Where do eusocial insects fit into soil food webs?

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24 **Abstract**

25 Social insects are an obvious example of soil macrofauna whose role in soil food webs
26 remains poorly understood. Termites and ants are among the most abundant
27 invertebrates found in many terrestrial ecosystems. Termites are functionally
28 detritivores while ants are functionally omnivores in most soil food webs although
29 variation in ant feeding habits and preferences can mean that some species are
30 functionally herbivores while others are predators. The areal abundance of termites and
31 ants in soils, their ecosystem engineering activities in soils and dead wood, and their
32 enormous variety of species interactions with soil organisms suggest that they are key
33 members of soil food webs. Identifying the species of social insects present in soil food
34 webs and quantifying their abundance by collecting whole colonies, whenever possible,
35 will allow quantification of their areal abundance. Using manipulative experiments to
36 test their impacts in combination with studying their areal abundance, diet, and
37 describing the interacting species found within their functional domains (nests,
38 galleries, gut faunae, etc.) it will be possible to better understand the impacts of social
39 insects on soil food webs.

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Food webs portray our understanding of the trophic relationships among producers, consumers and predators. In many belowground ecosystems, the trophic relationships among animal taxa are especially poorly understood or, more often, completely unknown (Briones, 2014; Wardle, 2006; Wardle et al., 2004). This knowledge gap calls into question whether it is yet practical or even possible to make generalizations about the role of soil fauna in many ecosystem processes (Bradford et al., 2014; Briones, 2014).

Social insects have been largely excluded from studies of belowground communities due to perceived paucity of data available on their areal abundance and trophic ecology (Fierer et al., 2009), yet the majority of social insects dwell in soil for much of their lives and what is known of their trophic ecology suggests that they are an important member of belowground food webs and affect soil ecosystem function (Cammeraat and Risch, 2008; Lobry de Bruyn and Conacher, 1990). Ants and termites are found mostly in soils, and even among bees and wasps there are many species that nest belowground, where they rear their young (Wilson, 1971). Ants and termites are among the most abundant macroinvertebrates found in almost all terrestrial ecosystems (Table 1, Brian, 1978; King et al., 2013), often outnumbering earthworms, so the remainder of this review will focus on these two groups of social insects. To move our understanding of belowground food webs forward, it is important to develop a conceptual framework for understanding how social insects fit into and shape belowground food webs.

Termites and ants are very distantly related insect taxa although they do share the evolution of eusociality: cooperative care of young, overlapping generations, and division of reproductive labor. Termites (Blattodea: Termitidae) are diploid, eusocial cockroaches, sister group to the subsocial roaches (Cryptoceridae) (Cameron et al., 2012; Djernaes et al., 2012) found at latitudes below 48 ° N and S, but especially abundant and diverse in the New and Old World Tropics (Brian, 1978; Eggleton, 2000). There are more than 2600 species of termites described in 281 genera with dozens of new species described each year (Kambhampati and Eggleton, 2000) and the vast majority of these species spend their entire lives in the soil (Holt and Lepage, 2000). A key aspect of termite ecology is that most species feed on dead herbaceous and woody material (Abe et al., 2000). This behavior is possible due to their associated gut faunas that permits digestion of lignocellulose (Brune, 2006).

Ants (Hymenoptera: Formicidae) are eusocial, haplodiploid aculeate (the clade recognizable by females having an ovipositor modified for stinging) Hymenoptera that are most closely related to the Apoidea, the spheciform wasps and bees (Johnson et al., 2013; Ward, 2014). There are currently approximately 13,000 described species of ants and there may be many as 40,000 species globally (Ward, 2014). The majority of ant species nest in soil but may forage above- and belowground. Except for the northern polar region (including Iceland and Greenland) and Antarctica, ants are found in all terrestrial ecosystems (Hölldobler and Wilson, 1990; Wilson, 1971). Ants are especially

abundant in the southern temperate, subtropical, and tropical ecosystems, worldwide, and are likely the most abundant insect group in many regions (Table 1; Andersen, 1997; Brian, 1978; King et al., 2013). Collectively, the diet of ants is extraordinarily diverse. The majority of ant species are omnivorous and highly opportunistic (Stradling, 1978) although there are also entirely predaceous and entirely herbivorous species found within the ants.

Despite the potentially overwhelming species-level diversity of these two taxa, it is possible to understand their functional role in belowground food webs by distilling existing knowledge about their diets (what they are eating), their predators (what is eating them), how their activity structures soil food webs beyond their trophic ecology and their areal abundance. Within this framework, I identify key areas of research that have yet to be addressed and suggest key hypotheses to be tested.

Diet of termites and ants

Termites

Termites are functionally considered detritivores in most food webs (e.g. Moore and Walter, 1988). Collectively, they feed primarily on recently dead or more fully decomposed plant matter in the form of logs, litter, or humus in the soil matrix that has already been colonized by fungi and bacteria, (Wood, 1978). Termites are hemimetabolous (incompletely metamorphosing) insects and all members of the colony

(immature and mature life stages) possess gut faunae that permits digestion of lignocellulose (Brune, 2006). Most termites feed directly on dead vegetation, including standing dead trees, shrubs and grasses, downed wood, litter, and humus but there are also fungus gardening termite species (in the subfamily Macrotermitinae) that feed dead vegetation to their fungus gardens, that they then consume (Rouland-Lefevre, 2000; Wood, 1978). A full review of termite diets has been presented by Wood (Wood, 1978 and references therein). It is important to note that as a condition of consuming lignocellulose, termites also regularly consume any fungi or bacteria that had colonized the material, and thus likely also act as important fungivores. Some termite species have even shown a strong preference for wood already colonized by certain wood-rot fungi (Wood, 1978). This intentional or incidental consumption of microbes and fungi may be significant, especially in the dead wood environment that is often mostly or fully colonized by fungi (Bradford et al., 2014).

Biogeographic region is an important consideration for understanding what termites may be eating as the feeding behaviors of termite species differ in temperate versus tropical regions. In the northern temperate Nearctic and Palearctic, termite fauna are dominated by lower termites that consume and nest in their food - dead wood (Eggerton, 2000; Maynard et al., 2015; Wood, 1978). Many of these species tunnel through the soil to find and consume dead wood resources above- and belowground and their nests are diffuse and inconspicuous (Abe et al., 2000). In the subtropical and

tropical regions grass, litter, and soil (humus) feeding termites predominate and thus, collectively, termites in these regions will be feeding on a much broader variety of lignocellulose resources beyond just dead wood (Eggerton, 2000). Many of these species build conspicuous mounds where the majority of the colony resides (Abe et al., 2000). A critical first step for understanding the role of termites in any given food web is to identify, if at all possible, the genera and species of termites present in the community. Once identified, it becomes easier to at least deduce general feeding and nesting habits as many are known (Inward et al., 2007).

The feeding behavior of a few species of economic interest (e.g. subterranean termites in the genus *Reticulitermes*, Formosan termites in the genus *Coptotermes*, and drywood termites in the genera *Cryptotermes* and *Incisitermes*) have been explored in laboratory and field studies (Judd and Corbin, 2009; Minnick et al., 1973; Morales-Ramos and Rojas, 2003; Rust and Reiersen, 1977; Waller et al., 1990). Collectively, these studies suggest that presence of repellent compounds (e.g. phenol, quinones, terpenoids), lignin content, moisture, physical hardness, and extent of wood rot fungus attack determine whether or not wood will be consumed. In brief, wood with fewer repellent compounds, with lower lignin content, softer woods, and wood that has been previously colonized by wood rot fungi is generally preferred for consumption by species of economic concern. However, the specific feeding behaviors and food

preferences under natural conditions of most species, especially non-wood feeding species that consume grasses, litter, and soil, are not known (Wood, 1978).

It is reasonable to describe the majority of termites found in a given belowground assemblage as detritivores. Their generalized feeding behavior (soil-, litter-, or wood-feeding) may also be revealed through genus and species-level identification (Bignell and Eggleton, 2000). Increased knowledge about the specific feeding preferences (species of consumed wood or grass, for example) of the termites present in an assemblage of interest would represent an important advance, revealing how their feeding affects, for example energy derived from root- or detritus-derived materials (Bignell and Eggleton, 2000). Consumption rates of wood, litter, or soil organic matter have been estimated for very few species, making it difficult to estimate impacts on carbon and nutrient cycling in ecosystems (but see Nash and Whitford, 1995). Traditionally, this information has been provided by direct observation of foraging, consumption of cellulose baits or bagged litter, and gut content analyses (Donovan et al., 2001; Wood, 1978), however, more recently, feeding habits have also been determined using isotope ratios of carbon and nitrogen (Tayasu et al., 1997).

Ants

Ants may be classified as either predators or generalist omnivores in belowground food web models (e.g. Moore and Walter, 1988). Functionally, the majority of ant species are

161 truly omnivorous (Hölldobler and Wilson, 1990; Stradling, 1978). With few exceptions,
162 ant colonies are highly opportunistic and flexible in their dietary choices because they
163 have energetic needs that are determined by both workers and larvae present in the
164 colony. Unlike termites, ants are holometabolous (completely metamorphosing) insects
165 and there is a distinct difference between the nutritional needs of the adult workers and
166 immature larvae in a colony. Adult ants do not grow and do not digest solid food items
167 due to the infrabuccal pocket and the proventriculus, structures in their alimentary
168 canal that prevent solids from passing beyond the crop (a food storage organ in the
169 foregut) into the midgut. Adult ant nutritional needs are met through consumption of a
170 liquid diet, often rich in carbohydrates but potentially also including lipids and amino
171 acids present in, for example hemolymph of insect prey (Hölldobler and Wilson, 1990).
172 In contrast, larvae are growing and are capable of consuming and digesting solid foods,
173 such as animal prey and carrion, and thus require a more protein- and lipid-rich diet.
174 Larvae may also operate as a 'digestive caste' for the colony, breaking down solid foods
175 and regurgitating amino acid- and lipid-rich liquid for consumption by workers, and
176 especially, egg laying queens (Tschinkel, 2006). The impact of the different diets of
177 colony members is that colony nutritional preferences for the majority of omnivorous
178 species will often shift over the course of the year if there are periods of high or low
179 larvae abundance, and thus high or low need for a protein-rich diet (Tschinkel, 2006).

Although ants are collectively functioning as omnivores in most belowground foodwebs, the role of particular species as functional herbivores or predators may have important impacts. Aboveground, ants frequently collect from honeydew-producing insects and may form mutualistic interactions with them (Styrsky and Eubanks, 2007). Belowground, root feeding bugs, such as scale insects (Hemiptera: Coccoidea) feed on phloem and produce honeydew and are likely a primary carbohydrate source for many ant species (Hölldobler and Wilson, 1990). Recent ¹³ C tracer studies have demonstrated that root-derived carbon is a critical energy source for ants (Gilbert et al., 2014). The presence of ants may significantly increase the abundance of hemipterans, thus further increasing their impact as both above- and belowground herbivores (Sanders and van Veen, 2011; Styrsky and Eubanks, 2007). In warm temperate, subtropical, and tropical regions, there are also a number of fungus-gardening ant species that maintain an obligate symbiosis with a macro- and microfungi and bacteria (Ishak et al., 2011; Rodrigues et al., 2011) that allows them to gather primarily live plant material from aboveground and move it belowground for breakdown. This symbiosis (maintenance of a fungus garden) permits lignocellulose degradation and nitrogen fixation while the macrofungi provide a food source for the ant colony (Meyer et al., 2011, 2013; Pinto-Tomás et al., 2009; Schoenian et al., 2011; Scott et al., 2010; Verchot et al., 2003).

Ants will act opportunistically as predators of many invertebrate groups including other predators such as spiders and harvestmen (Hölldobler and Wilson,

1990; Laakso, 1999; Tschinkel, 2006). There are also a number of temperate and tropical species that have been identified as specialized predators of oribatid mites, isopods, and millipedes (Dejean and Evraerts, 1997; Ito, 1998; Masuko, 1994; Wilson, 2005), thus impacting decomposer communities. Ants are also likely the most important predator of eusocial insects, especially other ants and termites, in most ecosystems (Deligne et al., 1981; Hölldobler and Wilson, 1990; Wilson, 1971). However, like termites, the specific feeding behaviors, especially feeding preferences, of most species are poorly known and likely respond to seasonal changes in colony-level nutritional needs (Tschinkel, 2006). Thus, improving our understanding of the specific feeding preferences of the species present in an assemblage of interest would add much toward understanding how ant feeding affects belowground food web dynamics (Laakso and Setälä, 2000; Sanders and van Veen, 2011). Identifying ants to genus, and in many cases to species, is possible in almost all locations (Ward, 2014) and thus represents a critical first step in understanding their role in belowground food webs. Additional, important information would, for example, include whether their feeding activity is taking place above- or belowground and what prey or plant-derived items are taken most frequently. Direct observation of foragers returning to the nest and gut content analyses are very useful for identifying prey selection (Muilenburg et al., 2008), while other analyses such as stable isotope analyses may be useful for identifying whether individual species are

acting primarily as herbivores, omnivores, or predators in a given community (Smith et al., 2009; Stradling, 1978).

Termites and ants as a food source

Termites and ants are prey for many other invertebrates, vertebrates, and fungi (e.g. fungal entomopathogens). A number of invertebrates, mammals, and birds are the most commonly documented predators of termites (Wood and Sands, 1978). However, it is ants that are undoubtedly the most important predators of termites (Deligne et al., 1981). The impact of ant predation is profound in many ecosystems, limiting decomposer and herbivore populations. Ant predation has been shown to limit termite productivity (e.g. Schaefer and Whitford, 1981) and activity, slowing organic matter decomposition rates (Parr et al., 2016).

Other ants, spiders, lizards, amphibians, and birds are the most commonly documented predators of ants (Hölldobler and Wilson, 1990; Petal, 1978). Many insect and invertebrate nest associates (inquilines), including flies, Lycaenid butterfly caterpillars, and beetles, prey upon ant larvae and pupae by mimicking colony odors or providing food rewards so that worker ants tolerate their presence within the nest (Hölldobler and Wilson, 1990). Predation on sexual forms (alates) during mating flights may function as an important limitation on populations as predation on individual

sterile workers has limited impacts on total populations of social insects (Deligne et al., 1981; King and Tschinkel, 2016; Petal, 1978; Tschinkel, 2006; Wood, 1978).

Belowground, the products of a colonial lifestyle, including fecal matter, salivary secretions, and midden materials (remains of food items, fecal materials, and corpses deposited above- or belowground) produced by ant and termite colonies may collectively be an important food source for many taxa and thus have a much greater impact on food web dynamics than predation of individual ants or termites (Petal, 1978; Wood and Sands, 1978). For example, plants and detritovore communities have both been shown to benefit from the input of above-and belowground refuse materials that provide key nutrients, such as nitrogen and potassium (Clay et al., 2013; Farji-Brener and Ghermandi, 2004). However, beyond noting the association between individual species nests and increases in fungal, plant, animal, and bacterial biomass (e.g. Wagner and Jones, 2004), little work has been done to reveal how ants and termites affect the composition of the communities that are utilizing the by-products of the colonial lifestyle as a food resource.

Nests as extended phenotypes structuring soil ecosystems

Although it is important to improve our understanding of what termites and ants eat, and what eats them, understanding the totality of their impacts on soil food webs requires a more holistic approach to studying their activities belowground. Describing

the species present and their interactions, including feeding activity, within the functional domains (Fig. 1) of social insect species provides a conceptual framework for structuring research aimed at understanding the entirety of their impacts belowground (Lavelle, 2002). It is widely recognized that plants influence belowground ecosystem processes by creating habitat for soil biota and that these "spheres of influence" or "functional domains" are the litter system and the rhizosphere which include the species present in the leaf litter (aboveground) and soil surrounding roots (belowground), respectively (Briones, 2014). These spheres of influence are considered mutualistic and complementary and differ in species richness and composition from one another and from the surrounding soil environment (Briones, 2014). Plant functional domains have associated invertebrate and microbial communities with their own food web dynamics and are also functionally distinct, providing key functions such as improving mycorrhizal associations and serving as the primary energy channel for belowground food webs (Briones, 2014; Grayston and Campbell, 1996). Social insect functional domains, the termitosphere and myrmecosphere, likely have similar characteristics, but little work has been done (but see Mora et al., 2005) since the concept was introduced (Lavelle, 2002) despite more recent calls for further research (Brussaard et al., 2007).

Functional domains in soils are typically discussed in the context of ecosystem engineers. Other than plants, the primary belowground ecosystem engineers are macroinvertebrates (Jiménez and Decaëns, 2006; Jouquet et al., 2006; Meyer et al., 2013;

278 Whitham et al., 2003). Earthworms have long been considered important soil ecosystem
279 engineers, affecting soil structure and regulating the distribution and composition of
280 belowground communities (Darwin, 1881; Drake and Horn, 2007; Thakuria et al., 2010).
281 The earthworm functional domain (the drilosphere) includes the biogenic structures
282 they create by burrowing through the soil and depositing casts, which have no direct
283 positive effect on themselves, but that affect soil community structure, and earthworms
284 are thus accidental engineers (Brown et al., 2000). Less studied, but usually more
285 abundant (Table 1), ants and termites create large and conspicuous nests in the soil,
286 whose effects directly impact the fitness of colonies as well as the structure of
287 belowground communities (Tschinkel, 2015, 2014), and are thus extended phenotype
288 engineers (Jiménez and Decaëns, 2006; Jiménez et al., 2008; Jouquet et al., 2006; Meyer et
289 al., 2013).

290 Although there have been few studies to quantify their impact (Cammeraat and
291 Risch, 2008), the biogenic structures created by social insects structure belowground
292 communities and food webs by, for example, serving as a resource for microbial
293 communities and their consumers (Petal, 1978; Wagner and Jones, 2004; Wood and
294 Sands, 1978). Different species may have functionally complementary impacts, too,
295 suggesting that biogenic structures and the activities of colonies, including dietary
296 preferences, are slightly different for most species (Mora et al., 2005). The biogenic
297 structures and collective activities comprise the functional domains of the species and

include the nests, galleries, carton materials, nest symbionts (e.g. fungus gardens), gut fauna, and activities of the individual members (such as feeding) of each species (Fig. 1) (King et al., 2013; Lavelle et al., 1992). When considered as a functional domain, social insect nests represent a largely unexplored frontier in belowground food webs and may serve as a structuring force for communities and, in turn, a domain through which a great deal of root and detritus derived energy is channeled to the heterotrophic communities found in soils (Lavelle, 2002; Lavelle et al., 1995).

Areal abundance

The areal abundance of social insects is largely unknown in many regions and completely unknown for most species due to the difficulties of excavating entire social insect colonies from soil (Brian, 1978; Smith et al., 2009). However, to effectively measure social insect areal abundance, it is crucial that whole colonies, and not just foraging workers, be counted to assess their abundance, biomass, and the flow of energy attributable to a species or genus (Abe et al., 2000; Brian, 1978; King et al., 2013). In the few examples (Table 1) where areal abundances have been assessed by excavating whole colonies, it is clear that social insects often have the highest abundance and biomass per unit area among all animal groups (above-, or belowground) in the warm temperate, subtropical, or tropical regions of the earth (Abe et al., 2000; Brian, 1978; King et al., 2013). For example, the average m^{-2} biomass of ants

318 in a site in Florida surpasses the m² biomass of most other animals ever reported,
319 anywhere on Earth (King et al., 2013). Considered together, ant and termite areal
320 abundance and biomass is truly extraordinary (Table 1; Brian, 1978; King et al., 2013)
321 and surpasses other macroinvertebrate biomass, such as earthworms. Given their
322 enormous potential for high areal abundance, an important step forward is for workers
323 studying belowground fauna to incorporate methods that permit quantification of the
324 composition, relative abundance, and biomass of ants and termites into their studies,
325 whenever possible.

326 Methods for whole colony excavations (Smith et al., 2009) and assessing the areal
327 abundance of social insects using whole colony counts and excavations (King et al.,
328 2013) are available and can readily be modified for use in many ecosystems and study
329 designs. Soils that are difficult or impossible to excavate by hand and species that nest
330 very deeply will prevent colony excavations in some regions, although there are some
331 behaviors, such as absconding from the nest, displayed by some species of ants when
332 confronted by specialized predators, such as army ants, that can be used to collect
333 whole colonies in areas where it otherwise may not be possible (Smith and Haight,
334 2008). Other approaches for collecting whole colonies include the use of baits or nesting
335 substrates (e.g. hollow wooden dowels for twig nesting species, artificial nest boxes for
336 litter nesting species) that are colonized by colonies that can then be observed or
337 collected (Herbers, 1986; Warren and Bradford, 2012; Wood, 1978). Even when colonies

cannot be collected directly it may be possible to estimate colony territory boundaries and crudely estimate colony size using, for example, molecular methods (microsatellite markers to determine relatedness and thus colony boundaries) to infer area occupied by colonies (Vargo and Husseneder, 2009) or mark-recapture methods, although the latter should be used with caution as they often produce unreliable estimates of colony size (Evans et al., 1998). In any sampling design where colony size or area occupied is of interest, some consideration of colony territory size should be made when determining sampling design. Large colonies (hundreds of thousands of workers) may occupy territories of large size and thus because of intraspecific competition for resources such as nest sites and food, colonies may be distant from one another (Adams, 2016). Many species, however, will occupy smaller areas and thus sampling on plots at the scale of 100 m² or less would be practical for capturing multiple colonies.

Testing social insect impacts

Our limited understanding of social insects in soil food webs has remained relatively unchanged for the past forty years so there are many opportunities to advance the field. Examples of recent advances include accumulating evidence that the abundance of invertebrates, including ants and termites, in brown food webs (food webs of detritus, including decomposers and their consumers) vary in response to ecosystem biogeochemistry (gradients of nitrogen, phosphorus, calcium, sodium), food

358 availability, and nest sites, suggesting a variety of bottom-up controls on total
359 abundance at local and regional scales (Kaspari and Yanoviak, 2009; Kaspari et al., 2014;
360 Shik and Kaspari, 2010). Additionally, predation by ants in both brown food webs and
361 herbivore assemblages reduces invertebrate abundance in many ecosystems, suggesting
362 top-down control in these food webs (Kaspari et al., 2011; Parr et al., 2016). Still lacking,
363 however, is detailed understanding of how social insects fit into soil food webs and
364 ultimately ecosystem processes such as decomposition, humification, nutrient cycling,
365 and plant production.

366 I suggest four key general hypotheses and alternatives that, if tested, will rapidly
367 improve our understanding of the impact of social insects in soil food webs in any
368 region. First, individual species of ants and termites act as keystone species whose
369 impacts on soil food webs are disproportionate to their abundance in the community.
370 An alternative is that species impacts are in proportion to their abundance and it is the
371 collective impact of the entire assemblage of social insects that have the greatest effect
372 on soil food webs. Second, the communities associated with the functional domains of
373 termites (the termitosphere) and ants (the myrmecosphere) differ substantially from one
374 another and from the rhizosphere, litter, and the drilosphere (earthworms).
375 Alternatively, functional domains differ substantially between species and it is thus not
376 possible to group them by taxa. Third, social insects function as ecosystem engineers by
377 contributing to soil structure formation through the movement of mineral and organic

378 soil components and the creation of hotspots of microbial activity. Alternatively, social
379 insects may limit microbial activity within their functional domains due to
380 antimicrobial secretions and behaviors that reduce microbial activity. Fourth, ants
381 collectively function in most soil food webs as predators, reducing the rate of
382 decomposition directly by limiting termite activity and population sizes. Alternatively,
383 top-down control by ants may be conditional depending upon the species present (e.g.
384 whether or not there are specialized termite predators present). Collectively, testing of
385 these hypotheses would provide the evidence necessary to better understand the role of
386 social insects in soil food webs at local scales.

377 Can these hypotheses be tested with current methods? Some can, and must, be
378 tested with an accumulation of indirect evidence gathered, for example, by sampling
379 within social insect functional domains to describe associated microbial, fungal, and
380 animal taxa and to allow comparisons with adjacent rhizosphere and litter
381 communities. However, methods are also available that permit manipulation of whole
382 colonies to directly test some of these hypotheses. Removal of colonies through
383 exclusion using fencing (Gibb and Hochuli, 2004), killing with hot water (Tschinkel and
384 King, 2007), transplantation of whole colonies (King and Tschinkel, 2013, 2008) or by
385 reducing or eliminating entire assemblages using pesticides such as poison baits (Evans,
386 2010; Parr et al., 2016) are all possible. Fencing or "caging" of colonies is also possible,
387 permitting detailed study of colony interactions with soil organic matter and mineral

398 soil components (Rink et al., 2013; Tschinkel, 2015). While these approaches may cause
399 non-target impacts (e.g. the use of pesticides may kill non-target arthropods or hot
400 water may sterilize soils) they nevertheless permit the types of experimental
401 manipulations necessary to tease apart social insect impacts from the impacts of other
402 taxa. If used in a variety of ecosystems and in combination with estimates of areal
403 abundance, tests of general hypotheses, as suggested above, using these methods also
404 permits scaling-up social insect impacts to ecosystem or regional scales.

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679 **Table 1.** Reported numbers of individuals m⁻² and biomass m⁻² for ants, termites, earthworms, and other macroinvertebrates across
680 Old and New World sites. Note that figures reported for Baroni-Urbani and Pisarski (1978), Wood and Sands (1978), Bignell and
681 Eggleton (2000), and King et al. (2013) include whole-colony sampling of ants and termites to estimate abundances. Modified from
682 King et al. 2013.
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Source (reference)	Ants m ⁻² /g m ⁻²	Termites m ⁻² /g m ^{-2***}	Earthworms m ⁻² /g m ^{-2***}	Other macroinvertebrates m ⁻² /g m ^{-2***}	Ants% / Termites % (maximum)**
<u>Wenk et al., 2016</u>					
Temperate deciduous forest (38° N, USA)	NA	NA	248/NA*	169/NA	NA
Temperate deciduous forest (42° N, USA)	NA	NA	0/NA	196/NA	NA
Temperate deciduous forest (44° N, USA)	NA	NA	0/NA	92/NA	NA
Temperate deciduous forest (45° N, USA)	NA	NA	9/NA*	99/NA	NA
<u>King et al., 2013</u>					
Temperate deciduous forest (41° N, USA)	0 - 22 / 0 - 0.102	0 / 0	0 - 3 / 0 - 0.300	18 - 83 / 0.108 - 4.003	2.5% / 0%
Temperate deciduous forest (35° N, USA)	1 - 19 / 0.001 - 0.018	0 - 6 / 0 - 0.005	0 / 0	10 - 47 / 0.098 - 5.186	0.3% / 0.09%
Mixed temperate deciduous/pine forest (33° N, USA)	2 - 1084 / 0.003 - 0.739	1 - 19 / 0 - 0.013	0 / 0	5 - 23 / 0.079 - 0.823	47% / 0.8%
Warm temperate broadleaf evergreen forest (29° N, USA)	111 - 8310 / 0.027 - 31.578	0 - 163 / 0 - 0.091	0 / 0	45 - 268 / 0.185 - 1.506	95% / 0.3%
<u>Bignell & Eggleton, 2000</u>					
Tropical forests (Africa, Asia, Neotropics)	NA	38 - 6957 / 0 - 33.264	NA	NA	NA
Tropical savannas (Africa)	NA	49 - 4402 / 0.216 - 2.990	NA	NA	NA
Temperate forests (Australia)	NA	NA / 0.810 - 1.350	NA	NA	NA
Temperate scrub & grasslands (Australia, USA)	NA	NA / 0.262 - 1.350	NA	NA	NA
<u>Wood & Sands, 1978</u>					
Temperate forest (Australia)	NA	600 / 0.810	NA	NA	NA

Semi arid savanna and grasslands (North America, Africa)	NA	0 - 9127 / 0 - 5.997	NA	NA	NA
Tropical savannas (Africa, Australia)	NA	70 - 4402 / 0.459 - 2.997	NA	NA	NA
Tropical Forests (Africa, Southeast Asia, Neotropics)	NA	87 - 4450 / 0.027 - 2.970	NA	NA	NA
<u>Baroni-Urbani & Pisarski, 1978</u>					
Various (mostly temperate Europe and USA)	0 - 115,825 / NA	NA	NA	NA	NA
<u>Kaspari & Weiser, 2012</u>					
Various (New World temperate to tropics)	NA / < 0.010 - < 1.000	NA	NA	NA	NA
<u>Lavelle & Spain, 2001</u>					
Various (worldwide "cold," temperate, and tropical)	NA	NA	~20 - 120 / ~0.6 - ~ 24.3	NA	NA
<u>Lavelle, 1984</u>					
Tropical grasslands (Ivory Coast, Mexico)	500 - 1400 / 0.273 - 0.525	2 - 1200 / < 0.100 - 0.756	230 - 700 / 3.345 - 7.350	147 - 558 / 0.240 - 14.370	0.9% / 1.4%
<u>Callaham & Hendrix, 1997</u>					
Appalachian Piedmont (33° N, USA)	NA	NA	0 -120 / 0 - ~ 8.250 *	NA	NA
<u>Shakir & Dindal, 1997</u>					
Various temperate forests (43°N, USA)	NA	NA	37 - 200 / 0.375 - 4.785*	NA	NA
<u>Suarez et al., 2006</u>					
Temperate hardwood forest (42°N, USA)	NA	NA	22 - 99 / 0.9660 - 8.085 *	NA	NA
<u>Hendrix et al., 1994</u>					
Southeastern pine forest (30°N, USA)	NA	NA	2 / 0.900	NA	NA
<u>Petersen & Luxton, 1982</u>					
Tundra	0 / 0	0 / 0	NA / 0.330	NA / 0.550	0% / 0%
Temperate grasslands	NA / 0.1	0 / 0	NA / 3.100	NA / 1.410	2% / 0%
Tropical grasslands	NA / 0.3	NA / 1.000	NA / 0.170	NA / 0.075	19% / 64%

Temperate coniferous forests	NA / 0.01	0 / 0	NA / 0.450	NA / 0.570	1% / 0%
Temperate deciduous forests	NA / 0.01	0 / 0	NA / 0.200 - 5.300	NA / 1.280	0.2 - 0.6% / 0%
Tropical forests	NA / 0.03	NA / 1.000	NA / 0.340	NA / 0.060	2% / 70%

684 *Majority exotic species.

685 ** Percent of maximum biomass (all macroinvertebrates) reported.

686 *** Conversion of fresh weights to dry weights (g) are estimates and followed that of Petersen and Luxton (1982): termite fresh
687 weight $\times 0.27$ = dry mass, earthworm fresh mass $\times 0.15$, ant fresh mass $\times 0.23$, and other macroinvertebrates fresh mass $\times 0.30$.

688 These conversions do not apply to the invertebrates sampled in this study as those were dried and weighed.

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698 **Figure 1.** Idealized functional domain of social insects is determined by the collective activities
699 of colony members and centered upon the nest constructed at and above the soil surface and
700 galleries excavated belowground. (1) Aboveground food and non-food items are brought into
701 the colony. (2) Belowground food and non-food items are brought into the colony. (3) Feces,
702 corpses, midden material, saliva, and other secretions are produced within the colony and serve as
703 a food and nutrient resource for the associated community inside the nest or aboveground if
704 moved out of the nest. Belowground community assembly occurs through the collective
705 activities of the social insects, including soil movement and associated microbial communities,
706 microbial growth (e.g. fungal hyphae), the arrival and activities of other micro- and
707 macroarthropods, and the collective interactions of the community members. The feeding
708 activities of social insect colony members and their associated gut fauna are also a part of their
709 functional domain. Modified from King et al. (2013).