

Chapter 8

Ants: Ecology and Impacts in Dead Wood



Joshua R. King, Robert J. Warren II, Daniel S. Maynard,
and Mark A. Bradford

Abstract Although rarely considered as a saproxylic insect group, ants are an important, highly abundant insect taxon in dead wood environments worldwide. Ants directly impact the dead wood environment primarily through nesting in standing dead trees, logs, stumps, and coarse and fine woody materials, contributing to the physical breakdown of woody materials. Ants indirectly impact the dead wood environment through predation of a wide variety of arthropods, particularly termites, and by serving as a food source for other animals, particularly birds (woodpeckers) and bears that physically break down dead wood to prey upon ant colonies. The known impacts of ant nesting and predation in dead wood are reviewed with a case study that provides new information on the role of abiotic factors affecting nesting site location in dead wood in the eastern temperate US forests. Results showed horizontal and vertical nest stratification of ant nests that shifted with spatial scale. At broad scales, climate determines disparate ranges among species across a latitudinal gradient. At the scale of a forest floor, however, microsite temperature, moisture, and biotic interactions affect nesting locations in downed logs. Future research aimed at better understanding the interactions between ants and other organisms in dead wood environments is necessary to improve our understanding of the importance of ants in shaping dead wood communities and ecosystem processes like decomposition.

J. R. King (✉)

Biology Department, University of Central Florida, Orlando, FL, USA

e-mail: joshua.king@ucf.edu

R. J. Warren II

Department of Biology, SUNY Buffalo State, Buffalo, NY, USA

D. S. Maynard

Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA

M. A. Bradford

Yale School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA

Foraging and nesting by ants belowground in soils and in live tree canopies has been thoroughly documented, and these are often considered primary domains of ants (Hölldobler and Wilson 1990). However, ants commonly nest and forage within downed and standing dead wood and have been shown to be the most, or among the most, abundant animal taxa in those environments (Wilson 1959; Lindgren and MacIsaac 2002; King et al. 2013). The term “saproxylic” refers to any species that depends either directly or indirectly on dying or dead wood, and thus this chapter is focused primarily upon ant activities in dead wood. Ant activity in live trees and shrubs (including myrmecophytic trees) and in ecosystems largely devoid of dead wood (e.g., some grasslands, deserts) is not considered.

Globally, forests sequester ~50% of the world’s terrestrial carbon (Mahli 2002), with dead wood constituting 10–20% of this C (Weedon et al. 2009). In certain regions, dead wood can account for 20–30% of the forest C stock and as much as 40% of forest respiration (Pan et al. 2011). Controls on the decay rate and partitioning of this dead wood pool are affected by organismal interactions in the dead wood environment, and understanding these interactions refines both regional and global C budgets (Boddy et al. 2008; Cornwell et al. 2009; Crowther et al. 2012; Warren and Bradford 2012; Bradford et al. 2014; Maynard et al. 2017). Ant activities in dead wood are important controls in forest ecosystems at all latitudes where standing and downed dead wood is abundant (Warren and Bradford 2012; Bradford et al. 2014; Parr et al. 2016).

Recent work has shown that wood-rot fungi and termites are key interacting players in determining the rate of wood decomposition at local scales in many forest ecosystems and that ants interact with both fungi and termites—and a multitude of other organisms—in dead wood environments (Abe et al. 2000; Warren and Bradford 2012; Bradford et al. 2014; Maynard et al. 2015; Neupane et al. 2015; Parr et al. 2016). Little is known, however, about the activity of ants in dead wood—which presents a major gap in our understanding of the natural history and ecology of this key group of organisms and their effects on a central, global ecosystem function: decomposition of dead wood. Here we review existing knowledge of the activities and impacts of ants in dead wood, present evidence of factors affecting the movement of and location of ant colonies in dead wood in eastern US temperate forests, and suggest key research needs to improve our understanding of the role of ants in shaping conditions and communities in dead wood environments.

8.1 Impacts of Ants in Dead Wood

8.1.1 Nesting Ecology

Ant nests take a number of forms, ranging from arboreal nests in preformed cavities in living trees, carton nests formed from processed (e.g., chewed and mixed with saliva or bound with silk) vegetative material, nests in soil or rock cavities, and nests in dead woody material of all sizes. Ant nests are a key component of their eusocial

life history; a nest is the extended phenotype of eusociality, used as a tool for organizing the colony social structure, including division of labor and protection of the colony members especially reproductive castes and young, and the nest acts as a thermoregulatory device that buffers temperature and moisture extremes (Tschinkel 2006, 2015). Accessible dead wood with cavities of dimensions appropriate for entrance or defense (Powell 2009) makes an ideal nesting substrate. Ants do not consume dead wood, and most ant species—with the exception of carpenter ants in the genus *Camponotus*—lack the ability to excavate sound wood. More commonly, ants occupy preformed cavities excavated, for example, by wood-boring beetles or termites. The creation of channels and occupancy and possible expansion of existing channels by ants may be an important component of the channelization and successional processes of the decomposition of wood (Ulyshen 2016). Channelization typically occurs after trees are mechanically damaged during mortality events (e.g., treefall due to wind, mechanical damage during harvest events by humans, fire scarring) which is followed by the initial stages of wood decay when fungi attack the pith, bark, and wood surface (Ausmus 1977). A large number of ant species frequently nest in wood, but the majority of species found in wood may also nest in soil in temperate and tropical forest ecosystems (Hashimoto et al. 2006; King et al. 2013). Standing trees, stumps, coarse woody material (CWM), and fine woody material (FWM, including stems, seedpods, acorns, etc.) with preformed cavities are all subject to colonization for nesting by ants (Herbers 1989; Hansen and Klotz 2005; de Souza et al. 2012).

Among the most conspicuous dead wood-nesting genera are carpenter ants in the genus *Camponotus*. This genus contains species that excavate cavities in heartwood of live trees and in dead wood (Hansen and Akre 1990; Hansen and Klotz 2005). This genus was recently revised and the subgenera *Colobopsis* and *Dinomyrmex* were elevated to genera (Ward et al. 2016) removing these largely arboreal genera from inclusion in the genus *Camponotus*. Currently, the genus *Camponotus* is estimated to contain over 1000 species worldwide. Many of the species in the genus nest in live trees; however, the remaining species nest in dead wood or soil and can be found in temperate, subtropical, and tropical forests across the globe (Hansen and Akre 1990; Wilson 2003). Many species of *Camponotus* are large-bodied, have large colony sizes (many hundreds to thousands of workers), and are predominately crepuscular or nocturnally active (Hansen and Klotz 2005).

Mature *Camponotus* colonies or founding queens enter dead wood that has become softened due to fungal decay or enter using holes and channels previously created by larger wood-boring beetle larvae such as Cerambycids or Buprestidae (Hansen and Klotz 2005). Once the wood is occupied, the workers channelize opportunistically through the softer parts of stumps, standing dead trees, and CWM (Akre and Hansen 1990; Hansen and Akre 1990). In human-built structures, damage by carpenter ants may also occur in rotting wood, sound softwood materials, or even in other soft building materials such as drywall (Akre and Hansen 1990). Among temperate species there is evidence of specialization among dead wood habitats. For example, some species prefer large logs or standing dead trees in the earliest stages of decomposition (Torgersen and Bull 1995), whereas others nest in

later-stage stumps and logs (Klotz et al. 1998) or small logs and CWM (Chen et al. 2002).

In north temperate, subboreal ecosystems where termites may be rare or absent, carpenter ants are often some of the first arthropods that channelize decaying wood (Hansen and Akre 1990; Hansen and Klotz 2005). In many north temperate ecosystems, *Camponotus* species are also among the most abundant ants in dead wood of all stages of decomposition, although a number of species in the genera *Formica*, *Myrmica*, *Temnothorax*, and *Lasius* are also common, often collectively comprising upward of 100% of species present in dead wood (Franch and Espadaler 1988; Torgersen and Bull 1995; Francoeur 1997; Swenson et al. 1999; Lindgren and MacIsaac 2002; Raley and Aubry 2006). Species in these genera have variable mature colony sizes, ranging from hundreds to tens of thousands of workers (Hölldobler and Wilson 1990; Hansen and Klotz 2005; King 2010; King et al. 2013). In open areas along forest edges or areas cleared by human activities, *Formica* species may become increasingly abundant as *Camponotus* species become less common and as wood becomes increasingly decayed and soft (Lindgren and MacIsaac 2002). As wood becomes more decayed and soft, species other than *Camponotus* may then be able to excavate wood to create nests, suggesting that decay stage of wood may be an important variable regulating ant distributions by governing nest-site availability. In regions outside the cool temperate zones, *Camponotus* remains a conspicuous member of the dead wood-nesting ant fauna although in the tropics they are only one of many genera that occupy dead wood environments (Wilson 1959; Hashimoto et al. 2006; De la Mora and Philpott 2010).

In warm temperate, subtropical, and tropical forests, the diversity of ant species increases and the predominant genera inhabiting dead wood environments shift away from *Camponotus*, *Formica*, and *Lasius*, which typically dominate dead wood nesting in cool temperate and boreal forests. In warm temperate zones, species in the genera *Aphaenogaster*, *Pheidole*, *Rhytidoponera*, *Solenopsis*, and *Temnothorax* become predominant genera in dead wood (Andersen 1986; Herbers 1989; King et al. 2013). Species in these genera also vary considerably in mature colony sizes, ranging from hundreds to tens of thousands of workers (Baroni-Urbani and Pisarski 1978; Hölldobler and Wilson 1990; Hansen and Klotz 2005; King 2010; King et al. 2013). In many tropical forests, the number of ant species found in dead wood is high, comprising up to ~20% of total ant diversity (including arboreal species) and ~50% of ground-dwelling species diversity (Hashimoto et al. 2006; Sagata et al. 2010). The genus *Pheidole* becomes especially common and abundant in dead wood of various sizes and decomposition stages in the subtropics and tropics (Wilson 2003, 1959; Levings and Franks 1982; Eguchi 2001; Watt et al. 2002; Eguchi and Yamane 2003; Hashimoto et al. 2006; De la Mora and Philpott 2010; Sagata et al. 2010; de Souza et al. 2012; Fernandes et al. 2012). A variety of specialist predators also become common nesters in dead wood environments. Species from the genera *Strumigenys*, *Gnamptogenys*, and *Cerapachys* are common, and mature colony sizes of many of these species tend to range from several tens to several hundreds of workers (Baroni-Urbani and Pisarski 1978; Hölldobler and Wilson 1990; King 2010).

In subboreal and cool temperate forests, a majority of species ($\geq 70\%$) use logs, stumps, and CWM (≥ 10 cm diameter) for nesting (Franch and Espadaler 1988; Higgins and Lindgren 2006, 2015; Higgins et al. 2017). These larger pieces of wood provide a substrate that warms rapidly when exposed to sunlight and retains heat after sunset, making these nesting locations favorable relative to soil for thermoregulation by colonies in cooler climates (Higgins and Lindgren 2006, 2012). Standing dead trees, logs, stumps, and CWM are nesting sites for many species in warmer climates as well, although the diversity of species in leaf litter, soil, and in live trees surpasses the diversity of ants nesting in larger pieces of dead wood (Wilson 1959; Levings and Franks 1982; Watt et al. 2002; Hashimoto et al. 2006; De la Mora and Philpott 2010; Sagata et al. 2010). Fine woody material (≤ 10 cm diameter) including small twigs and even seed pods and nuts are used by ants in the temperate (Booher et al. 2017) and especially tropical zones (De la Mora and Philpott 2010; de Souza et al. 2012; Nakano et al. 2012). These substrates are an important nesting site for a large diversity of species and may be occupied at various stages of decomposition (De la Mora and Philpott 2010; Booher et al. 2017). It is likely that these dead wood substrates are favored by many small-bodied ant species because they represent a contained, defensible location for an entire small colony that provides consistent humidity and temperature conditions relative to other nesting sites, such as soil (Wilson 1959; Booher et al. 2017).

Suitable nesting sites in dead wood may be limiting at local scales due to the inability of many species to excavate sound wood or to limited availability of preformed cavities of appropriate size (Herbers 1986; Powell 2009; Sagata et al. 2010; Booher et al. 2017). For example, when FWM nesting sites are experimentally increased in forest plots, nest site occupancy typically increases up to $\sim 20\%$ whether in tropical or temperate forest (Kaspari 1996; Foitzik et al. 2004; Sagata et al. 2010). The most likely competitors for nesting sites for ants in dead wood are other ants (Hölldobler and Wilson 1990; Sagata et al. 2010). However, multiple species may often occupy the same wood piece, and many dead wood pieces (large or small) are often unoccupied, suggesting that factors other than competition may be driving dead wood occupancy rates (Franch and Espadaler 1988; Sagata et al. 2010; Higgins and Lindgren 2012). Termites may also compete with ants for dead wood space but also appear to inadvertently provide nesting sites in dead wood for ants, especially in the tropics (Wilson 1971; Hölldobler and Wilson 1990; Dejean et al. 1997; Mertl et al. 2012; Warren and Bradford 2012; Warren et al. 2012). Co-nesting of termites and ants in single dead wood pieces has been observed in temperate and tropical forests (Buczkowski and Bennett 2008; Mertl et al. 2012). In temperate forests, much of the co-nesting is likely occurring between multiple piece nesting termites (the “lower” termites) that feed upon and nest within dead wood and a variety of ant genera with similar nesting requirements (Buczkowski and Bennett 2008; Lubertazzi 2012; Maynard et al. 2015). In tropical forests, termite communities are much more diverse, and thus a much broader diversity of ants and termites are likely to co-nest in dead wood pieces (Mertl et al. 2012). The creation of physical barriers by termites and specialized antipredatory strategies against ant predators likely make co-nesting possible (Jaffe et al. 1995; Buczkowski and Bennett 2008; Oberst et al. 2017).

8.1.2 *Ants as Predators and Prey*

The majority of ants are broadly omnivorous and highly opportunistic in their diet, taking prey or plant-derived food resources according to colony needs (e.g., high demand for protein during reproductive phases) or simply because of availability (Stradling 1978; Hölldobler and Wilson 1990; Tschinkel 2006). It is likely that the interactions between ants and termites impact the decomposition process, potentially affecting nutrient cycling rates and even the pathways by which C and nitrogen enter the soil (Warren and Bradford 2012; Bradford et al. 2014). Ants, as a group, long have been recognized as the most important termite predators wherever termites occur (Wood and Sands 1978; Deligne et al. 1981; Hölldobler and Wilson 1990). Species from almost every ant subfamily prey upon termites, whether opportunistically or as specialized predators (Wood and Sands 1978; Deligne et al. 1981; Hölldobler and Wilson 1990).

Ants may be an especially important limiting factor for termite populations as they are a specific predator on termite kings and queens in dead wood, preying upon alates (winged reproductives) during mating flights and during the founding stage when termite colonies are especially vulnerable, due to small colony size (Blake 1941; Basalingappa 1970). Some of the most common ants in dead wood are substantial termite predators. For example, species from the genus *Aphaenogaster* often are among the most common dead wood nesting species in eastern US forests, and termites from the genus *Reticulitermes* are an important part of their diet (Buczowski and Bennett 2007; King et al. 2013). The genus *Pheidole* often is the most abundant group of ants in dead wood in the warm temperate through tropical zones, and the genus contains a number of species that prey on termites (Sheppe 1970; Deligne et al. 1981; Hölldobler and Wilson 1990). Although many of these ant genera are generalist predators in dead wood and likely opportunistically preying upon adult worker termites, or even whole colonies, their high abundance and common occurrence in dead wood in forests worldwide likely limits termite activity (Wood and Sands 1978; Deligne et al. 1981; Wilson and Brown 1984; Wilson and Hölldobler 1986; Hölldobler and Wilson 1990; Raimundo et al. 2009).

Other ant species are specialized predators of termites with morphological, physiological, and behavioral adaptations that suggest that termites are their primary prey item (Deligne et al. 1981; Traniello 1981; Hölldobler and Wilson 1990; Lemaire et al. 1990). The entire Ponerinae genus *Centromyrmex* (15 species) is termitophagous and has morphological adaptations, including short, stout legs apparently adapted to moving through narrow, tubular termite galleries, making this a conspicuous, if not especially common, group of termite predators from the New and Old World tropics (Weber 1949; Kempf 1966; Bolton and Fisher 2008). Other termitophagous ant species (several genera) form hunting parties that specialize upon raiding termite nests (and, in some cases, other ant nests) in which they attack and eat termite colony members (Wheeler 1936; Levieux 1966; Longhurst et al. 1978, 1979; Leal and Oliveira 1995; Yusuf et al. 2014; Lampasona 2015). Termitolestic species, in the genus *Solenopsis* and *Carebara*, are very small ant

species that specialize in stealing the eggs and young nymphs of termite colonies (Wheeler 1936; Deligne et al. 1981). These highly specialized termite predators are widespread throughout the subtropical and tropical regions of the New and Old World regions.

Ants likely also are the most important predators of other arthropods in dead wood due to their abundance and their foraging activities in most terrestrial environments (Petal 1978; Hölldobler and Wilson 1990; King et al. 2013; King 2016). For example, ant species prey upon oribatid mites, isopods, millipedes, and wide variety of larvae, such as fly larvae commonly found in dead wood environments (Wilson and Brown 1984; Masuko 1994; Dejean and Evraerts 1997; Ito 1998; Wilson 2005). Moreover, ants surpass other predatory macroinvertebrate groups, such as spiders and predatory beetles, both in total abundance and impact on arthropod prey populations (Kajak et al. 1972; Petal 1978). Ant predation may eliminate as much as ~50% of the individuals produced per unit area per year for some groups of arthropods, such as flies and bugs, (Kajak et al. 1972; Petal 1978). Spiders and other predators, such as beetles, also are common ant prey items, and thus ant predation likely has cascading impacts throughout dead wood communities, although these impacts may be localized nearest colony activity (Petal 1978).

Ants, due to their enormous abundance in dead wood in forests, are important sources of food for other animals, including vertebrates. Ants comprise a major component of the diet of a variety of birds, especially woodpeckers that forage in dead wood. More than 50% of their diet may be composed of ants foraged from dead wood (Levieux 1972; Torgersen and Bull 1995; Raley and Aubry 2006; Horn and Hanula 2008). A variety of reptiles, frogs, and especially dead-wood-dwelling salamanders depend upon ants as a major component of their diet (Hamilton 1932; Anderson and Mathis 1999; Caldwell and Vitt 1999; Hirai and Matsui 2000; Moseley et al. 2005). Specialist ant- and termite-eating mammals (monotremes, marsupials, and eutherians) that occur in forests and woodlands primarily consume ants and termites in dead wood, and these insects typically comprise greater than 90% of their diet (Calaby 1960; Redford 1987). Bears, including black, brown, sun, and sloth bears, are another group of mammals that depend upon ants in dead wood as a key component of their diet (Swenson et al. 1999; Mattson 2001; Große et al. 2003; Bargali et al. 2004; Steinmetz et al. 2011). Among other taxa, ants in dead wood are food for a wide variety arthropods, invertebrates, and even fungi (Petal 1978; Roberts and Humber 1981; Hölldobler and Wilson 1990).

8.2 Colony Movement in Dead Wood

Ant colonies move, and, in some cases, species may be highly transient to the point that entire colonies change location on a regular basis (Smallwood 1982a; Miyata et al. 2003; McGlynn et al. 2004; Moyano and Feener 2014). The regular movement of colonies, at the population scale, represents an important ecological phenomenon affecting the spatial distribution of colony impacts, including predation,

channelization, availability as a prey item, and, ultimately, the rate of ecosystem processes such as dead wood decomposition (Kaspari et al. 2011; Bradford et al. 2014).

Frequent colony relocation may be prompted by a number of factors including thermoregulation, competition, predator avoidance, and resource acquisition (McGlynn et al. 2004; Jones and Oldroyd 2006; Tschinkel 2014). Colony relocation among microhabitats (e.g., soil, decomposing wood, under rocks, leaf litter) might be considered “horizontal” movement, but it often corresponds with “vertical” positioning along a continuum from the soil column to the upper reaches of fallen logs or even into trees (Ofer 1970; Miyata et al. 2003; Hashimoto et al. 2006; Lubertazzi 2012; Moyano and Feener 2014). In tropical, subtropical, and temperate forests, temperature and moisture levels are heterogeneous both across the forest floor and, vertically, from soil to leaf litter, to tree trunks, and to canopy (Christy 1952; Warren 2010; Warren and Bradford 2011). Microhabitat conditions also change with season, as do colony requirements (e.g., many subtropical and temperate species need warmer temperatures for brood development), prompting nest relocation for optimal temperature and moisture regulation (Carlson and Gentry 1973; Smallwood and Culver 1979; Smallwood 1982b; Miller 1994; Kuriachan and Vinson 2000; Chen et al. 2002; McGlynn et al. 2010; Warren et al. 2010, 2012). Many eusocial colonies also move vertically on a seasonal basis as they shift from winter hibernacula to summer nests (Talbot 1951; Ofer 1970; Snyder and Herbers 1991; Miller 1994; Banschbach et al. 1997; Laskis and Tschinkel 2009) or daily to maximize optimal temperature and moisture for colony health and brood development (Headley 1949; Roces and Nunez 1989; Cabrera and Kamble 2001; Houseman et al. 2001; Pranschke and Hooper-Bùi 2003; Higgins and Lindgren 2006, 2012; Jones and Oldroyd 2006; Penick and Tschinkel 2008; Moyano and Feener 2014).

8.2.1 A Case Study of Ant and Termite Colony Movement in Eastern US Forests

Despite our understanding of segregation of nesting locations at local scales, we still have relatively little understanding of fine-scale vertical and horizontal nesting choices and how those choices may change under different climatic conditions. Whereas horizontal segregation (Levings and Traniello 1981; Rytí and Case 1992; Brown 1999) or vertical segregation at a coarse scale such as litter versus arboreal strata (Lynch 1981; Longino and Nadkarni 1990; Zelikova et al. 2008) has been examined, vertical colony placement across the scale of soil to downed dead wood (~1 m) among co-occurring, interacting ground-dwelling social insects (ants and termites) rarely has been examined. We examined horizontal (presence/absence, abundance) and vertical (soil up to downed dead wood) nest placement, across a regional climate gradient in eastern US temperate forest, for the three dominant

social insects inhabiting soil and CWM: the woodland ant species *Aphaenogaster rudis* and *Pheidole dentata* and the temperate forest termite *Reticulitermes flavipes*. We examined the relative contribution of abiotic (temperature, moisture, CWM class) versus biotic (interspecific interactions between *R. flavipes*, *A. rudis*, *P. dentata*, and other ants) variables in predicting horizontal and vertical nest placement at both broad and fine spatial scales.

8.2.2 Methods

8.2.2.1 Study Sites

King et al. (2013) conducted a forest arthropod survey from Connecticut to Florida (in eastern US temperate mixed forests) and found that macroinvertebrate abundance and biomass in dead wood was dominated by ants and termites. Species of the *Aphaenogaster fulva-rudis-texana* species complex (Umphrey 1996) include *A. picea* Wheeler and *A. rudis* Enzmann (hereafter “*A. rudis*”). These species dominated dead wood ant communities in the northern portion of the latitudinal gradient and then gave way to *Pheidole dentata* Mayr as the dominant ant in the southern reach of eastern US forest—coinciding with a marked increase in *Reticulitermes flavipes* Kollar termite colonies from north to south (King et al. 2013; Maynard et al. 2015). Working in the same study sites and sampling plots as King et al. (2013), ant and termite colonies were sampled in August to September 2011. The four study locations spanned ~12° latitude (approximately 1600 km): Yale-Myers Forest (Connecticut, 41°57'N 72°07'W), Coweeta Hydrologic Laboratory (North Carolina, 35°03'N 83°25'W), Whitehall Forest (Georgia, 33°53'N 83°21'W), and San Felasco State Park (Florida, 29°43'N 82°26'W).

8.2.2.2 Study Species

Aphaenogaster rudis is a widespread and abundant species complex that ranges from southern Canada to Georgia and west to the Mississippi River (Lubertazzi 2012; King et al. 2013) in the eastern United States. *Aphaenogaster rudis* are dietary generalists acting as scavengers, predators, and keystone woodland seed dispersers (Ness et al. 2009). Colonies are typically monogyne (single queen) with fewer than 500 workers. Nests are constructed in a variety of substrates but most commonly in rotten wood extending into the soil (personal observations, King et al. 2013). *Pheidole dentata* is an abundant, widespread ant species mainly located in forests in the southeastern United States but reaching as far northward as Maryland and westward to Texas (Wilson 2003). *Pheidole dentata* have two physical worker castes, soldiers as well as workers, and may have multiple queens (polygyne), although they are typically monogyne. Colonies are >ca. 600 workers. Nests are

constructed in a variety of substrates, especially rotten wood, and extend into the soil. *Pheidole dentata* workers are scavengers and generalist predators.

Reticulitermes flavipes, the eastern subterranean termite, occurs throughout the eastern United States, but its density increases greatly moving southward (Emerson 1936; Maynard et al. 2015). *Reticulitermes flavipes* feed on dead wood, but, unlike the ant species, reproductive members of the colony often remain belowground (Thorne et al. 1999). However, the vast majority of the colony and the standing biomass of *Reticulitermes* colonies—when temperatures are warm enough to facilitate feeding (i.e., $\sim >10$ °C)—are found in aboveground dead wood connected by subterranean tunnels (Abe 1990; Korb 2007; King et al. 2013).

8.2.2.3 Sampling

Two 10×10 m plots were established on two north- and two south-facing slopes (except at YMF, where slopes face east-west) at each of the four study sites ($n = 8$ plots per study site and $32,100$ m² plots across all four locations). Study ants and termites were sampled in all CWM (dead wood >10 cm dia.) within each plot, with an emphasis on collecting whole colonies (ants) or feeding groups (subterranean termites) of social insects. Although termite foraging congregations may or may not be true “nests,” they were measureable units typically representing the majority biomass of the colony (Deheer and Vargo 2004; Vargo and Husseneder 2009; King et al. 2013). All CWM was measured along the center axis for length, and at either end for diameter. We categorized the state of decay in each individual CWM using the “class” index developed by Pyle and Brown (1998), where class I is sound wood and class V is heavily decayed to the point of almost becoming soil. See King et al. (2013) for more detailed methodology. The nest height of all colonies from the soil surface also was measured. Given that nest height is constrained by the diameter of available CWM, we also calculated relative nest height as the proportion of available diameter height used (i.e., nest height/CWM diameter). In each plot, soil temperature was measured at 5 cm depth and volumetric soil moisture (Campbell HydroSense™) to 12 cm depth across 10 distinct sub-locations.

8.2.2.4 Horizontal Nest Placement Analysis

We used analysis of covariance (ANCOVA) models in the R statistical program (Team 2014) to evaluate *R. flavipes*, *A. rudis*, and *P. dentata* abundance at the plot scale ($n = 32$). None of the ants we sampled occupied the same piece of CWM, so the abundance data were, in effect, analogous to presence/absence data. The biotic variables included in the model were *R. flavipes*, *A. rudis*, *P. dentata*, and other ant (“other,” *Camponotus*, *Lasius*, *Nylanderia* spp.) abundance. Because ants eat termites, the ant species were included as predictors in the *R. flavipes* models, but *R. flavipes* was not included in ant statistical models because its presence should not deter ant colonization. Given that *A. rudis* and *P. dentata* ants never occurred in the

same CWM, the influence of *P. dentata* presence on *A. rudis* plot-level abundance was evaluated, but the directional effect is unknown, making it redundant to include *A. rudis* as a predictor in *P. dentata* models. The abiotic variables were temperature, moisture and CWM class. We also used ANCOVA models to evaluate *R. flavipes*, *A. rudis*, and *P. dentata* abundance at the scale of individual CWM pieces ($n = 156$). Because the ant species never occurred in the same log, we used individual species presence and the same abiotic variables.

We included site ($n = 4$) as a factor in all ANCOVA models to capture unmeasured variance across sites as well as to evaluate contingent responses (interaction effects with site). We also evaluated second-order terms for the abiotic variables to examine intermediate responses. We used the “car” package (Fox and Weisberg 2011) in R to test for collinearity among fixed effects and found that soil moisture and temperature were collinear (variance inflation > 8), so they never were included in the same model. The inclusion or exclusion of variables was based on Akaike’s Information Criterion (AIC) values (Akaike 1973), calculated using maximum likelihood with the best-fitting parameters ($\Delta 2\text{AIC}$) retained. We then evaluated the slope value of retained fixed effects and considered coefficients with p -value ≤ 0.05 significant. We considered coefficients with p -value ≤ 0.10 to be “marginally significant” (Hurlbert and Lombardi 2009) and used this higher threshold given the noise in environmental data that decreases statistical power but, if randomly distributed, does not affect estimates of coefficient (or effect) size (Bradford et al. 2016).

8.2.2.5 Vertical Nest Placement Analysis

We used analysis of variance (ANOVA) models to evaluate differences among *R. flavipes*, *A. rudis*, and *P. dentata* nest height and relative nest height. We also used ANOVA to examine differences in CWM diameter by site. Post hoc tests for individual differences were done using Tukey’s “Honest Significant Difference” tests. We evaluated *R. flavipes*, *A. rudis*, and *P. dentata* nest heights at the plot scales using ANCOVA models. We used an approach similar to that previously outlined for horizontal nest placement, except that interspecific ant influences on nest height could not be evaluated at the scale of individual CWM pieces because the ants did not co-occur in the same log.

8.2.3 Results

8.2.3.1 Study Species Occurrence

Whitehall Forest was the only location where we found all three study species (Table 8.1) in our plots. *Reticulitermes flavipes* was not found at Yale-Myers (Connecticut) but does occur in that region and at that site (pers. obs.); similarly

P. dentata was not found at Coweeta (North Carolina mountains) but also occurs in that region. The species distributions largely correspond with broad-scale climate drivers. Termite abundances correlated with increased temperature, increasing from the northernmost Yale-Myers site down to the southernmost San Felasco State Park site (Table 8.1). *Aphaenogaster* abundances directly correlated with precipitation and peaked at the Coweeta Hydrologic Lab; whereas *P. dentata* occurred most at the driest site, Whitehall Forest (Table 8.1).

8.2.3.2 Horizontal Nest Placement: Plot Scale

The best-fit model ($\Delta\text{AIC} < 2.0$) predicting *R. flavipes* abundance at the plot scale retained temperature and site, but only the positive effect of temperature was significant (temperature, $df = 1$, $SS = 1,525,934$, $F\text{-value} = 4.192$, $p\text{-value} = 0.050$; site, $df = 3$, $SS = 1,202,618$, $F\text{-value} = 1.101$, $p\text{-value} = 0.366$). We only found termite colonies in plots with soil temperature $>20^\circ\text{C}$. The best-fit model for *A. rudis* abundance retained moisture and site, but only the positive effect of moisture was marginally significant (moisture, $df = 1$, $SS = 1,082,269$, $F\text{-value} = 3.305$, $p\text{-value} = 0.080$; site, $df = 3$, $SS = 1,412,467$, $F\text{-value} = 1.438$, $p\text{-value} = 0.254$). *Aphaenogaster* ants were most abundant where plots contained 5–20% soil moisture. The best-fit model for *P. dentata* abundance retained temperature and site, and the positive effect of temperature and site (given increased *P. dentata* abundance at Whitehall Forest and San Felasco) were significant (temperature, $df = 1$, $SS = 637,037$, $F\text{-value} = 4.402$, $p\text{-value} = 0.045$; site, $df = 3$, $SS = 1,326,041$, $F\text{-value} = 3.054$, $p\text{-value} = 0.045$). We only found *P. dentata* in plots with temperature $>23^\circ\text{C}$.

8.2.3.3 Horizontal Nest Placement: CWM Scale

The best-fit model ($\Delta\text{AIC} < 2.0$) for *R. flavipes* abundance at the CWM scale contained *A. rudis* and *P. dentata* presence, temperature, temperature², CWM class and a *P. dentata* \times site interaction term. The significant interaction term ($df = 1$, $SS = 404,152$, $F\text{-value} = 11.267$, $p\text{-value} = 0.001$) indicated that *R. flavipes* abundance was not impacted by *P. dentata* presence in CWM at San Felasco (mean \pm SE, present = 544.71 ± 237 termites; absent 182.1 ± 83 termites), but decreased with *P. dentata* presence in CWM at Whitehall Forest (present = 6.8 ± 7 termites; absent 42.8 ± 18 termites). *R. flavipes* abundance decreased with *A. rudis* presence in all CWM ($df = 1$, $SS = 154,849$, $F\text{-value} = 4.317$, $p\text{-value} = 0.040$) (Fig. 8.1). We also found that *R. flavipes* abundance in CWM increased marginally significantly with temperature ($df = 1$, $SS = 101,905$, $F\text{-value} = 2.841$, $p\text{-value} = 0.094$), but CWM class and the temperature² terms were not significant.

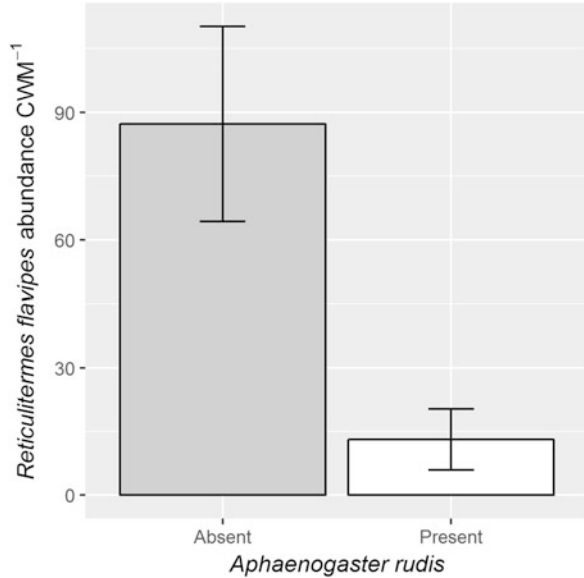
The best-fit model ($\Delta\text{AIC} < 2.0$) for *A. rudis* abundance retained *P. dentata*, other ants, soil moisture, CWM class, and site, but only the negative effect of *P. dentata* presence was marginally significant and the positive effect of soil

Table 8.1 Site conditions and social insects

Site (latitude)	Climate ^a		<i>Reticulitermes</i> spp.		<i>Aphaenogaster</i> spp.		<i>Pheidole dentata</i>	
	Temp (°C)	Prec (cm)	Colonies	Individuals	Colonies	Individuals	Colonies	Individuals
Yale-Myers Forest (41)	8.8	121.2	0	0	8	3865	0	0
Coweeta Hydrologic Lab (35)	12.5	183.0	12	1782	26	5720	0	0
Whitehall Forest (33)	16.6	119.5	13	2354	8	1617	6	4621
San Felasco State Park (29)	20.6	128.2	13	6262	0	0	7	2902

^aMean annual 1981–2000; PRISM Climate Data (<http://www.prism.oregonstate.edu>)

Fig. 8.1 *Reticulitermes flavipes* (subterranean termites) abundance in logs with the presence versus absence of *Aphaenogaster rudis* ants (values are means \pm SE). The termite abundances are significantly lower in coarse woody material (CWM) containing the ants



moisture significant (*P. dentata*, $df = 1$, $SS = 71,039$, $F\text{-value} = 3.160$, $p\text{-value} = 0.076$; moisture, $df = 1$, $SS = 527,843$, $F\text{-value} = 23.480$, $p\text{-value} < 0.001$). *Aphaenogaster rudis* colonies contained (mean \pm SE) 78.3 ± 14 individuals in CWM without *P. dentata* but never occurred in logs with *P. dentata* present (Fig. 8.2). The best-fit *P. dentata* model included CWM class and site, but only the site effect was significant ($df = 3$, $SS = 132,566$, $F\text{-value} = 2.966$, $p\text{-value} = 0.034$).

8.2.3.4 Vertical Nest Placement: Plot Scale

No significant differences occurred between species in nest height ($df = 2$, $SS = 257$, $F\text{-value} = 1.585$, $p\text{-value} = 0.211$) (Fig. 8.3a), but significant differences occurred in relative nest height ($df = 2$, $SS = 0.880$, $F\text{-value} = 4.363$, $p\text{-value} = 0.016$) (Fig. 8.3b). Tukey multiple comparison of means indicated *R. flavipes* relative nest height (0.54) was significantly greater ($adjusted\ p\text{-value} = 0.011$) than *A. rudis* relative nest height (0.31) (Fig. 8.3b). There was no difference in the diameter of the CWM colonized by the three species ($df = 2$, $SS = 0.014$, $F\text{-value} = 0.015$, $p\text{-value} = 0.611$).

The best-fit model ($\Delta AIC < 2.0$) for *R. flavipes* nest height at the plot scale retained *A. rudis*, *P. dentata*, other ants, soil moisture, CWM class, and site, but none of the effects were significant. The best-fit model for *A. rudis* nest height retained *R. flavipes*, soil moisture, CWM class, and site, but only the positive effect of *R. flavipes* significantly correlated with *A. rudis* nest height ($df = 1$, $SS = 3539$,

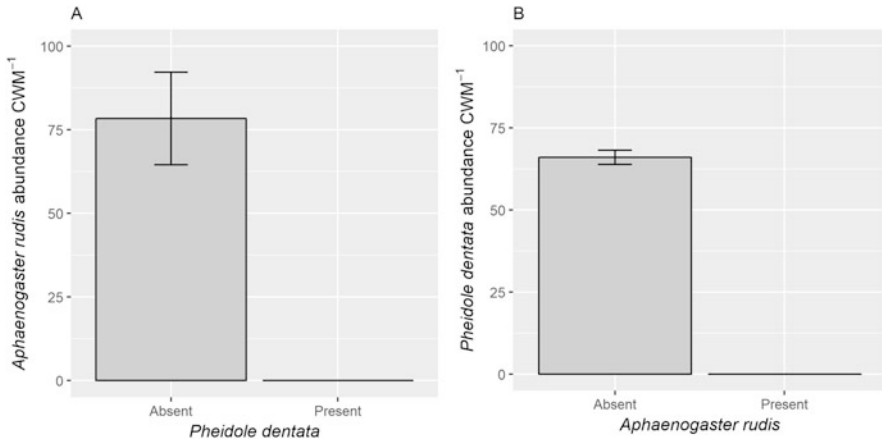


Fig. 8.2 *Aphaenogaster rudis* (a) and *Pheidole dentata* (b) ant abundance in logs in the absence versus presence of the other species. These two species did not coexist in the same piece of coarse woody material (CWM)

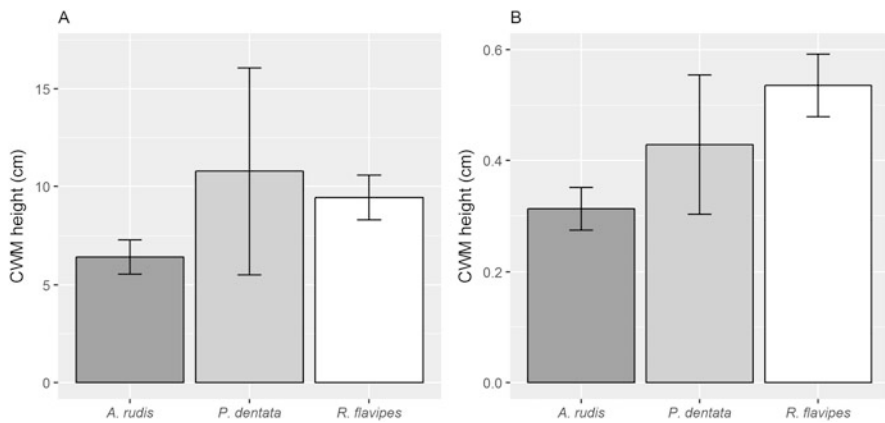


Fig. 8.3 Nest height (a) and nest height as a proportion of log diameter (b) for the dominant termites (*Reticulitermes flavipes*) and dominant ants (*Aphaenogaster rudis* and *Pheidole dentata*) [values are means \pm SE] in eastern US temperate forest floors. None of the genera differed in absolute height of nests (a), but the *R. flavipes* colonies were significantly higher in larger logs than *A. rudis*—suggesting the termites used a greater proportion of available height than the ants

F -value = 29.233, p -value = 0.001) (Fig. 8.4). The best-fit model for *P. dentata* nest height retained soil temperature, temperature² and site, with only the temperature terms significant (temperature, $df = 1$, $SS = 1814$, F -value = 9.893, p -value = 0.014; temperature², $df = 1$, $SS = 674$, F -value = 3.675, p -value = 0.092; indicating a curvilinear response (Fig. 8.5)).

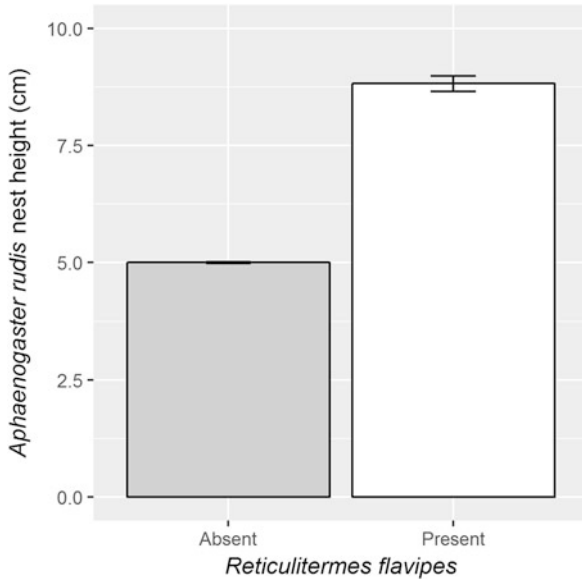


Fig. 8.4 Nest height of *Aphaenogaster rudis* ants where *Reticulitermes flavipes* termites were present and absent. The ants appeared to move their nests much higher in coarse woody material where termites also occurred

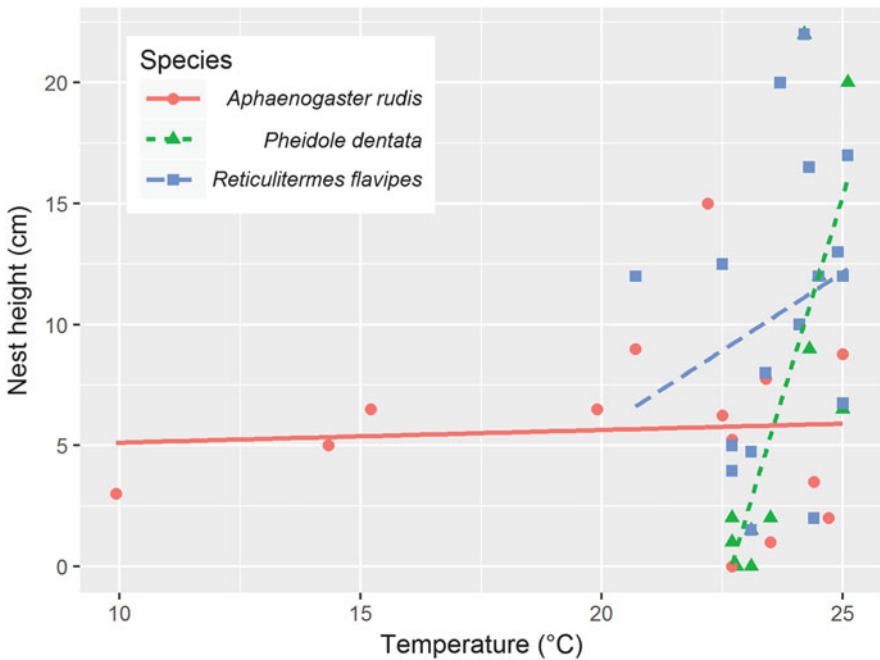


Fig. 8.5 Scatterplot showing *Aphaenogaster rudis*, *Pheidole dentata*, and *Reticulitermes flavipes* nest height increases with temperature. Whereas all species' nest height increased with temperature, only the slope value for *P. dentata* differed significantly from zero

8.2.4 Discussion

Our results suggest that the spatial scale of interest determines conclusions about the strength of biotic versus abiotic influences on eusocial insect nest placement. At broad scales (km), the distribution of *R. flavipes*, *A. rudis*, and *P. dentata* corresponded with climate. *R. flavipes* and *P. dentata* abundances increase with latitudinal increases in soil temperature, whereas *A. rudis* distributions peaked with high soil moisture. Similarly, at plot-level scales (*m*), temperature most influenced *R. flavipes* and *P. dentata* nest locations across the forest floor whereas moisture most influenced *A. rudis*. Temperature and moisture remained important at the scale of an individual log (*cm*), with interspecific interactions appearing to govern which species occupied the logs. None of the ant species, including additional ant species grouped together as “other ants,” shared a log. *Reticulitermes flavipes* shared logs with *A. rudis* and *P. dentata* colonies but had significantly fewer termite workers present in the logs when they did. The consistency of the lack of co-occurring ants and reduced termite abundances in the presence of ants suggests that experiments are needed to verify underlying mechanisms for this relationship.

8.2.4.1 Horizontal Nest Placement

Aphaenogaster rudis appeared limited by moisture, preferring CWM in locations with moderately moist soils, whereas *R. flavipes* and *P. dentata* only occurred in CWM in locations with the warmest soils. These interspecific microclimate requirements seem to map onto the broad-scale species distributions and the general natural history of this group of ants (Lubertazzi 2012).

Ant and termite species interact at very local scales (Hölldobler and Wilson 1990), and notably there was a conspicuous lack of shared logs between ant colonies, and a significant drop in *R. flavipes* abundance in logs shared with *A. rudis* (and site-specific effects in those shared with *P. dentata*). These findings suggest that local, negative biotic interactions influenced habitat selection for nests. Interestingly, at Whitehall Forest where *A. rudis* and *P. dentata* overlap, Giladi (2004) found that *P. dentata* dominated active floodplain habitat where *A. rudis* was absent, suggesting that negative interactions occur at scales greater than an individual log. In sum, these results suggest that manipulative field studies are required to definitively decouple biotic and abiotic drivers among these species.

We find dramatic declines in *R. flavipes* abundance in dead wood also colonized by *A. rudis*, whereas *P. dentata* appear to have contingent effects. Many ant species will prey upon termites (Feener 1988; Dejean and Feneron 1999; Bayliss and Fielding 2002; Buczkowski and Bennett 2007, 2008), and *R. flavipes* abundance decreases with *P. dentata* presence at Whitehall Forest. However, *R. flavipes* abundance is much greater at San Felasco, and it increases with *P. dentata* presence. In fact, because the density of termites is much greater in the southern range of *P. dentata*, any predatory impact may be relatively less, allowing greater microscale

coexistence. Another possibility is that *P. dentata* outcompetes and excludes more effective termite predators, thereby alleviating an important top-down control on local termite abundances.

8.2.4.2 Vertical Nest Placement

Nest placement in logs helps regulate colony microclimate. Obvious vertical adjustments to microclimate are movements downward during winter to avoid freezing temperatures (Talbot 1951; Ofer 1970; Snyder and Herbers 1991; Miller 1994; Banschbach et al. 1997; Laskis and Tschinkel 2009) or during summer to avoid desiccation (Wilson 1971; Gordon et al. 2013). We only found one vertical microclimate response: *P. dentata* increased its nest height exponentially with temperature, likely maximizing optimal temperature conditions for colony functions such as brood development, queen egg laying, and even food storage (Tschinkel 2006; Gayahan and Tschinkel 2008).

All three species generally placed their nests at similar heights, but *A. rudis* used less available log diameter than *R. flavipes*. Given that ants use logs as housing for nests whereas *R. flavipes* also consumes dead wood as food, *R. flavipes* may occupy more log space to fully exploit consumable resources. *Aphaenogaster rudis* ants are also desiccation intolerant (Smallwood 1982b) and require highly mesic forest conditions for nesting (Warren et al. 2012). Given that dead wood dries from the top down, using the warmer, upper portions of the wood requires greater moisture to avoid desiccation, necessitating lower colony placement by *A. rudis* in drier locations. In addition, because *A. rudis* does not generally excavate wood itself, it is largely limited to those portions of the wood that have already been excavated by other soil animals. Interestingly, *A. rudis* locates colonies relatively higher in wood where termites are present, possibly a response to a food resource. Termites can fend off ants in dead wood colonies by filling in spaces and positioning soldiers at openings (Buczkowski and Bennett 2008), so an alternate possibility is that *A. rudis* nests higher to occupy abandoned tunnels in logs once occupied by termites.

8.3 Conclusions and Future Work

The drivers of horizontal and vertical colony locations in dead wood on a forest floor appear to change with scale for eusocial insects. At broad spatial scales, climate seems to shape disparate ranges among species across a latitudinal gradient, but we cannot rule out that a shift in interacting species (or some other unmeasured factor) also acts as an influence on range distributions. At the scale of a log, in contrast, biotic interactions appear to predominate, with species excluding one another, but not without some microclimate influences. Our results therefore highlight that the habitat distributions of dominant eusocial insects in eastern US temperate forest likely are structured by biotic and abiotic forces acting at different strengths

depending on measurement scale. These results suggest that measures taken at a single spatial scale may misrepresent the strength of biotic or abiotic drivers and may lead to incorrect predictions about how eusocial insects will respond to climate change both within and among sites. This scale dependence of biotic vs. abiotic influence on eusocial insect distributions and abundance is likely also true for dead wood nesting ants in tropical forests (Kaspari 1996). Admittedly, our data are observational but suggest the need for experiments to tease apart and quantify biotic and abiotic influences on nest placement and how nest movements affect key ecosystem processes that are mediated by these species.

At the broadest scales, salvage logging, wildfire due to forest mismanagement, and land conversion present significant threats to dead wood environments and all of the species they support (Andrew et al. 2000; Watt et al. 2002; Majer et al. 2007; Ulyshen and Hanula 2009; Lemperiere and Marage 2010; Lindenmayer et al. 2012; Luke et al. 2014; Boucher et al. 2015). These threats lend urgency to improving understanding of the species and their interactions in dead wood. There are major gaps remaining, but a critical step in furthering our understanding of the role and importance of saproxylic insects is to better understand the most abundant taxa, like ants and termites, in dead wood, worldwide. We suggest three key areas of research for improving our understanding of the role of ants in dead wood environments. First, ants appear to act as top-down predators in dead wood, but their impact upon prey abundance and diversity in dead wood has only rarely been measured (Deligne et al. 1981). Quantifying their impacts as predators upon key groups, such as termites, in dead wood in relation to stage of decomposition should thus be a research priority. Second, because the impacts of ant nesting and other ant activities in dead wood are transitory, it is critical to understand the relationships between ant species and decay stage of dead wood. This is a necessary first step in understanding their impacts on the rate of decomposition, as the arrival and duration of ant impacts in decaying wood may create alternate pathways in carbon and nutrient cycling (e.g., redirecting termite- to fungal-mediated wood decomposition). This area of research is closely related to the third key area of research: the impact of ant nesting and activity upon microbial communities in dead wood. Ants may have important impacts upon microbial community assembly and succession in the dead wood environment because they produce a number of antimicrobial compounds that likely impact both fungal and bacterial communities, especially in the vicinity of their nests (Fernandez-Marin et al. 2006; LaRosa et al. 2012; Tranter et al. 2014). Thus, because of their high abundance in dead wood, through their interactions with other saproxylic insects like termites, and their potential impacts upon microbial communities, ants likely play a key role in the decomposition process of dead wood, worldwide. However, the magnitude and direction of these ant-mediated ecosystem effects are almost entirely unknown.

Acknowledgments We thank Ella Bradford, Ben Gochnour, Lindsay Gustafson, Sarah Huber, Mary Schultz, and Anna Wade for field and lab assistance. This is the Termite Ecology And Myrmecology (TEAM) working group publication number 3. Research was supported by US National Science Foundation grants to M.A.B. (DEB-1021098), J.R.K. (DEB-1020415) and the Coweeta LTER Program.

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