



Where do eusocial insects fit into soil food webs?



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ABSTRACT

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

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Table 1
Reported numbers of individuals m^{-2} and biomass m^{-2} for ants, termites, earthworms, and other macroinvertebrates across Old and New World sites. Note that figures reported for Baroni-Urbani and Pisarski (1978), Wood and Sands (1978), Bignell and Eggleton (2000), and King et al. (2013) include whole-colony sampling of ants and termites to estimate abundances. Modified from King et al. (2013).

Source (reference)	Ants $\text{m}^{-2}/\text{g m}^{-2}$	Termites $\text{m}^{-2}/\text{g m}^{-2c}$	Earthworms $\text{m}^{-2}/\text{g m}^{-2c}$	Other macroinvertebrates $\text{m}^{-2}/\text{g m}^{-2c}$	Ants/Termites % (maximum) ^b
Wenk et al., 2016					
Temperate deciduous forest (38° N, USA)	NA	NA	248/NA ^a	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 ^a	99/NA	NA
King et al., 2013					
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%
Bignell and Eggleton, 2000					
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
Wood and Sands, 1978					
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
Baroni-Urbani and Pisarski, 1978					
Various (mostly temperate Europe and USA)	0–115, 825/NA	NA	NA	NA	NA
Kaspary and Weiser, 2012					
Various (New World temperate to tropics)	NA/<0.010–<1.000	NA	NA	NA	NA
Lavelle and Spain, 2001					
Various (worldwide “cold,” temperate, and tropical)	NA	NA	–20–120/–0.6––24.3	NA	NA
Lavelle, 1984					
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%
Callahan and Hendrix, 1997					
Appalachian Piedmont (33° N, USA)	NA	NA	0–120/0–8.250 ^a	NA	NA
Shakir and Dindal, 1997					
Various temperate forests (43° N, USA)	NA	NA	37–200/0.375–4.785 ^a	NA	NA
Suarez et al., 2006					
Temperate hardwood forest (42° N, USA)	NA	NA	22–99/0.9660–8.085 ^a	NA	NA
Hendrix et al., 1994					
Southeastern pine forest (30° N, USA)	NA	NA	2/0.900	NA	NA
Petersen and Luxton, 1982					
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%

^a Majority exotic species.

^b Percent of maximum biomass (all macroinvertebrates) reported.

^c Conversion of fresh weights to dry weights (g) are estimates and followed that of Petersen and Luxton (1982): termite fresh weight $\times 0.27$ = dry mass, earthworm fresh mass $\times 0.15$, ant fresh mass $\times 0.23$, and other macroinvertebrates fresh mass $\times 0.30$. These conversions do not apply to the invertebrates sampled in this study as those were dried and weighed.

(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

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