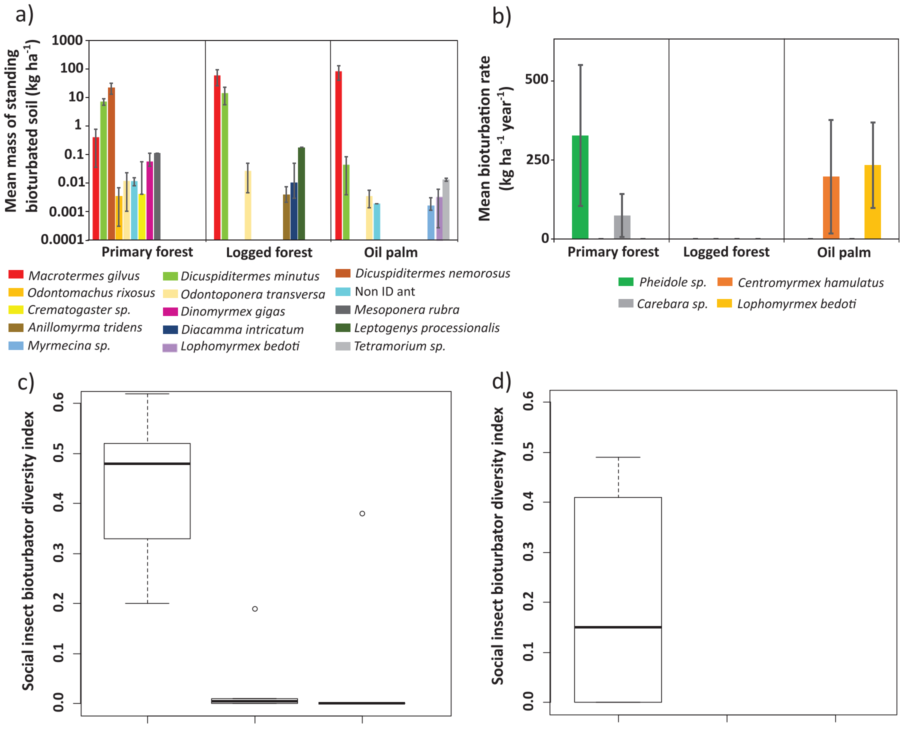

Fig. 4. Bioturbator diversity index and mass of standing bioturbated soil and bioturbation rates of social insects across different land uses. (a) Visualization of all social insect species generating standing bioturbated soil. All the SEM values are available in Supplementary material 6. Note the logarithmic y-axis. (b) Visualization of social insect small-scale bioturbation rate (note that no termite bioturbation was found in any habitat and no ant bioturbation was found in logged forest). The error bars represent the standard errors of means. (c) The bioturbator diversity index for social insects (ants and termites) identified to species level for standing bioturbated soil. (d) The bioturbator diversity index for social insects (ants and termites) for bioturbation rate. 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 open points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles.

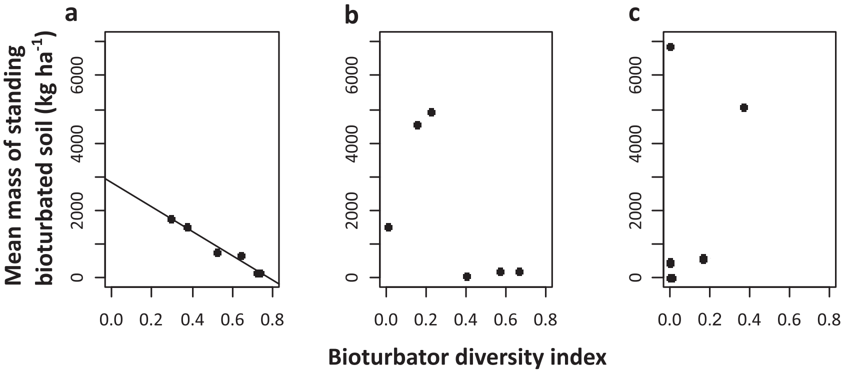

Fig. 5. The mass of standing bioturbated soil in relation to bioturbator diversity index in (a) primary forest, (b) logged forest and (c) oil palm plantation. Points represent individual plots (N = 6 per habitats) at which standing mass of bioturbated soil and diversity of bioturbating animals were measured. The fitted line denotes a significant relationship.

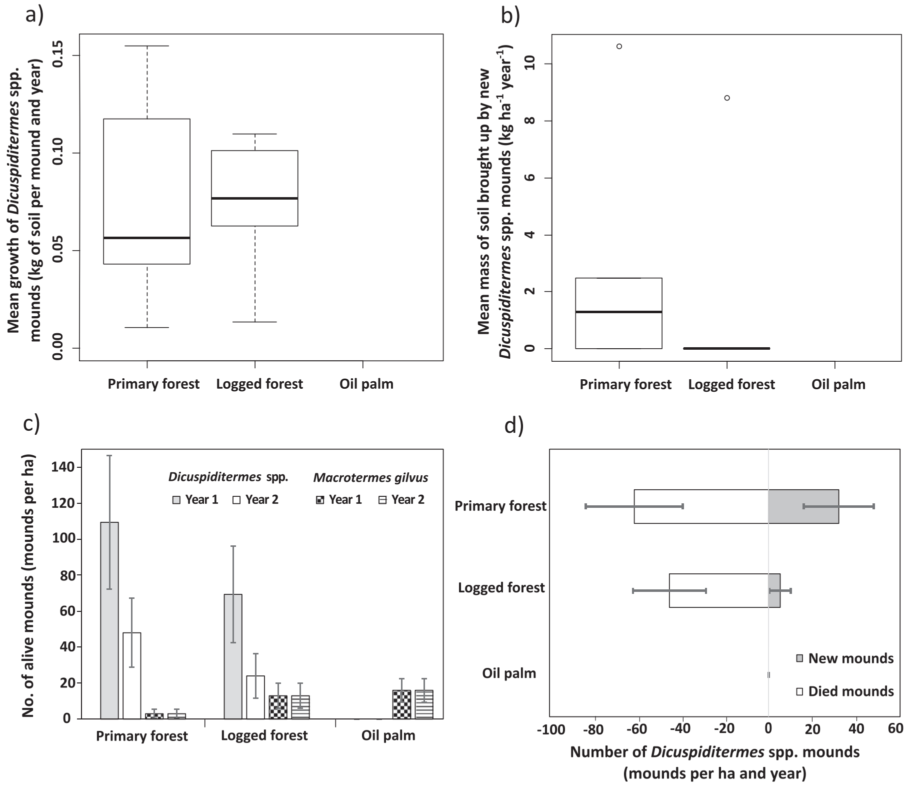

Fig. 6. Termite mound dynamics. Note that no growth or turnover of *M. gilvus* mounds was recorded during the one-year study period hence all such data presented here relate only to *Dicuspiditermes* spp. mounds. (a) The growth of *Dicuspiditermes* spp. termite mounds across different land uses measured over a one-year period. (b) The mass of soil brought up to the surface by newly emerged *Dicuspiditermes* spp. mounds. 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 open points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles. Note that the absence of the upper whisker for primary forest is because the 75th percentile is the same value as the maximum value in the data, once the upper outlier is excluded. (c) Termite mound densities and relative changes over a one year period measured on 25 m × 25 m plots. (d) Number of recently dead and newly created *Dicuspiditermes* spp. mounds on 25 m × 25 m plots after one year.

small spatial and temporal scales.

4.1. Termites as a dominant generators of standing bioturbated soil

Most of the standing bioturbated soil was produced by the mound-building activity of termites, with a single termite species, *Macrotermes gilvus*, dominating in the disturbed habitats. The second most important bioturbator in primary forest and logged forest was the soil-feeding termites *Dicuspiditermes* spp., which build phallic-shaped mounds from organic matter-rich soil. This finding supports a long-standing claim, that termite mounds trap significant amounts of soil (e.g. Dangerfield et al., 1998; Tilahun et al., 2012), although such measurements necessarily neglect the bioturbation taking place in underground mound spaces for these species and also all bioturbation performed by strictly hypogeic termites. Additionally, the aboveground mounds of *M. gilvus* are made of sand/silt and clay soil and have a thick outer wall. Hence they had proportionally higher bulk density (1.66 g cm^3) than the lighter mound material of *Dicuspiditermes* spp. (0.53 g cm^3), with more hollow spaces represented by chambers and tunnels. *Dicuspiditermes* spp. were absent or rare in oil palm plantation (with only one dead nest found), probably due to high temperature, low humidity and patchy food resources.

4.2. Earthworms as a dominant driver of bioturbation rate

Our results highlight the importance of termites for standing bioturbated soil in this system, and that the density of mound material (not only the volume of the mound) should be taken in account during such comparisons. The bioturbation rate (on a small scale) however, was mainly driven by earthworms (Oligochaeta), contributing 63–99% of the total bioturbation across all habitats through production of small soil casts (details of other bioturbator groups are given in Supplementary material 3). Note however, that this does not reflect the bioturbation of the whole earthworm community, but probably only the activity of anecic (mainly vertically moving) earthworms (Lamandé et al., 2003; Whalen et al., 2004). Earthworms generated the greatest proportion of small-scale bioturbation in all three habitats, and were the only small-scale bioturbator in logged forest. This shows the importance of earthworms for maintaining small-scale bioturbation rate over short time periods when other organisms are absent. This is especially important because of the ecosystem services earthworms are known to provide: facilitation of water and gas transport, incorporation of litter into the soil, and breaking down soil organic matter, with impacts on vegetation dynamics and diversity (Jouquet et al., 2006).

4.3. Variability in standing bioturbated soil across habitats

The lack of difference between habitats in standing bioturbated soil probably relates to increases in the creation of aboveground soil structures by termites, which balances the decreases in the activity of other bioturbator groups. An additional factor is the high variability in these measures among plots, reflecting spatial patchiness. Indeed, the standing bioturbated soil was mainly generated by termites in all three habitats, although *M. gilvus* was not a dominant species in primary forest, in contrast to logged forest and oil palm plantation (Fig. 4a; Supplementary material 4). However, the two *Dicuspiditermes* termite species, combined with a diverse range of other bioturbating animals, generated similar levels of standing bioturbated soil in primary forest compared to logged forest and oil palm plantation. Compared to primary forest, the amount of soil brought up by *M. gilvus* was higher in logged forest and highest in oil palm plantation, where it accounted for the majority of total standing bioturbated soil (see above). In oil palm, *M. gilvus* was able to compensate for the amount of standing bioturbated soil in logged and primary forest attributable to other bioturbators. It seems that *M. gilvus* replaces other termites in more degraded habitats and becomes the main species producing long-lived above ground soil structures. The dominance of *M. gilvus* in disturbed habitats is explicable in terms of it being a fungus-growing and wood/litter-feeding species and hence, in contrast to most rainforest termite species, it can tolerate the high temperatures and low air humidity typical of disturbed areas (Bandeira et al., 2003; Eggleton and Tayasu, 2001; Hassall et al., 2006; Jones et al., 2003; Luke et al., 2014). A similar increase in the relative importance of *M. gilvus* in oil palm plantation as compared with primary and logged forest has been observed in terms of litter decomposition (Foster et al., 2011).

4.4. Termite mound dynamics

In primary and logged forest greater numbers of mounds died than were created during the year, which might be due to the hot, dry El Niño conditions. However, this effect was more extreme in logged forest. There were almost six times fewer new *Dicuspiditermes* spp. mounds in logged forest than in primary forest, but only 1.4 times fewer newly dead mounds. Taken together, there were 1.6 times more living mounds in primary forest, with fewer mounds dying and more mounds created, compared with logged forest (Fig. 6c). This might be due to disturbance from past logging activities, which could physically damage mounds. The mounds in logged forests could also suffer from a higher frequency of treefalls (we observed this on at least two plots), from soil compaction caused by logging vehicles (Edwards et al., 2014), and possibly by more extreme impacts of the two-year El Niño event (NOAA, 2019) in more degraded forest. The higher number of newly-created mounds in primary forest could result from the higher overall mound densities in this habitat and hence greater production of alates. We did not record any growth or turnover of *M. gilvus* mounds in any habitat. Furthermore, our measurement did not record any termite sheeting in this species (temporary protective soil layers build over food items and passageways) which is known to contribute greatly to overall termite bioturbation (Kooyman and Onck, 1987; Lee and Wood, 1971). This means that either mound growth is very slow for *M. gilvus*, or that termites favour more humid conditions for mound and sheetings building than those experienced during El Niño (Woon et al., 2019). However, when compared to *Dicuspiditermes* spp., there were disproportionally fewer *M. gilvus* mounds in all the habitats, and mound dynamics are expected to be slower. Additionally, *M. gilvus* mounds decompose slowly (Coventry et al., 1988), as the mound material is very dense. Hence, we would expect that the less dense *Dicuspiditermes* spp. mounds should decompose faster than those of *M. gilvus*, especially in humid conditions (supported by personal observation of Jiri Tuma).

4.5. Bioturbation rate and its relation to mass of standing bioturbated soil

The mean values of small-scale bioturbation rate were double or even triple those of large-scale standing bioturbated soil, when extrapolating to annual values in forested habitats, but not in oil palm (Supplementary material 5). This emphasizes the potential importance of bioturbators at small temporal and spatial scales. However, these values were extrapolated from a five-day observation period, and so we would advise caution in interpreting these results. We would recommend future work be conducted with repeated measurements of these bioturbation rates throughout the year (details of the methods and discussion on limitations are available in the Supplementary material 3). Despite this limitation, our measurements of growth of termite mounds indicates such a low rate of bioturbation generated by this group ($42.7\,\mathrm{kg\,ha^{-1}\,year^{-1}}$in primary forest and $28.6\,\mathrm{kg\,ha^{-1}\,year^{-1}}$ in logged forest), that the annual termite bioturbation figure is still an order of magnitude less than even the five-day small-scale short term bioturbation rate (not multiplied up to annual time scale). Previous work has emphasized the importance of termites as apparent bioturbators in tropical ecosystems (Holt and Lepage, 2000; Seymour et al., 2014). However, our work shows that small-scale bioturbators such as worms and ants, previously thought to be important mainly in temperate and drier sub-tropical systems (Persson et al., 2007), can contribute greatly to tropical bioturbation, with probably more rapid breakdown of bioturbated structures and hence possible incorporation back into the soil profile (which is one reason why this has been poorly documented). However, more measurements are needed during wetter periods, since growth of termite mounds might increase after rains, because termites are generally more active in humid conditions (Dibog et al., 1998). This is important, because the balance between species that slowly produce longer-lived mounds (termites) and those that rapidly produce smaller short-lived structures (worms and ants) is affected by habitat change (Fig. 4a, this paper; Luke et al., 2014).

4.6. The relationship between diversity of bioturbators and its relation to bioturbation

Bioturbation is mediated by a more diverse community in less disturbed habitats, with a greater number of groups/species contributing similar amounts. Unexpectedly, in primary forest plots with higher bioturbator diversity, standing bioturbated soil was lower (Fig. 5). This is caused by termites bringing up, proportionally, the majority of soil in primary forest (note that the diversity index was calculated using proportions of soil brought up, rather than direct measures of abundances). Therefore, when there were fewer termite mounds in the area, the remaining bioturbators did not compensate for the bioturbation done by termites, despite the bioturbator diversity index being higher (because termites did not dominate). However, our method did not distinguish between different kinds of bioturbation qualitatively and the question remains whether the overall bioturbation caused by higher variety of bioturbators is more beneficial for the soil environment and nutrient cycling. There could also be some degree of competition for soil as a living space, or even in terms of soil nutrients, which would also explain our results, with termites outcompeting other bioturbating species.

4.7. Redundancy of bioturbators across habitats

It appears that the dominant bioturbator *M. gilvus* is able to maintain soil mounds in logged forest and to a greater extent in oil palm plantations. However, it remains unclear whether this species can balance the contribution of other bioturbators in the system in terms of nutrient redistribution and maintenance of soil quality. Because *M. gilvus* mounds are very dense clay structures, they are very long-lived, and their importance in terms of nutrient dynamics might not be as great as their imposing appearance suggests. The dominance of this species also means that aboveground bioturbation in oil palm plantations depends almost entirely on one species, which could make this converted habitat potentially vulnerable to species extinctions (Mack et al., 2000) and to loss of the ecosystem services provided by *M. gilvus*. However, such resilient bioturbating termite species may be vital for the initial recovery of disturbed habitats, for example by providing better soil hydrological functions (i.e. water infiltration), or decomposing dead plant matter (Dawes, 2010; Foster et al., 2011). In contrast, small-scale bioturbators like ants and earthworms still performed relatively well in plantations, highlighting their significance for contributing to total bioturbation in disturbed habitats. Logged forest represented an intermediate habitat. Some primary forest groups could still survive, for example efficient bioturbators such as soil-feeding termites, earthworms and cicadas, but there was also a higher density of *M. gilvus* mounds, keeping the standing bioturbated soil levels high. Hence, bioturbator redundancy remained high when the primary forest was logged, but not when the forest was converted to oil palm plantation.

5. Conclusion

Our work indicates that aboveground bioturbation in the tropics may be dominated by an important group of “hidden bioturbators”, whose small structures are rapidly broken down after construction, and hence whose importance has previously been underestimated. Although amounts standing of bioturbated soil and bioturbation rate did not differ between habitats, in oil palm plantation, the standing bioturbated soil was created almost exclusively by one species of termite – *Macrotermes gilvus*. Primary and logged forest, on the other hand, maintained a high diversity of bioturbators. This reliance on a single bioturbator species in oil palm plantation over larger scales is of concern because it leaves this important ecosystem process vulnerable to future extinction events.

Data availability

Full datasets for all analyses in this paper are available at https://doi.org/10.5281/zenodo.3344504.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2019.07.002.

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Supplementary material 1

SAFE project sites at which the bioturbation survey plots were located, and their GPS coordinates.

Sampled sites	GPS coordinates	Mean altitude (m a.s.l.)
OG2	4.747133 - 116.972182	279
B	4.729231 - 117.616939	428
F	4.699606 - 117.546201	445
LFE	4.740113 - 117.589789	494
OP1	4.656591 - 117.453272	405
OP2	4.647143 - 117.441597	471
OP3	4.640273 - 117.453208	306

Supplementary material 2

Field bioturbation assessment protocol

This guide aims to provide a straightforward method for estimation of terrestrial bioturbation activity performed by various soil organisms from appearance of soil above ground level. It can be used to compare the relative importance of various macro- and megafauna performing bioturbation, and to compare bioturbation values between habitats or biomes. The protocol described here is implemented in Tuma et al. (In preparation).

Methods:

1. Plot establishment

Individual sampling plots were of dimensions 25 m x 25 m. Preliminary observations indicated that this size is small enough for effectively surveying all activity within each plot, but sufficiently large for recording the potentially clumped distribution of particular structures created by bioturbation (e.g. cicada turrets). The number of replicates of these plots will depend on the particular research question, the expected magnitude of effect sizes, and the expected within habitat heterogeneity. The replicates should be randomly distributed within the sampled habitat, unless the aim is to sample a specific place in the area of interest. Before starting the survey, the plot should be marked using tape or string on its edges and corners. Two different kinds of surveys are then carried out within each plot. One for measuring larger structures over the entire 25 m x 25 m plot (3. Standing bioturbated soil), and a second for measuring creation of smaller structures in a 1 m by 1 m sub-plot (4. Bioturbation rate).

2. Types of soil structures

In advance of the whole procedure, it is recommended to make several trial surveys. During these, one can learn to recognise the structures present in the habitat. The soil casts can be dissected to see the internal organisation and in some cases to find and sample the animal creating it, in order to become familiar with types of structures. In most cases the bioturbator can then be placed in a broad taxonomic/functional category solely from the appearance of the cast. The variability between and within groups of bioturbators from our field sites in Sabah (Malaysia) is depicted in Figures 1 - 4.

For example, earthworms typically produce shaped casts, compressed, smooth soil structures, roughly mirroring the shape and the size of the earthworm itself. The casts of large tropical earthworms could be mistaken for cicada emergence turrets. However, cicada turrets have a large cavity in the middle of the cast. Ant mounds are, in contrast, formed by loose grains formed in variously shaped heaps and mounds. For ants it is also possible to use a bait dropped near the mound structure (e.g. crushed biscuit) and observe whether the resulting foraging trail leads to the mound. A voucher sample of the ant species can then be obtained. These examples demonstrate the importance of observing the structures, learning their most common shapes, and trialling the procedure beforehand.

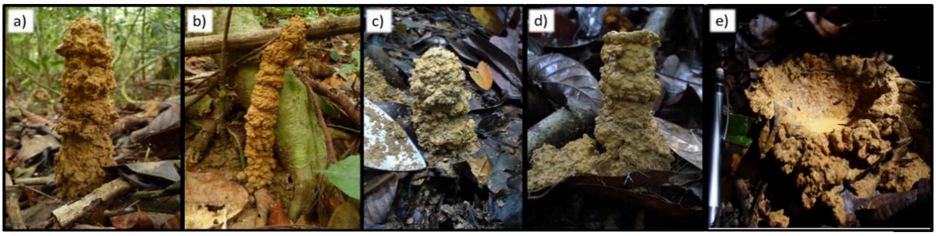

Figure 1. Diversity of cicada turrets around emergence holes. a) – c): different sizes and shapes of capped turrets, d) fresh, uncapped turret, e) a turret damaged by rain, but still recognizable.

Figure 2. Diversity of earthworm casts. a)-c) different shapes of yellow, clay-rich casts, extruded by large earthworms. d) large, red/brown casts, created by large earthworms ingesting clay which is rich in iron. e) smaller, dark-brown/black casts produced by small earthworms living in upper soil layers rich in organic matter.

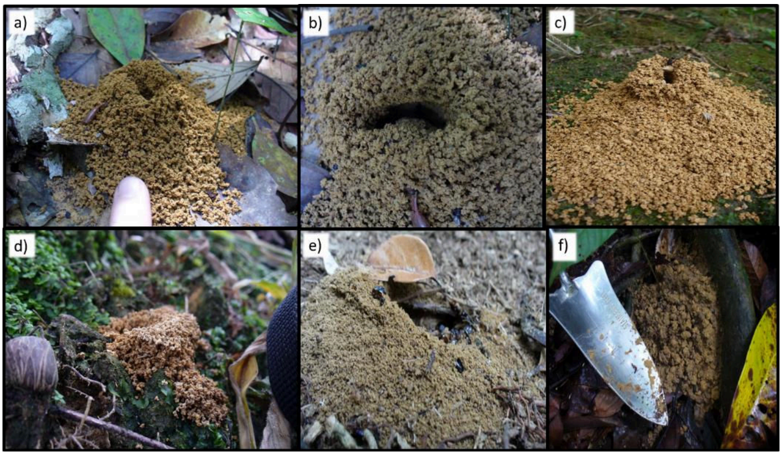

Figure 3. Diversity of ant nests. a) excavated soil around the nest entrance of *Diacamma intricatum*. b) typical U-shaped, slit-like entrance of a *Diacamma intricatum* nest. c) nest entrance of *Odontoponera transversa*. d) small heap of soil around another *Odontoponera transversa* nest. e) soil wall with food remnants around nest entrance of *Pheidole* sp. f) a structure superficially like an ant nest, but classed as 'burrow' created by unidentified digging.

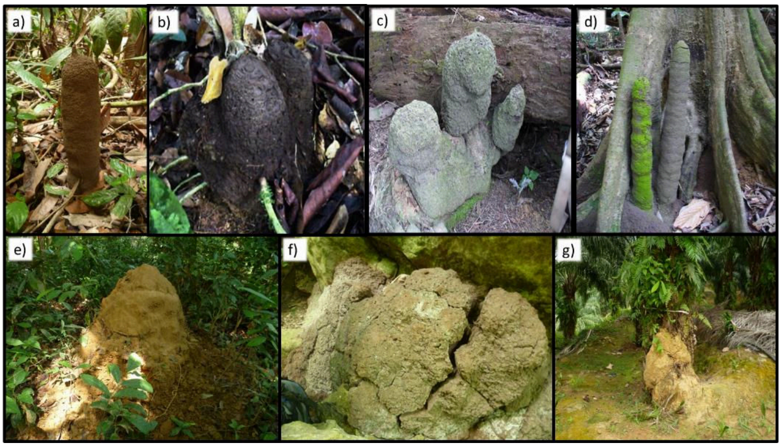

Figure 4. Diversity of termite mounds. a) *Dicuspiditermes minutus* typical mound. b) *D. nemorosus* typical mound. c) *Dicuspiditermes minutus* in oil palm plantation d) *Dicuspiditermes* sp. in logged forest (SAFE site 'LFE' plot). e) *Macrotermes gilvus* mound in primary forest. f*) M. gilvus* in logged forest – a mound made from soil rich in iron (SAFE site 'F'). g) *M. gilvus* mound in oil palm plantation attached to an oil palm tree.

3. Standing bioturbated soil (large-scale)

Searching for the soil structures created by bioturbation should be done in one or two-meter strips, depending on undergrowth density and terrain complexity, starting from a corner of the 25 m by 25 m plot. A good approach is to mark the strips that have already been surveyed by attaching tape to the vegetation, especially in dense vegetation.

It is unmanageable to collect all of the smaller soil structures on the soil surface as they are covered by litter, too small to spot, or difficult to distinguish from soil between dead leaves that were not necessarily generated by bioturbators. Therefore it is useful to set a minimum threshold for dimensions (mainly height) of the soil structures to be collected. In our study, we set the threshold to 6 cm. This excluded mainly epigeic and small anecic earthworms, some ant mounds and other small burrowers falling below this threshold. However, these were recorded in 1 m x 1 m plots (see section 4 below).

The soil structures should be collected in separate plastic bags, each type into an individual bag for each plot. It is recommended to use a small trowel for scooping the soil. The whole structure above the soil surface should be collected, including the soil stacked between living or dead leaves, and the soil that has been splashed or scattered around, but clearly originated in the focal soil structure. Usually, it is possible to distinguish this soil from the unchanged soil as the bioturbated soil is often of different colour and texture. The individual samples of collected soil should be oven dried at 80°C for 48 hours and weighed.

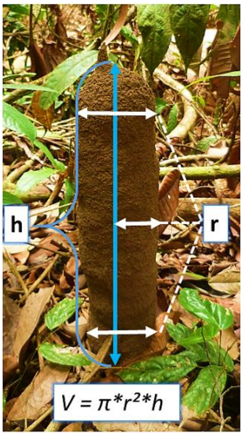

Figure 5. Measurement procedure on *Dicuspiditermes minutus* mound in order to calculate the total volume of aboveground soil trapped in the mound.

Figure 6. Reference soil core taken from *Dicuspiditermes minutus* mound to obtain specific volumetric weight for estimation of total mound weight.

Larger soil structures, represented mainly by termite mounds, cannot be collected easily. In such cases, the dimensions of the mound are measured and the weight calculated through a “specific volumetric weight” approximation. First, the dimensions of the mounds in the field are measured. This depends on the most usual shape of the mounds, as it needs to be decided what geometric object will be used to estimate weight of each mound. For the termite *Macrotermes gilvus*, we measured the height and the diameter of the mound and applied the formula for cone volume calculation: $V = \pi * r^2 * h / 3$ (A). Then the density of the mound material was measured by inserting a sampling tube with known dimensions into the mound body thus obtaining a known volume of the mound substrate (Fig. 6). We sampled three mounds for each termite species across all habitats and took an average value for volumetric weight. These voucher samples are then oven-dried at 80°C for 48 hours and weighed. We then calculated the volume of the tube for the specific volumetric weight sampling (B) and divided it by the weight of the dry soil in this tube from *M. gilvus* voucher mound (C). Then we calculated the estimated total weight (D) of the sampled mound as $D = A * C / B$ (g). In case of the termite *Dicuspiditermes* spp., the mound volume was measured in the same way, but using an equation for the volume of cylinder, instead of a cone (Fig. 5). Note that the method described in this section estimates total standing bioturbated soil over a large area, rather than measuring the rate of soil turnover.

4. Bioturbation rate (small scale)

The second type of measurement considers the bioturbation done by smaller animals, which are not included in the survey of the 25 x 25 m plot. This method also allows measurement of the rate of bioturbation (as distinct from the standing amount of bioturbated soil measured in the larger plots). For these smaller animals, the plot dimensions are 1 m x 1 m. Two 1 m^2 plots should be established at the edge of the 25 m x 25 m plot, but outside of it, in order to record small and large scale bioturbation in similar microhabitat conditions (Fig. 7). These two plots are placed avoiding any of the large structures that would have been surveyed in the 25 m x 25 m plot survey. Again, the perimeter should be marked using colourful string or tape. Before starting surveys, it is necessary to remove all leaf litter and dead plant material from the plot as well as all the soil structures formed by previous bioturbation (see Fig. 8). These are mostly small coprolites (typically of brown/black colour), smaller ant mounds (e.g. from *Pheidole* spp., *Carebara* spp., *Diacamma* spp.), small heaps of soil created by beetle larvae, solitary wasps and other animals. The aim of this clearing is to remove any soil structures that could later be misidentified as new bioturbation on this plot. In certain cases it is difficult to judge if a particular structure has been created by bioturbation, or sometimes it is be too demanding to remove it without severely destroying the plot. In such cases, these structures are marked with colourful toothpicks in order to avoid counting them later as newly emerged structures. This completes the first phase of the survey.

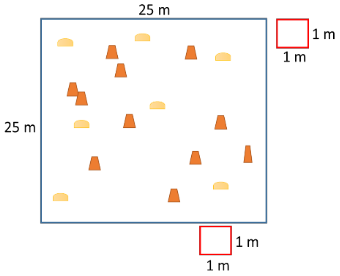

Figure 7. The layout of the bioturbation survey plots in the field. The blue square represents 25 x 25 m plot for surveying the standing bioturbated soil. The two red squares represents 1 x 1 m plots for survey of bioturbation rate done by smaller organisms.

The second phase involves re-visiting the plot after five days. This is long enough for new structures to emerge, but also not excessively long for the effect of the rain to wash away the bioturbated material. Rain is the main limiting factor in this kind of measurement, as it restricts the maximal time between the setup and re-visit of the plot.

The survey phase is based on the same principle as for the larger plot described above. Although the searching has to be done at a smaller scale in order to record even minimal bioturbation. The structures were collected in separate bags and their animal-group identity recorded. The soil was then dried and weighed in the same way as for the large-scale method.

The bioturbation rate values obtained by the small-scale method represent temporal information about soil reworking. However, this is not true for the measurement of the large-scale bioturbation. We therefore propose that for future projects, the large and small-scale surveys are performed repeatedly through the year, or at least, the surveys repeated in the main seasonal periods, in order to record the changes in bioturbation in relation to the main environmental conditions (e.g. dry and wet season). The impact of environmental conditions on bioturbation could then be assessed, and total yearly bioturbation could be more accurately calculated.

Figure 8. Established 1 m^2 plot for small-scale bioturbation rate survey. Note that the plot is marked with bright coloured string and the litter and pre-existing bioturbated structures are removed.

Termite mound dynamics

5. Termite mound growth

To obtain information on relative growth of termite mounds we used plastic sticks with measuring scales, which were pushed horizontally and vertically in the body of the mound (Fig. 9: a). The sticks should be firm and pointed as the mound material can be very dense and difficult to penetrate. It is also easy to damage the mound, so inserting the sticks has to be done carefully. Opening the mound during this procedure can provoke the termites to cover not only the opening, but also the scale itself. The sticks should be long enough and extending above the mound surface to be still visible after one year of mound growth. The scales (cm) on the sticks should be carved/incised into the scale body as the field conditions can otherwise obscure scale marks. The position of the scales have to be recorded and photographed for future reference. A variety of mound sizes should be chosen for the mound growth measurement, as smaller or younger mounds can grow faster than older ones (Jiri Tuma, personal observation). After one year, the mounds with the measuring sticks should be checked and the level of mound material covering the scale should be recorded (Fig. 9: b). By this method, the initial size and the relative change of mound size can be determined, and hence the amount of up-lifted material incorporated into the mound structure can be calculated using cone/cylinder formula and specific volumetric weight of the mound material (calculation described in section 3. Standing bioturbated soil, see above).

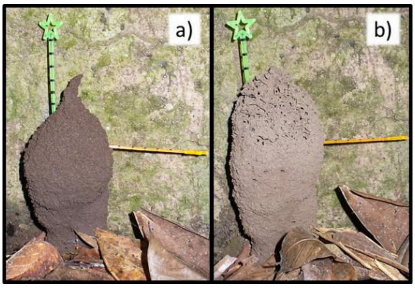

Figure 9. a) Sticks with measuring scales inserted in the body of a *Dicuspiditermes* spp. termite mound. b) The growth of the mound after one year – new soil mass covers the measuring scales. Note, that the vertical scale would not have been high enough in this case had the mound not died, as small mounds have the potential to completely overgrown the scale. Note broken appearance of the mound after one year, due to death of the colony.

6. Termite mound turnover

This assessment is based on section 3, in which all the standing termite mounds in the 25 m x 25 m plots were measured. To obtain the mound turnover in these plots, all the standing mounds should be marked with firm stick and a colourful flag with a mound specific number, or customized labelling. Additionally, the position of the individual live mounds in the plot should be recorded as well as the prominent features of the plot (logs, big trees etc.) for better navigation within the plot. After one year, the plot should be re-surveyed. The newly emerged mounds should be recorded and the state of the labelled mounds checked. If the mound fell to the ground, or is abandoned and in a bad state, the decomposition processes begins and it can be classified as dead in case of *Dicuspiditermes* spp. In case of large and stable mounds, as *Macrotermes gilvus*, the state of the mound should be inspected in detail. The mound has to be opened to confirm the presence of living individuals inside, or for the state of the symbiotic fungus. By this method, the number of surviving, newly-emerged and newly-dead mounds, in the plot over the course of one year can be obtained and thus the turnover rate of termite mounds can be calculated. Note that this method will not detect any mounds that have appeared and died within the course of one year.

5. Concluding remarks

By combining all these approaches, it is possible to obtain a representative picture of bioturbation in terrestrial habitats. It is also possible to calculate the comparative contribution of different macro and mega faunal groups to the overall bioturbation. However, a user of this guide should be aware of the limitations of this method and take them in account when interpreting the results. With the method we developed, we obtained a “snapshot” of aboveground bioturbation present. Principally, we did not aim to evaluate the bioturbation activity of any particular animal in detail apart from for termite mound dynamics. This method also necessarily underestimates total bioturbation values in following aspects:

1. The method measures only aboveground soil presence and it is known that underground soil mixing can reach significant, but mostly unknown share of the overall bioturbation (Hasiotis and Halfen, 2010; Minter et al., 2012).

2. It omits very small bioturbation done by certain meso- and micro-fauna, such as small earthworms and Enchytraeidae, dipterian larvae, nematodes etc.

3. In order to obtain a complete picture of bioturbation in certain habitat, multiple measurements during the year, both of standing and of mixing rate would have to be taken to record the creation and decay of more temporal structures (such as cicada turrets and earthworm casts). Nevertheless, we believe that our combined method for measuring terrestrial bioturbation can be of use when the habitats are compared within the same region and over the same time frame.

A simplified outline of the procedure for bioturbation estimation:

1. Preliminary identification of structures done by bioturbation and their creators present in studied system.

2. Establishing the survey plot for large-scale standing bioturbated soil measurement.

3. Large-scale survey. Collection of bioturbated soil structures and separation of them according to the animal group.

4. Sampling of the larger (non-collectable) structures for ‘specific volumetric weight’ and measuring the dimensions of these structures.

5. Establishing the plots for small-scale bioturbation rate survey. Marking the plot, removing the litter layer and existing bioturbation structures, marking larger, bioturbation-like structures for future reference.

6. After a period of five days, surveying the plots for small-scale bioturbation activity, identification, collection and separation of the collected bioturbated structures into bioturbator groups.

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Supplementary material 3

A more detailed explanation of the results relating to different soil fauna contributing to bioturbation in our system. Note that references to figures reference to the main manuscript.

Apart from termites, the other animal groups contributing to standing bioturbated soil were cicadas, earthworms, other unidentified bioturbators and ants. **Cicada** larvae build a soil turret from clay around the emergence holes in their last year of underground life (Béguin, 2017). They contributed to total bioturbation in our large scale assessment by between 0 – 2.7 %. The highest mean weight of soil represented by cicada turrets was found in logged forest, followed by primary forest and there was none found in oil palm plantation. This situation probably reflects the availability of food resources and environmental conditions cicadas require in the assessed habitats, as cicada larvae rely on young saplings and trees (Chiavacci et al., 2014). There are enough saplings and low vegetation available in forested habitats but not in the plantation. Additionally, sapling density can be connected with sun-affected spots along with continuous treefall gap dynamics (Arihafa and Mack, 2013). The logged forest has a more open canopy due to physical damage from the removal of large trees, skid trails and logging roads (Douglas, 1999). Cicadas prefer these areas, as there is significant re-growth triggered by better light conditions (Chiavacci et al., 2014). Finally, the absence of cicada turrets in intensively managed oil palm plantations could be caused by the absence of any tree saplings and other vegetation on which cicadas could feed.

Earthworms (Oligochaeta) are widespread bioturbators in humid habitats that produce casts. Their contribution to total bioturbation in our standing bioturbated soil assessment was: 0–2.26 %, but 63 – 99 % at for small scales bioturbation rate. The mean weight of collected casts for standing bioturbated soil was highest in primary forest and comparable with logged forest values. There was no bioturbation caused by large earthworms in oil palm plantations measurable by our method. Note, that only the larger coprolites (> 6 cm in height) were collected during standing bioturbated soil assessment. Tropical earthworms in general depend on litter quality, organic matter content in the soil, humidity, and seasonality (Dey and Chaudhuri, 2014), but they also vary in species composition, depending on land use (Guéi and Tondoh, 2012). The lack of large earthworm activity in oil palm can be explained by the very poor litter layer, as this condition directly results in low input of organic matter into the soil and an absence of humid microclimate near the soil surface (Turner and Foster, 2009; Brühl and Eltz, 2010). However, we found a number of smaller earthworm casts in oil palm plantation the bioturbation rate assessment, so there must be another factor negatively affecting large earthworms in oil palm habitats.

Ants are known as major bioturbators in a number of habitats (Mandel and Sorenson, 1982; Carlson and Whiteford, 1991; Nkem et al., 2000; Persson et al., 2007; Evans et al., 2011). Nonetheless, their contribution to total bioturbation in our standing bioturbated soil assessment was the least: 0 - 0.5 % and 0 – 26.2 % for small scale bioturbation rate. We did not see any tall soil ant mounds with complex internal structure. Most of the soil excavated by ants and deposited on the soil surface appeared to be just ‘soil dumps’, rather than true functional structures that are created in some places e.g. in the temperate zone (*Formica, Lasius*). Only the slit-shaped and turret-like entrance of *Diacamma intricatum* and soil walls around nest entrances of *Carebara* sp. and *Pheidole* sp. seemed to serve as protection of the nest entrance hole. In the contrast to this, the soil scattered around *Odontoponera transversa* nest entrance in oil palm was loose and seemed to be only temporary, being easily washed away by rain. Hence, ants appear to be important bioturbators at small scales, with unexplored bioturbation potential as they often do not form permanent aboveground mounds.

There was a significant bioturbation caused by animals that we were not able to identify (**Other** category). Generally, the bioturbated soil was found in heaps, mounds or placed without order, but was evidently excavated. Based on our experience and on animals present in these habitats, we speculate that this bioturbation was generated by rodents, lizards (e.g. Agamidae), snakes, myriapods, solitary wasps, beetles and other digging insects, including their larval stages. The contribution to standing bioturbated soil of this group was 0 – 3.3 %, and 0 – 11% for small scale bioturbation rate. Bioturbators in this category performed well in forested habitats, but not in oil palm plantations. This could be attributed to lower overall animal diversity in oil palm (Fitzherbert et al., 2008; Turner et al., 2011) in the standing bioturbated soil assessment. This trend is supported also by our results concerning bioturbator diversity (Fig. 3). Hence, there is decreased probability that a given animal living in oil palm plantations would act as an efficient bioturbator. On the other hand, oil palm plantations are known for cases of hyper-abundances of particular species (Senior et al., 2013), so there is a theoretical potential that a hyper-abundant, or even invasive species would be an efficient bioturbator. This raises the question, if we could consider the termite *M. gilvus* termite as a disturbed habitat species but also an efficient bioturbator in oil palm plantations.

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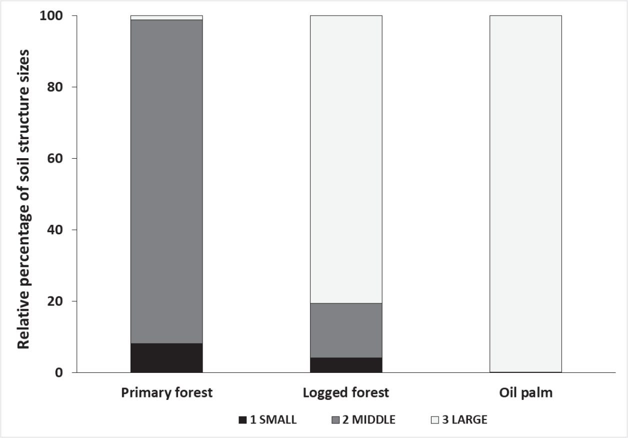
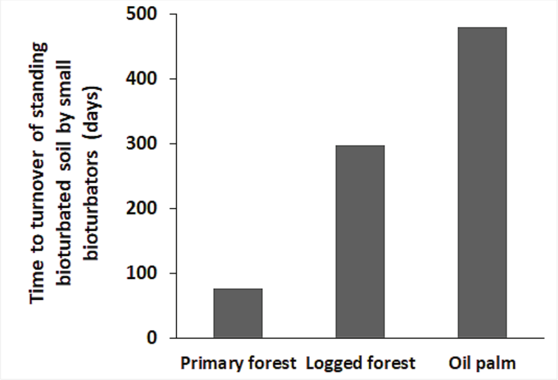
Supplementary material 4



Proportional representation of structure sizes across different land uses measured on large scale (standing bioturbated soil). The categories were established as: SMALL – all soil bioturbated structures above six centimetres from soil surface belonging to 'ANTS', 'CICADAS', 'WORMS' and 'OTHER' category. MIDDLE – *Dicuspiditermes* spp. mounds and LARGE – *Macrotermes gilvus* mounds.

Supplementary material 5



The potential of small bioturbating organisms (bioturbation rate) for turnover of all aboveground soil structures created by large-scale bioturbators (standing bioturbated soil). The minimal time to the total turnover of standing bioturbated soil by small-scale bioturbators was calculated as the mean mass of standing bioturbated soil divided by one-day mean of bioturbative performance of small scale bioturbators (days). Because some plots had either zero standing soil or a rate of zero, we were only able to make these calculations for values summed across all plots in each habitat, and hence no statistical comparisons were possible.

Supplementary material 6

Standard error of mean values (SEM) of standing bioturbated soil generated by social insects, measured on large scale (Fig.4a).

Ant/termite species	**Primary forest**	**Logged forest**	**Oil palm**
Macrotermes gilvus	0.373	34.504	43.971
Dicuspiditermes minutus	1.874	8.787	0.040
Dicuspiditermes nemorosus	8.971	0.000	0.000
Odontomachus rixosus	0.003	0.000	0.000
Odontoponera transversa	0.011	0.023	0.002
Non ID ant	0.011	0.000	0.002
***Crematogaster* sp.**	0.004	0.000	0.000
Dinomyrmex gigas	0.052	0.000	0.000
Mesoponera rubra	0.104	0.000	0.000
Anillomyrma tridens	0.000	0.004	0.000
Diacamma intricatum	0.000	0.010	0.000
Leptogenys processionalis	0.000	0.164	0.000
***Myrmecina* sp.**	0.000	0.000	0.002
Lophomyrmex bedoti	0.000	0.000	0.003
***Tetramorium* sp.**	0.000	0.000	0.012

Standard error of mean values (SEM) of bioturbation rate measured at small scale (Fig.3b).

Category	**Primary forest**	**Logged forest**	**Oil palm**
ANTS	211.5	0.0	185.6
WORMS	1041.3	1125.8	624.3
OTHER	0.0	0.0	161.0

THESIS SUMMARY

Thesis Summary

Human-caused habitat change threatens biodiversity and ecosystem stability worldwide (McGarigal et al., 2005; Sala et al., 2000). Pristine habitats are being converted to production land at increasing speed (FAO, 2017). These land use changes are a result of the demands of a growing human population. However, they adversely affect environmental conditions, biodiversity, ecosystem functions and services provided by species and therefore stability of impacted ecosystems (Bommarco et al., 2013; Dobson et al., 2006). Tropical forests are under imminent threat from conversion to agricultural land. This is of concern because a large portion of world's biodiversity is found in the tropics, centred on a number of important biodiversity hotspots (Myers et al., 2000). Logging and conversion of forest, mainly to agricultural land such as pastures for cattle or for various crops such as soya or oil palm, are the main drivers of tropical habitat loss (Kissinger et al., 2012).

The demand for palm oil products is rising, due to diversification of the oil's use, high profitability and relatively low price (Henderson and Osborne, 2000). Because of this demand, more land will be needed for establishing new plantations, which will lead to clearance of primary or logged forests at increasing rates. This is a major contributor to large-scale deforestation in South-East Asia, which has the highest rate of forest clearance of any tropical region. It is predicted that by 2100, there will remain only one quarter of the original forests in SE Asia (Sodhi et al., 2004). In Malaysia, logged forests are typically considered as "degraded" habitats, assigned as areas suitable for cultivation by local authorities (Casson, 2000). However, selectively logged forests still preserve relatively high biodiversity and show fast recovery of vital ecological functions (Douglas, 1999; Fitzherbert et al., 2008).

In this thesis I target soil-dwelling tropical ants and termites because of their high biomass, diversity and the numerous ways that they affect their environment. Ants affect both soil processes (Frouz and Jílková, 2008) and seed dispersal (Lengyel et al., 2009). They are also important scavengers, particularly in the tropics where they can remove up to 61% of the food items on the forest floor (Griffiths et al., 2018; Tan and Corlett, 2012). Ants are significant predators of a range of soil invertebrates, and can therefore shape entire soil invertebrate communities (Kaspari et al., 2011). Soil termites likewise provide a range of ecosystem services, but their main function differs from that of ants. Termites are important decomposers of organic matter including dead wood, leaf litter, bark, lichens, straw and mammalian dung (Bignell and Eggleton, 2000; Noble et al., 2009). For example, termites were responsible for decomposition of 24% of annual litter production and 60% of annual wood fall on savannah in Nigeria (Collins, 1981). Termites also affect the formation, heterogeneity and fertility of soils by accumulating nutrients in their nests and by bioturbation, i.e. mound building and sheeting activity (Brauman, 2000; Harit et al., 2017).

Ants and termites are considered as suitable indicator groups for understanding habitat change (Brown Jr, 1991). For example, ants have been used as an indicator group for rainforest quality (Lawes et al., 2017). Thus, in this thesis, I focus on changes in communities of soil ants and termites along tropical habitat degradation gradient and on the ecosystem functions they affect.

Main findings and conclusions

In **first chapter** I conduct a literature review of the importance of ants and termites for ecosystem processes and food webs, focusing on interactions between ants and termites and how this interaction can affect ecosystem functioning. I propose that ant predation on termites is the most important, most widespread, and most studied type of interaction between these two groups. This predation affects populations of termites and as a consequence, it can limit the decomposition rate of dead plant organic matter. I also highlight the importance of opportunistic predation from ants, in addition to the relatively well-known termite specialist predators. The role of these opportunists in regulating termite populations might be underemphasized, in comparison to specialist predators. I review the most useful methods for exploring ant-termite predation and how these can be applied to reveal the consequences of this interaction for ecological processes. I propose that a combination of methods, including DNA barcoding, exclusion experiments and field observations, are necessary for assessing the effect of this interaction on entire ecosystems.

In the **second chapter** I present new field data on the distribution of tropical soil-dwelling ant and termite communities in differently degraded habitats and explore the predation of ants on termites using DNA barcoding of ants. The abundance of ants was highest in logged forest while termite abundance showed no clear differences between habitats. The species richness and Shannon diversity index of ants was comparable between primary and logged forest but was much lower in oil palm plantation. Termites had more species in the logged forest than in primary or oil palm plantation. These results emphasize the value of the logged forest for supporting species diversity while oil palm plantations showed a lower number of species and were susceptible to invasive species. Furthermore, oil palm was predominantly occupied by the invasive ant *Anoplolepis gracilipes*, and there was only one termite species - *Macrotermes gilvus*. In addition, randomly selected ant individuals (from 12 genera) from soil pits were analysed for termite DNA in their bodies using DNA barcoding. I found that from 124 ant individuals, 32% contained termite DNA and this percentage was similar across habitats. However, termite predation rates differed across ant genera. This means that overall ant predation on termites is similar even in the most degraded habitats. Hence I speculate that the predatory pressure of ants on termite populations and the influence of this pressure on the ecosystem functions termites provide is resilient to habitat change.

Since I found that ant and termite communities vary across the gradient of anthropogenic change I predicted that this would affect ecosystem processes. In the **third chapter**, I focus on the process of bioturbation: the turnover of soil material by soil-dwelling organisms, which is one of the most important ecosystem functions soil-dwelling ants and termites provide. I developed a protocol to identify the main bioturbators and estimate aboveground animal-driven bioturbation. I assess how bioturbation rates and amount of standing bioturbated soil differs across a habitat degradation gradient in Borneo. I found that termites were responsible for 97.0% of standing bioturbated soil across all habitats, while short-term small-scale bioturbation was mainly driven by earthworms (87.3%). Furthermore, the standing bioturbated soil in oil palm was almost exclusively generated by a single species of termite – *Macrotermes gilvus*, while bioturbation in primary forest and logged forest was maintained by a high diversity of animal groups. From my findings in the second chapter, this termite species is not the only one found in soil in disturbed habitats. However, it becomes more important in maintaining vital ecosystem processes with increasing disturbance. Conversely, the reliance on a single bioturbator species in oil palm plantation over larger scales is of concern because it leaves this important ecosystem process vulnerable to future extinction events.

Significance of the thesis and future perspectives

Taken together, my work emphasizes the role of soil-dwelling ants and termites and their interaction in mediating essential ecosystem processes in Borneo. I show the decline of ant and termite species diversity and also functional diversity in oil palm plantations compared to primary and logged forests. Logged forest was still a valuable habitat maintaining not only ant and termite species diversity but also bioturbation levels and diversity of bioturbator groups. These findings thus support the policy of maintaining logged forests for their high conservation value. This also raises concerns for the future sustainability of expanding oil palm plantations, especially in the face of current global change, along with anticipated species extinctions and potential loss of the vital ecosystem processes that ants and termites provide.

The next step is to identify ant species capable of supressing termite populations. This is important both because this suppression will affect the ecosystem processes termites provide, and because suppression could lower the economic damage termites cause on buildings and crops. This is potentially of importance when dealing with invasive economically important termite species, where identification of an ant species that could act as a biocontrol agent would be useful. In general, we should target generalist ants as these species can have significant, but underestimated impacts on termite populations in comparison with more well-known termite-preying specialists. With modern methods as PCR-based gut content analyses, in consort with traditional field observations, and most importantly, field-based manipulations of communities, the potential of ant species as regulators of termite populations can be evaluated. This will be especially important in the places where termites are likely to expand, due to ongoing climate change. Such methods, particularly the next generation high throughput barcoding of predator gut contents, will allow us to put ant-termite interactions in a broader context. For example, by screening for a wider range of ant prey items, we can explore the degree to which supposed termite specialists also exploit non-termite prey. Screening of non-ant predators for termite DNA in their guts will allow to understand the importance of ants as termite predators relative to other groups.

Ants and termites could be used as indicator groups of global change. They have important roles in food webs and ecosystem processes and affect vital ecosystem components. Thus, if the biology of individual species is revealed, we can predict the way that ant- and termite-driven ecosystem processes will shift in face of anthropogenic global changes. With respect to climate change, such work could involve either laboratory-based experiments using captive colonies, or to overcome the limitations of such tests (see Chapter I), field-based experimental warming could be used (see Reed et al., 2020 for the first example of this in the tropics).

Animal-driven soil bioturbation, along with processes such as litter decomposition or productivity, should be added to the list of vital ecosystem processes that are measured as standard. This is because bioturbation affects key parameters such as soil fertility and water infiltration. It will be necessary to assemble further different methods to estimate total soil bioturbation of meso-, macro-, and megafauna at a site, to complement the work presented in Chapter III. Further work looking at temporal and spatial variability of bioturbation is also needed. Similarly, the contribution of individual species (or animal groups) can be evaluated, so that bioturbation can be added to the list of ecosystem functions and services they provide. By this, the real contribution of ants and termites to total bioturbation can be estimated at local and ecosystem scales. With this improved knowledge, we can make general predictions about how changes in species diversity will affect key ecosystem processes, especially in cases when different altitudes, experimental treatments or habitats are compared. It would also be fruitful to explore further the role of bioturbating organisms in highly degraded landscapes such as oil palm plantations, with a view to exploring how their presence affects yield. For example, the *Macrotermes gilvus* that I found in oil palm plantation have potentially positive impacts on productivity via soil mixing, and possibly also bringing up of groundwater to upper soil layers where it would be more easily accessible for palm roots.

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CURRICULUM VITAE

Curriculum vitae

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Research and Education

2014 – Present: Ongoing PhD study, University of South Bohemia and research under Institute of Entomology and Institute of Soil Biology, Biology Centre of the Czech Academy of Sciences, CZ).

2017 : Internship. Natural History Museum, London. Identification of termites from soldier caste with Paul Eggleton.

2014 : Master's degree in Soil Biology, University of South Bohemia. MSc. thesis: "Nest building activity of the ant *Lasius niger* and its influence on bioturbation".

2012 : Bachelor's degree in Environmental Protection, University of South Bohemia. BSc. thesis: "Nest building activity of the ant *Lasius niger* and its influence on bioturbation". (Thesis later extended substantially to form master's degree thesis).

2008 : High school in Spálené Poříčí (CZ) – Main field of study: Nature and Environment protection.

Conferences

ISB (Institute of soil Biology) - **Soil Interaction workshop -** České Budějovice, Czech Republic, 2019: DNA barcoding reveals a predatory link between tropical ants and termites.: **talk**

CSPE (Czech Ecological Society), Olomouc, Czech Republic, 2019: Ant-termite interactions: an important but under-explored ecological linkage.: **talk**

CEWSZ (Central European Workshop of Soil Zoology),
České Budějovice, Czech Republic, 2019: How ant and termite interactions change in differently degraded tropical habitats?: **talk**

ATBC (Annual meeting of the Association for Tropical Biology and Conservation), Montpellier, France, 2016: Changes in bioturbation related to logging of rain forest and conversion to oil palm plantation in Borneo.: **talk**

Zoo Days České Budějovice, Czech Republic, 2016: Bioturbation on habitat degradation gradient in Borneo.: **talk**

EGU (European Geosciences Conference) Vienna, Austria 2015: Nest building activity and bioturbation of the ant *Lasius niger* (L.).: **poster**

Other talks and outreach

Šumava, National Park, (CR), 2019. Invited scientist. “Ant ecology and species identification.”

Centre for eco-education, Olomouc (CR), 2019. Invited scientist. “Ants as a suitable soil-animal group for eco-education.”

Elementary school, Plzeň (CR), 2018. Invited scientist. “Ants as ecosystem engineers.”

Publications

Tuma, J., Luke, S. H., Davies, R. G., Eggleton, P., Klimes, P., Jones, D. T., Konvickova, H., Maraví, P. M., Segar, S., Fayle, T. M. (In preparation) How does rainforest logging and conversion to oil palm affect soil-living ants and termites and ant-termite predation rate?

Tuma, J., Eggleton, P. & Fayle, T.M. (In press) Ant-termite interactions: an important but under-explored ecological linkage. *Biological Reviews*

Tuma, J., Fleiss, S., Eggleton, P., Frouz, J., Klimes, P., Lewis, O.T., Yusah, K.M. & Fayle, T.M. (2019) Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation. *Applied Soil Ecology* 144, 123–133.

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Šimek, M., Bryndová, M., Elhottová, D., Jílková, V., Lukešová, A., Kyselková, M., Pižl, V., Tajovský, K., **Tůma, J**. and Vosátka, M. Functional organization of soil. In: Šimek, Miloslav et al. Living soil: biology, ecology, management and degradation of soil. Praha: Academia, 2019. Volume 2, p. 469–542. ISBN 978-80-200-2976-8. [in Czech]

Awards

2018 – Best student presentation (PhD conference, Biology of Ecosystems department, CZ)

2019 – Joint second placed best published first author paper by PhD student (Institute of Entomology, CZ)

2019 - Best student presentation (PhD conference, Biology of Ecosystems department CZ)

Language skills

TOEFL English certification (fluent), German (intermediate); Malay (basic)

Special courses

Stable Isotope Course: 2016 University of South Bohemia + Weihenstephan-Triesdorf University - Freising (GE): Use of stable isotopes in physiological and environmental studies, labelling and tracing stable isotopes in biological systems.

Ant Course 2016, Maliau Basin, Sabah, Malaysia: Collection techniques, identification and preparation of ants. Introduction to filed sampling of ants. Led by Brian Fisher.

Supervision of students

Josef Němec – bachelor student ("Effect of wind throws on ant *Formica aquilonia* population on Kleť mountain").

Teaching

Soil zoology course, University of South Bohemia: I am responsible for lectures about ants and termites and their effects for soil ecosystem. Course is organised by Soil Biology Institute.

Vomáčka I; II, (field course for freshmen), University of South Bohemia: I take part in this course by presenting ants as important arthropod group. I present to students basic field sampling methods along with determination of soil fauna.

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