Insect. Soc. (2012) 59:215–221
DOI 10.1007/s00040-011-0208-4

Insectes Sociaux

RESEARCH ARTICLE

Ant colonization and coarse woody debris decomposition in temperate forests

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Received: 12 July 2011 / Revised: 5 November 2011 / Accepted: 8 November 2011 / Published online: 19 November 2011

Abstract Ants are ubiquitous, abundant and have widespread impacts on ecological communities and ecosystem processes. However, ant effects on coarse woody debris decomposition are unexplored. Several ant species colonize coarse woody debris for nesting, and this puts them in contact with fauna and microbes that utilize coarse woody debris as habitat and food, potentially influencing nutrient cycling and, ultimately, forest productivity. We report results from a field experiment employing 138 artificial ant nests (routed pine blocks) across five locations in southeastern US deciduous forests. We examine the correspondence between ant, termite and wood-eating fungi colonization and variation in coarse woody debris decomposition. After 1 year, nests colonized by ants had 5% more mass than those not colonized. Ant colonization corresponded with significantly less termite- and fungal-mediated decomposition of the nests. Without ants, termites removed 11.5% and fungi removed 4% more wood biomass. Ants, termites and wood-eating fungi all colonized pine nests where temperatures were highest, and ants also preferred higher soil moisture whereas termites and fungi responded negatively to high soil moisture when temperatures were higher. Ants reduce termite colonies through predation, and may inhibit fungi through the secretion of antimicrobial compounds. Our results indicate that interactions between forest understory ants, termites and fungi may influence the rate of coarse woody debris decomposition—biotic interactions that potentially influence forest structure and function.

Keywords *Aphaenogaster* · Coarse woody decomposition · Myrmecochory · *Reticulitermes* · Wood-rotting fungi

Introduction

Few terrestrial ecosystems lack ants. Given their vast numbers and diverse roles as predators, prey, scavengers and mutualists, they are tightly woven into the fabric of ecological communities (Hölldobler and Wilson, 1990). Their activities influence the structure and function of communities and can have ecosystem-level effects (Hölldobler and Wilson, 1990; Wagner and Jones, 2006; Sanders and van Veen, 2011). *Aphaenogaster* is one of the most abundant ant genera in eastern US deciduous woodlands (Mitchell et al., 2002; Giladi, 2004; Ellison et al., 2007; Warren et al., 2010), and *A. rudis* is considered a keystone mutualist based on its role as a dominant seed disperser (Ness et al., 2009). This role means that its activities influence both the abundance and distribution of many understory plant species (Zelikova et al., 2008; Ness et al., 2009; Warren et al., 2010). Less is known about *Aphaenogaster*'s interactions with other woodland species, and its potential roles in forest ecosystem function.

Decomposing wood provides essential habitat for numerous forest species, including mammals, birds, reptiles, amphibians and arthropods (reviewed in Lofroth, 1998; Evans, 2011). *Aphaenogaster* spp. maintain mobile colonies often found in coarse woody debris (Talbot, 1934; Beattie, 1978; Lynch et al., 1980; Smallwood, 1982). Termites and fungi utilize dead wood as a food resource, reducing its biomass and making nutrients available for plant uptake (Gentry and Whitford, 1982; Gilbertson, 1984). Well-established positive and negative interactions exist between

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termites and wood-rotting fungi (reviewed in Gilbertson, 1984), but less is known about how ants interact with these species. *Aphaenogaster* spp. do prey heavily on termites (Buczkowski and Bennett, 2007, 2008) and ants also secrete antimicrobial compounds that inhibit some fungal species (Beattie et al., 1985; Beattie et al., 1986; Zettler et al., 2002). In turn, these ant traits might influence coarse woody debris decay by both termites and fungi, but there is little existing research into these links.

In conducting artificial nest box studies to identify *Aphaenogaster* spp. microhabitat distributions, we noticed that termites rarely infested those nest boxes colonized by *Aphaenogaster* spp., and wood-rotting fungi appeared less common and abundant in these nests. These observations suggested that ant colonization of the pine nest boxes might inhibit decomposition by hindering termite and fungal activity, so we delayed retrieval of nest boxes for a year. Given that temperature and moisture impact ants, termites and fungi, as well as wood decomposition rates (Ainsworth et al., 1973; Hölldobler and Wilson, 1990; Hudson, 1992; Dunn et al., 2007; Sanders et al., 2007; Suiter et al., 2009; Evans, 2011), we evaluated nest mass loss as a function of ant, termite and fungal colonization across spatial variation in soil temperature and moisture. We took advantage of an existing experimental infrastructure, with 138 nest boxes across five locations in southeastern US forests, to examine how these interactions might influence coarse woody debris decomposition.

Methods

In February 2009, we placed artificial ant nests into forest understories across five sites in a suite of plots designed to assess how *Aphaenogaster* dispersal services and nesting are influenced by biotic and abiotic factors (Warren et al., 2010; Warren et al., 2011), and the nests were left in the field until January 2011 to evaluate ant influence on nest decomposition rates. All five sites were in 60- to 80-year-old mixed hardwood forests. Two sites were located in the Piedmont region of Georgia, USA: the Middle Oconee River watershed (MO) in the State Botanical Garden of Georgia (33°54′08″N, 83°22′58″W, 190–210 m elevation) and Whitehall Forest (WHF) (33°53′41″N, 83°21′68″W, 150–240 m elevation). WHF is ca. 2 km from MO. The other three sites were located in the southern Appalachian Mountain region of North Carolina, USA: Betty's Creek (BC) watershed in the Cowee Mountains (35°17′10″N, 85°17′27″W, 777–790 m elevation), an experimentally watered site (EXP) ca. 400 m from BC (35°16′18″N, 83°17′52″W), and the Coweeta Hydrological Laboratory (CWT) (35°02′12″N, 83°23′91″W, 750–1025 m elevation). CWT is ca. 30 km from BC and EXP. The North Carolina sites are ca. 100 km north of the Georgia sites and have lower MAT and higher MAP (~17°C, ~122 cm in Georgia; ~13°C, ~183 cm in North Carolina).

Artificial ant nests consist of white pine blocks (15 × 12 × 2 cm), and similar pine wood blocks have been used in other studies to simulate coarse woody debris decomposition (Boddy, 2001). Ant nesting chambers were created by routing 1.5 cm deep grooves into the wood with access via a 10 × 4 mm chamber entrance between the wood and a 1.5-mm Plexiglas plate. The nests were placed Plexiglas side up for observation of colonies, but covered with ceramic tiles (16 × 16 cm) to block sunlight and secure the nests in the leaf litter. We placed the nests in contact with the surface soil and flush with the forest litter layers. At MO and BC we established five, 20-m transects at 100-m intervals perpendicular to a small stream. Along each transect, we placed a nest at each 5-m interval ($n = 5$ per transect, $n = 25$ per site). At WHF and CWT we placed nests at the corners of eight 5 × 7 m grids located across north- and south-facing slopes. At the EXP site we placed nests within a 5 × 7 m grid. Overall, we used 138 nests, and all nests were spaced at least 1 m apart.

We used mean weekly abiotic measurements ($n = 4$) in June 2010 to assess relative differences in soil temperature and moisture at each nest, which is an effective means of describing relative, spatial differences in abiotic variables (e.g., Warren, 2010; Warren et al., 2010; Warren et al., 2011; Warren and Bradford, 2011). Volumetric soil moisture percentage was measured with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT, USA); we used the average of five points within 1 m^2 of each nest in our data analysis. Ambient soil temperature was measured at each nest with a T-shaped digital thermometer inserted 8 cm into the soil; we used the average of five points per nest for data analysis.

We observed two *Aphaenogaster* spp. in this study: *A. rudis* Enzmann, found at the Georgia sites, and *A. picea* (Wheeler), found at the North Carolina sites, and two species of termite, *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks). In the North Carolina sites we also observed a second ant species, *Lasius alienus* (Foerster), colonizing nests, but it only occupied a small proportion (8 nests). Because *L. alienus* nests did not constitute a large-enough sample size to compare their effects with those of the *Aphaenogaster* spp., we grouped these species together for the purposes of analyses. Ant species were identified using Fisher and Cover (2007) and Creighton (1950); termite species were identified using Sheffrahn and Su (1994). Fungi grew on many nests but the presence of wood-rotting fungi was scored only when we observed both hyphae and skeletonization of wood, the latter being a result of preferential feeding on high-cellulose, low lignin inter-growth ring tissue (Hudson, 1992). Termites also initially target the low lignin wood tissue when colonizing the nests where they contact the soil, but the termite damage is distinct from fungi because they subsequently remove the lignin-rich wood, and they replace consumed wood with soil. To estimate highest possible initial dry mass of the nest boxes, we used the maximum mass (150 g) of 12 nest boxes not placed in the field. Mass loss was recorded after collected nests were cleaned of all debris and organisms and oven dried (at 65°C) to constant mass. However, our estimates of wood degradation by fungi are likely underestimates given that it was not practical to physically remove hyphae from wood-rotting fungi that undoubtedly penetrated the internal wood tissue (Swift, 1973; Jones and Worrall, 1995).

We accounted for divergence in study designs using mixed effects models that combine all data but assumed that each of the five sites acted as an independent unit within the data set. Given that the clustering of nests in transects and grids might introduce spatial autocorrelation, we evaluated the relationships between the organisms, the artificial nests and the abiotic environment using site as a random effect. Nest colonization by ants, termites and wood-rotting fungi (all scored as present or absent) was analyzed using generalized linear mixed models (GLMMs) assuming a binomial error distribution with overdispersion <1.0. Nest degradation (proportion biomass loss in g) as a function of ants, termites and wood-rotting fungi and their interactions was analyzed using linear mixed models (LMMs) assuming Gaussian error distributions.

To assess how habitat variables might help explain nest colonization, we used LMMs assuming Gaussian error distributions. Across the five sites, we compiled nest abundance by sub-category (transects and grid rows) and calculated colonization abundance and mean soil temperature and moisture by these subsets ($n = 34$ subsets). To account for differences in available nests, we used the total nests per subset to weigh the means in the LMMs so that variance from data points in subsets with greater available nests was given greater weight in the model analysis. We used absolute soil moisture percentage from the observational and experimental plots to account for experimental watering (that is, we measured the actual soil moisture after experimental watering rather than just including a treatment effect so that both observational and experimental soil moisture was that experienced by the ants). Soil temperature and moisture, along with interaction terms, were included in the models as fixed effects, and second-order terms were included to account for unimodal responses. Site was included as a random effect. Second-order and interaction terms were removed from the LMMs if not significant (sensu Engqvist, 2005). The mixed models were fit using the Laplace approximation in the 'lme4' package for the 'R' statistical program (R Development Core Team, 2009). Because it is difficult to interpret continuous interaction terms, and impossible to interpret the main effects, we created abiotic interaction plots by re-centering the variables and plotting main and interaction effects. We considered coefficients with p value <0.05 significant and coefficients with p value <0.10 marginally significant (sensu Hurlbert and Lombardi, 2009).

Results

Ants colonized 57% of the nests (29% *A. picea*, 22% *A. rudis*, 6% *L. alienus)*, termites colonized 14% (8% *R. flavipes*, 6% *R. virginicus*) and wood-rotting fungi colonized 51% of nests. (Note that some nests were not colonized and others were colonized by multiple organism groups, so the percentages do not total 100%.) The ants colonized a similar percentage of nests in Georgia (56%) and North Carolina (58%), whereas termites colonized far more nests in Georgia (32%) than North Carolina (1%). Nest utilization by wood-rotting fungi was somewhat higher in Georgia (60%) than North Carolina (46%). In only two instances did ants and termites utilize the same nest, and in both cases termites colonized after the nests were abandoned by ants. Artificial nest colonization by ants and termites was negatively correlated (coeff. $= -2.27$, SE $=$ 0.66, $z = -3.45$, $p = 0.0006$), as was colonization by ants and wood-rotting fungi (coeff. $= -0.97$, SE $= 0.38$, $z = -2.61$, $p = 0.009$). Nest colonization by termites and wood-rotting fungi was positively correlated (coeff. $=$ 1.38, SE $= 0.66$, $z = 2.08$, $p = 0.04$).

Given the relationships between ant, termite and fungal colonization, we assessed whether the presence of an organism group influenced nest decomposition. Mean biomass loss for all nests was 51.4 ± 14.4 g, and biomass loss appeared somewhat higher in Georgia (56.0 ± 14.4 g) than North Carolina (48.2 ± 16.1 g), likely due to the much higher presence of termites at the warmer Georgia sites. Indeed, nests colonized by termites had the greatest mean mass loss (Fig. 1). A simple comparison of means where an organism group had been/was present versus absent revealed significantly lower biomass loss when nests were colonized by ants (Fig. 1a), whereas biomass loss was significantly higher when nests were colonized by termites (Fig. 1b) and wood-rotting fungi (Fig. 1c). In order to elucidate potential interactions between the ants and other organisms in affecting mass loss, we constructed LMMs to partition variance across the presence or absence of ants, termites and fungi. Because of high collinearity between termite and fungal colonization (variance inflation factors >7) these were evaluated in separate models. Ants and termites very rarely occupied the same nests, reflected by an insignificant ant × termite interaction term (coeff. $=$ -0.05, SE $= 0.10$, $t = -0.56$, $p = 0.58$). When evaluated

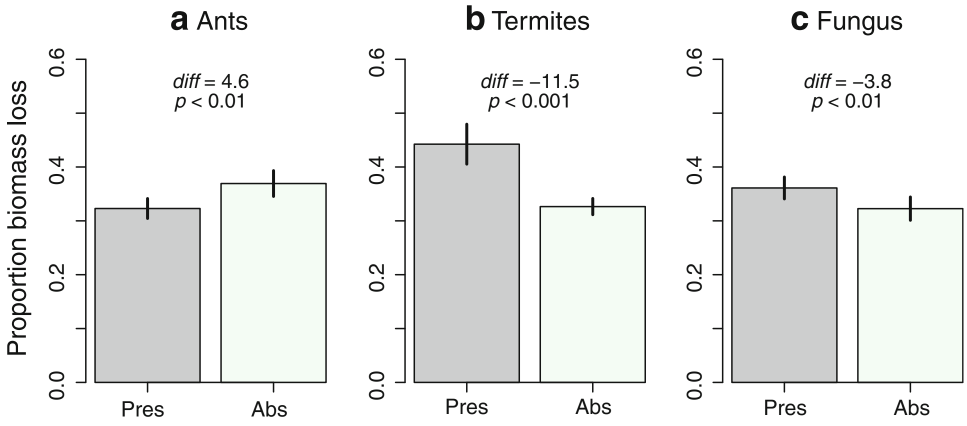

Fig. 1 Proportional change in wooden-nest mass with the presence (pres) or absence (abs) of **a** *Aphaenogaster picea*, *A. rudis* and *Lasius alienus* ants, **b** *Reticulitermes flavipes* and *R. virginicus* termites and **c** wood-rotting fungi. Differences in mean biomass loss (±95% CI)

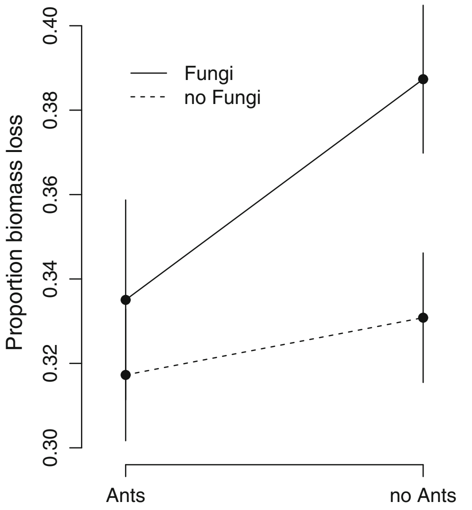

Fig. 2 Interaction plot of ant × fungal effects on the proportion of wood-nest mass loss. The marginally significant ($p < 0.10$) interaction term indicates that ants and fungus do not affect biomass loss independently. Whereas fungal colonization does not impact nest biomass loss when ants also are present, when ants are absent from nest boxes fungal colonization reduces biomass significantly. This interaction is highlighted by the fact that the *lines* used to connect the data points are not parallel to one another. Point values are means ± 95% CI

in the same LMM as termites, the impact of ants on nest biomass was minimal (coeff. = 0.03, SE = 0.03, $t = 1.20$, $p = 0.23$) whereas nest biomass decreased considerably with termite presence (coeff. = −0.16, SE = 0.04, $t = -3.71$, $p = 0.0003$). Ants and wood-rotting fungi often did occupy the same nests, and there was a marginally significant ant × fungus interaction term (coeff. = 0.10, SE = 0.06, $t = 1.77$, $p < 0.08$). This interaction indicated that the presence of ants corresponded with significantly less nest biomass loss by wood-rotting fungi (Fig. 2).

Overall, increased temperature best predicted nest colonization by ants, termites and wood-rotting fungi, but these relationships were complicated by interactions with soil moisture. For ants, there was a significant soil temperature × moisture interaction term (coeff. = 0.026, SE = 0.007, $t = 3.59$, $p = 0.001$), indicating that ant colonization increased far greater with high temperature and soil moisture than either abiotic variable alone (Fig. 3a). Conversely, for termites the significant temperature × moisture interaction term (coeff. = 0.011, *SE* = 0.006, $t = 1.755$, $p = 0.09$) indicated that higher soil moisture decreased colonization at higher temperatures (Fig. 3b). Fungal colonization exhibited a similar pattern to that as termites as the significant temperature × moisture interaction term (coeff. = 0.013, SE = 0.008, $t = 1.717$, $p = 0.09$) also indicated that higher soil moisture decreased colonization at higher temperatures (Fig. 3c).

Discussion

Ant species in the *Aphaenogaster* genus are exceedingly abundant and widespread in eastern US deciduous forests (Mitchell et al., 2002; Giladi, 2004; Ellison et al., 2007; Warren et al., 2010; Warren and Bahn, 2011). Ness et al. (2009) suggested that the *Aphaenogaster* genus plays a key role in these forests through its dispersal of understory herbs, which comprise approx. 50% of the plant diversity in these systems (Handel et al., 1981; Beattie and Hughes, 2002; Gilliam, 2007). We find that *Aphaenogaster* spp. also may play a critical role in mediating habitat availability for other organisms, as well as by inhibiting decomposition of coarse woody debris through negative effects on the activities of termites and wood-rotting fungi. Notably, *Aphaenogaster* ants, *Reticulitermes* termites and wood-rotting fungi are all highly abundant in many temperate forest systems, suggesting these interactive effects on wood decomposition may occur across broad spatial scales.

The interaction between ants and termites seems easily explained: *Aphaenogaster* spp. eat termites (Buczkowski and Bennett, 2007, 2008). *Reticulitermes* termites are highly abundant and widespread (Nutting, 1990), and

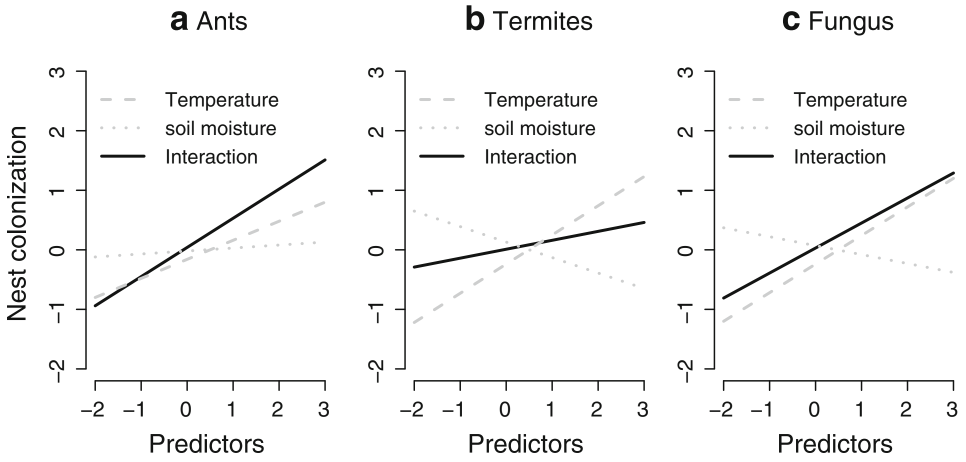

Fig. 3 Continuous interaction plots of the effects of soil temperature and soil moisture on ant (**a**) termite (**b**) and fungus (**c**) colonization of wood nests. All variables are standardized for plotting

termite colonies provide a concentrated, localized protein source for ants (Wood and Sands, 1978). However, in intact colonies, the *Reticulitermes* soldier caste can fend off *Aphaenogaster* foragers so that the termite colonies are not destroyed (Buczkowski and Bennett, 2008). This might explain why we observed nests colonized by either ants or termites, with the two instances where termites colonized the same nest as ants occurring only after ants had abandoned the nests. Further work is needed to quantify ant impacts on termite demography and dispersal, and how these interactions impact ecosystem processes. In addition, *Aphaenogaster* ant colonies are highly mobile, and we minimized nest checking to minimize colony stress, so a future assessment of *Aphaenogaster* impact might include ant occupancy time as a predictor of nest biomass retention.

The observed effects of ants on wood-rotting fungi may be less direct than with termites. Ants are the only insects with metapleural glands (Hölldobler and Wilson, 1990), which are specialized organs that produce and secrete antimicrobial compounds (Beattie et al., 1985; Beattie et al., 1986). Because they live in dense, closely related populations that reside within the dark, moist ground conditions conducive to growth of microbial pathogens, metapleural secretions are important for ant fitness (Bailey, 1920; Alexopouclous, 1962; Ainsworth et al., 1973; Beattie et al., 1985; Beattie et al., 1986; Stow and Beattie, 2008). As such, any effect of metapleural secretions on wood-rotting fungi is probably a by-product of ant defense against pathogenic fungi. Indeed, metapleural chemicals inhibit soil fungal mycelia development (Beattie et al., 1985; Beattie et al., 1986), and ant mounds contain less fungal diversity than soil without ant colonies (Zettler et al., 2002). These effects have been investigated for soil fungi, but we did not find any literature pertaining to wood-rotting fungi. In future work, it will be important to score total fungal biomass in the wood (based on chitin) to provide a continuous versus discrete estimate of potential fungal activity (e.g., Jones and Worrall, 1995).

Whereas the interior of coarse woody debris appears the preferred nesting habitat for *Aphaenogaster* spp. (Buczkowski and Bennett, 2007; Warren et al., 2011), ants also nest in leaf litter and beneath rocks (Talbot, 1934; Beattie, 1978; Lynch et al., 1980). This places them in direct contact with the soil, and the impacts of *Aphaenogaster* on soil processes have been the main focus of ant ecosystem research (e.g., Zettler et al., 2002; Zelikova et al., 2011). In utilizing coarse woody debris, *Aphaenogaster* ants occupy habitat also favored by termites and wood-rotting fungi. As a highly abundant organism in eastern deciduous forests, *Aphaenogaster* spp. may influence ecosystem processes when colonizing coarse woody debris via interactions with termites and fungi. Future research is required to assess this possibility.

Across our five sites, we find that termites consume more wood biomass in a year, but wood-rotting fungi are more widespread and colonize 3.5 times more nests. Termites only colonized a large proportion of nests at the two more southerly sites (in Georgia). The extent to which *Aphaenogaster* inhibits the decomposition of coarse woody debris may then be dependent on geographic location, and the associated environmental conditions, with greater relative effects on wood decay rates where termites are present. What is clear from our data is that *Aphaenogaster* presence corresponds with reductions in the microhabitat distribution of both termites and wood-rotting fungi, and thus corresponds with reduced decomposition of our artificial nest boxes. In addition, our data indicate that the ants, termites and fungi all favor coarse woody debris in warmer microhabitat, suggesting they may overlap both in their preferences for biotic (dead wood) and abiotic (temperature) habitat. However, whereas *Aphaenogaster* colonization appears augmented by higher soil moisture, wetter conditions mitigate termite and fungal colonization. These data suggest some habitat segregation between *Aphaenogaster* and the organisms along soil moisture gradients or, as suggested by the inverse colonization patterns reported here, a preference by *Aphaenogaster* spp. for relatively wetter habitat reduces its occupancy by termites and fungus. As higher temperature and moisture also favor more rapid decomposition rates, this preference may make the effect sizes of ant–fungal and ant–termite interactions dependent on abiotic conditions, as other effects of *Aphaenogaster* appear to be (e.g. Warren et al., 2010).

Our study arises from field observations of colonization patterns of artificial ant nests. As such, future work is required to establish the precise mechanisms, generality and magnitude of how the ants influence the decomposition activities of termites and fungi. For example, ants in the genus *Lasius* occupied a small percentage of nests, and further work is required to establish whether *Aphaenogaster* and *Lasius* impacts on the decay of coarse woody debris are functionally equivalent. Also, by characterizing fungal colonization by presence or absence of wood damage, our estimates of ant effects on the activities of wood-rotting fungi are likely underestimates. Indeed, wood-rotting fungi convert decomposed biomass into chitin, and we estimated fungal colonization by outer decomposed wood, so we may have underestimated the mass loss of wood by including inner-wood fungal biomass (Swift, 1973; Jones and Worrall, 1995). Future research needs to quantify fungal biomass in coarse woody debris colonized and not colonized by ants. It would also be important to identify fungal taxa because metapleural gland secretions can have taxon specificity (Beattie et al., 1986; Zettler et al., 2002), and so may influence whether more or less effective wood-rotting fungi colonize nests.

Coarse woody debris plays a critical role in shaping the structure and function of forests, through provision of habitat for microbial, invertebrate and vertebrate species, stabilization of soils, and as a stable nutrient source. In the forest floor, ants are equally ubiquitous, and those in the genus *Aphaenogaster* likely play a key role given their abundance and also dispersal of understory plant seeds. Our observations suggest these ants—through their nesting preferences—also influence the abundance and distribution of termites and wood-rotting fungi, with consequences for the decay rates of coarse woody debris. How these consequences influence the availability of habitat for other species, and ecosystem-scale rates of wood decomposition, is unresolved. Additional work is needed to investigate how the shared preference for woody debris and warmer microsites by the ants, termites and fungi may affect forest structure and function in a changing climate.

Acknowledgments We thank Joshua King and Neil McCoy for advice on nest box construction, Jim Affolter and the State Botanical Garden of Georgia for site access and two anonymous reviewers for manuscript comments. Funding was from the National Science Foundation (award DEB-0823293) to the Coweeta Long Term Ecological Research Program and from the Yale School of Forestry and Environmental Studies.

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