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
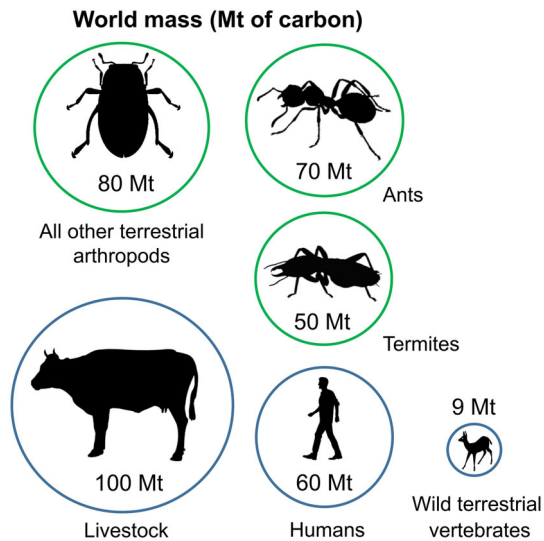
World mass (Mt of carbon)

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 excavation 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
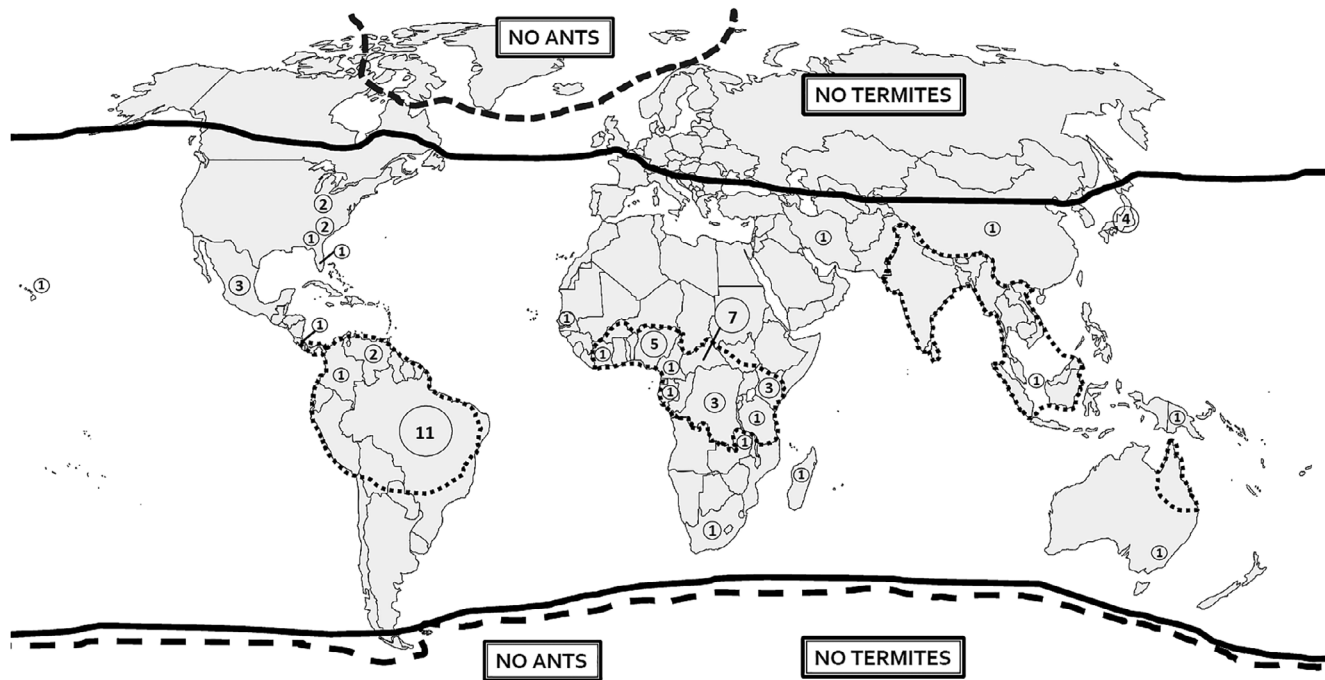
Fig. 2. Global geographical co-occurrence of ants and termites, joint diversity hotspots and number of studies describing ant and termite interactions. Dotted lines mark the areas where ant and termite biodiversity hotspots overlap [data on termite generic diversity from Eggleton, 2000; ant species diversity 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
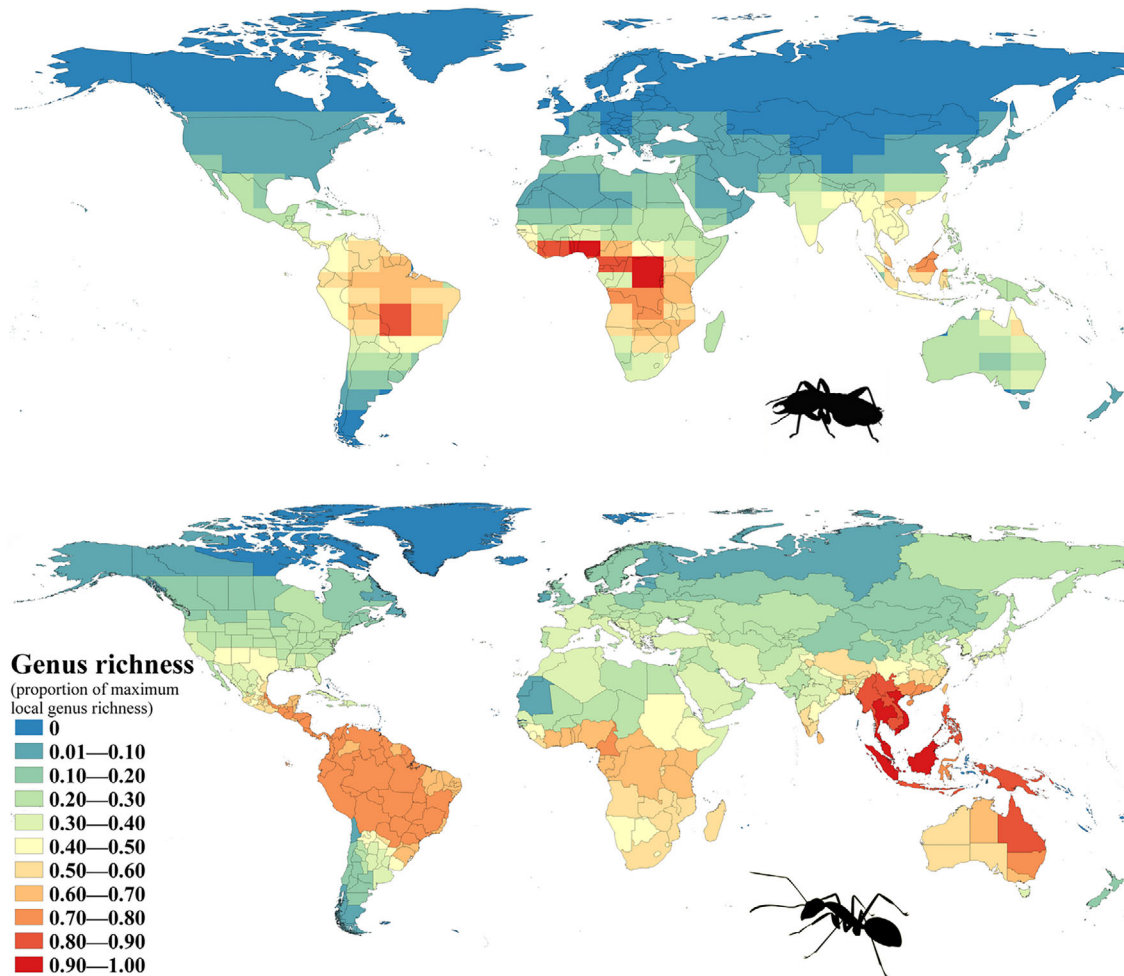
Fig. 3. Global genus richness patterns for termites (top) and ants (bottom). The colour fill is scaled relative to the maximum local richness for each of the groups (termites = 65, ants = 116). For termites, genus counts are taken from an updated version of the map in Eggleton, Williams & Gaston (1994), 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
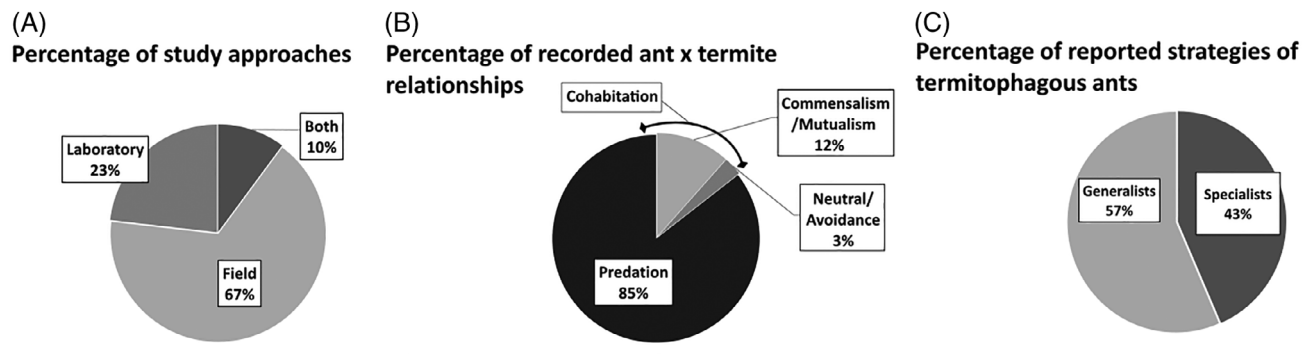
(A)
Percentage of study approaches

(B)
Percentage of recorded ant x termite relationships

(C)
Percentage of reported strategies of termitophagous ants

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 involvement 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

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

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

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.

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
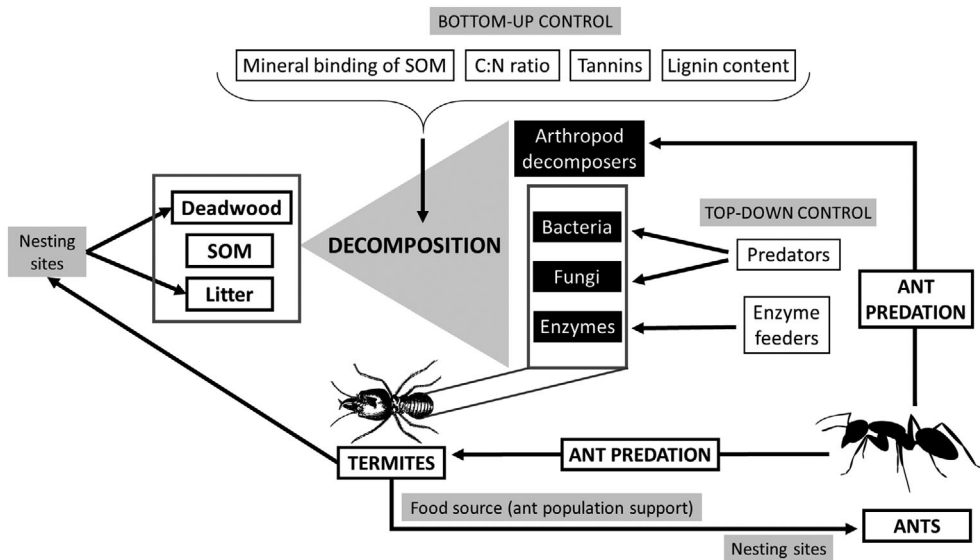

Fig. 5. Schematic outlining the role of ant predation of termites on the processes involved in soil organic matter (SOM) decomposition based on ideas from Allison (2006) and DeSouza, Araújo & Reis-Jr (2009). Ants are likely to be important predators of termites. This means that ants are likely to affect 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

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.