

Contrasting effects of insect exclusion on wood loss in a temperate forest

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Abstract. Experimental efforts to determine how insects influence terrestrial wood decomposition are few, especially in temperate regions. To address this need, a five-year exclusion study was conducted in northern Mississippi, U.S.A., to quantify insect contributions to wood decay using one-meter loblolly pine (*Pinus taeda* L.) bolts. The study included three treatments: (1) “partially protected” bolts that were placed on cypermethrin-treated soil to exclude subterranean termites (Isoptera: Rhinotermitidae: *Reticulitermes* spp.) while permitting colonization by beetles (Coleoptera) and other saproxylic taxa, (2) “fully protected” bolts that were placed on cypermethrin-treated soil and enclosed within screen cages to protect against all insects and (3) “unprotected” bolts that were not subjected to either exclusion treatment. The full insect community consumed approximately 15–20% of wood volume in unprotected bolts, about six times more than in partially protected bolts from which termites were excluded. There were no differences in specific gravity (based on initial wood volume) or mass loss among treatments, however. It is not clear whether these findings are due to an inhibition of microbial decomposers by insects (e.g., antimicrobial compounds secreted by termites or ants), a stimulatory effect of the exclusion treatments (e.g., cypermethrin stimulating fungal growth or cages favorably altering wood moisture), or some combination of both. When based on final water-displaced volume, specific gravity was significantly higher for unprotected bolts than for those fully protected, probably because termites selectively consume the least dense wood. By the end of the study, about 20% of the final dry weight of unprotected bolts consisted of termite-imported soil. Wood volume consumed and soil content decreased with distance from the ends of the bolts whereas water content exhibited the opposite pattern. We detected a significant negative relationship between water content and volume consumed by termites, possibly because water content decreases with increasing wood density and termites tend to avoid high density wood. While insects clearly consume large volumes of wood in southeastern U.S. forests, our results suggest they do not act to accelerate mass loss beyond what is achieved by microbial decomposers. More research is needed to confirm this, however—especially given the uncertainties inherent to exclusion studies.

Key words: arthropods; biodiversity; coarse woody debris; dead wood; ecosystem services; invertebrates; saproxylic taxa.

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INTRODUCTION

Despite the broad importance of dead wood to forest carbon budgets (Turner et al. 1995),

nutrient cycling (Harmon et al. 1986), and biodiversity (Stokland et al. 2012), the decomposition of this substrate remains, in many respects, a poorly understood process. For example, the

diverse assemblage of arthropods associated with dead wood has long been suspected to accelerate decomposition but the magnitude and nature of this influence have only rarely been investigated (Ulyshen and Wagner 2013). Potential contributions to the process include consuming and excavating wood (Edmonds and Eglitis 1989), hastening wood fragmentation through mechanical weakening (Blackman and Stage 1924), facilitating fungal colonization through tunneling (Swift and Boddy 1984) and vectoring fungal decomposers (Dowding 1984, Swift and Boddy 1984). The net effect of these activities on wood decomposition and the relative importance of each should vary greatly at both regional and local scales depending on faunal composition (e.g., Schuurman 2005, Warren and Bradford 2012) and abiotic conditions (e.g., temperature, humidity, resource quality, etc.). In addition to quantifying ecosystem services provided by saproxylic arthropods (Ulyshen 2013), research aimed at elucidating such patterns may help explain decay rate variability and benefit efforts to model global carbon and nutrient budgets (Schuurman 2005, Cornwell et al. 2009).

Wood-consuming arthropods can be found wherever trees grow but the composition of this fauna varies widely. Aided by symbiotic protists and fungi capable of digesting cellulose, termites dominate the wood-feeding arthropod community in many warm temperate or tropical regions. The importance of these insects to wood decay has been discussed for many decades (Lee and Wood 1971, Wood 1976, 1978, Wood and Sands 1978, Longman and Jenik 1987) but relatively few efforts have been made to quantify their contributions to the process. A number of studies carried out primarily in Africa and Asia, however, suggest termites (especially the fungus-farming macrotermitines) may consume a large proportion of the dead wood produced annually (Abe 1978, 1980, Buxton 1981, Collins 1981, Schuurman 2005). Whereas termites are concentrated in warmer regions, beetles associated with dead and dying wood are distributed much more widely. A number of studies indicate these organisms can also be important contributors to the decay process (Leach et al. 1937, Edmonds and Eglitis 1989, Müller et al. 2002, Angers et al. 2012).

The forests of the southeastern United States

experience a warm climate and receive considerable amounts of rainfall. While supporting a high diversity of other saproxylic insects as well (Hanula 1996, Ulyshen and Hanula 2009), the most economically important wood-consuming arthropods native to the region are the five currently-recognized species of subterranean termites (Rhinotermitidae: *Reticulitermes* spp.) (Lim and Forschler 2012). Although studied extensively in urban settings where they are major structural pests, very little is known about their ecology in forests. For example, we know of only two studies that provide information on the contributions of termites to wood decay in forests of the region. Gentry and Whitford (1982) estimated that termites removed 3–20% of the mass from wooden blocks within nine months in South Carolina. Similarly, Warren and Bradford (2012) reported an 11.5% greater loss of mass from wooden blocks due to termites after 23 months in Georgia and North Carolina. Because both studies used wooden blocks instead of naturally-occurring substrates, however, these results may not provide an accurate representation of what happens in nature (Ulyshen and Wagner 2013).

Here we report the results from a five year exclusion study aimed at quantifying the contributions of termites and other insects to the decomposition of loblolly pine (*Pinus taeda* L.), one of the most important timber species in North America (Schultz 1997). Our main objectives were to (1) compare volumetric and gravimetric wood losses between bolts from which insects were or were not excluded, (2) determine the relative importance of termites and other insects to the decay process and (3) examine how insect activity and wood moisture content varied from the ends to the centers of experimental bolts.

METHODS

Location and design

Thirty-four loblolly pine (*Pinus taeda* L.) trees measuring 21–33 cm in basal diameter and 19–23 m tall were selected from a 1-ha site in a 24-yr-old plantation on the Noxubee National Wildlife Refuge (NWR) in Noxubee County, MS. After felling in June 2005, each tree was cut into 1-m bolts beginning at a top bole diameter of 20 cm.

A disk 20 cm thick was cut between each 1-m bolt for use in estimating the dry weight (i.e., weight after drying for at least 2 d at 102°C), initial water content, and specific gravity (i.e., oven-dry weight/wet volume) of the preceding bolt. These measurements were made on 2.5 cm thick disks taken from the centers of the 20-cm disks within 2 months after felling.

In total, 187 bolts were cut and these were numbered by tree and bole location. The minimum and maximum wood diameters were measured on both faces of each bolt using a ruler. They were then transported to a nearby stand dominated by loblolly pine and mixed hardwoods. An 11 by 17 study grid was established at the site, with cell centers separated by 10 m. One bolt was placed at the center of each cell in an east/west orientation. Forty-seven grid cells were randomly selected for the “fully protected” treatment. At the center of each, a 1 × 2 m area of soil was treated with 0.5% cypermethrin (Demon TC, 160 mL per 8 L water) to exclude subterranean termites (Fig. 1D). The termiticide was administered as the trees were felled at the beginning of the experiment and again in February 2007. Bolts assigned to this treatment were also enclosed within a 30.5 × 30.5 × 111.8-cm cage covered with Lumite woven polyester mesh (Synthetic Industries, Gainesville, GA; 965-μm mesh opening) to prevent aerial insect colonization (Fig. 1A, B). The mesh cages were placed over frames made of plastic tubing and staked down along the edges. The enclosed bolts were in direct contact with the cypermethrin-treated soil.

Bolts placed in the remaining cells were completely exposed to insect attack and belonged to the “unprotected” treatment (Fig. 1C). After one month, 109 (79%) of the unprotected bolts had been colonized by termites as determined visually after gently rolling each bolt a quarter of a turn. A third treatment was then added to the study by moving the 31 remaining unprotected bolts (i.e., those that had not been attacked by termites) to the nearest insecticide-treated plot. As they were not enclosed within cages, these “partially protected” bolts continued to undergo beetle attack. Although the addition of this treatment was an afterthought and did not conform to proper randomization, it provided a unique opportunity to compare the relative

importance of termites and beetles to wood loss. The extent to which the insecticide treatment excluded beetles and other insects from colonizing partially protected bolts cannot be determined from this study.

Measurements

Of the 187 original bolts, 146 were sampled over a five-year period with sampling taking place every four months (15 sampling periods in total). Each bolt was sampled a single time over the course of the study using a randomly determined schedule. The remaining 41 bolts were excluded from the study due to deviations from the intended treatments based on visual inspections made prior to data collection. For example, “fully protected” bolts that had been attacked by beetles small enough to fit through the mesh openings (e.g., several species of scolytine weevils) were eliminated. The total number of bolts sampled from each treatment varied over time as shown in Appendix A. Within two days of collection, a band sawmill (Lumbermate 2000) was used to cut each bolt into 9 disks (~2.5-cm thick) with the fifth representing the center of the bolt (Fig. 1E). The separation between disks was about 7.5 cm. Due to extensive termite damage, it was necessary at 32 months and thereafter to secure disks prior to cutting with plastic bands (Catamount Nylon Cable Ties). By 56 months, the unprotected bolts were too degraded to cut into 2.5 cm disks. Instead, they were cut into five ~20-cm disks using a chainsaw, the second and fourth of which were used in measurements.

Once cut and cleaned of debris, the disks were weighed and their minimum and maximum thicknesses and wood diameters measured. They were then placed in an oven for at least two days at 102°C to obtain dry weights. Because it remains unclear which method of calculating water content provides the most biologically meaningful information (Harmon et al. 1986), we calculated water content for wet and dry weights separately to ease comparisons with other studies. Accomplishing accurate dry weight measurements for unprotected bolts became increasingly complicated over time due to the tendency of termites to pack their galleries with soil. For the first 32 months, small dental tools and pressurized air were used to remove

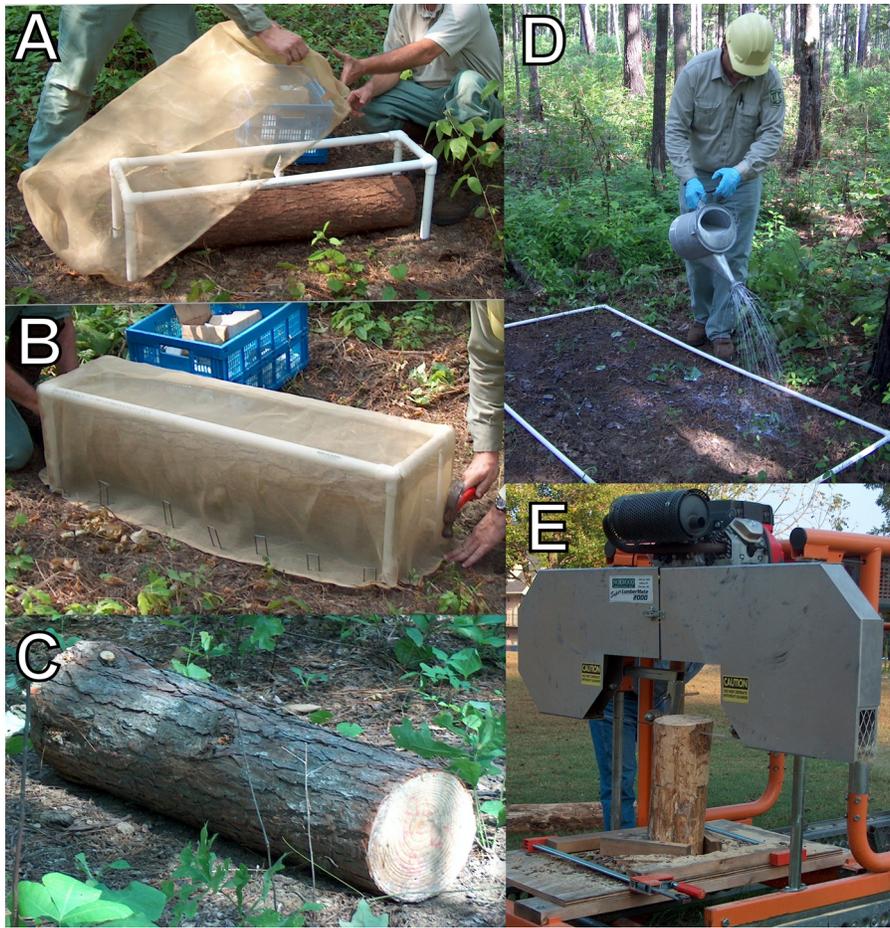


Fig. 1. Bolt being enclosed within mesh cage (A); completed cage (B); unprotected bolt (C); applying cypermethrin (D); cutting disks (E).

this material. Subsequently, the dried disks were incinerated using a propane gas burner (Ulyshen and Wagner 2013) and the resulting soil weight was subtracted from the total disk dry weight. To properly account for missing wood, specific gravity (designated herein as “specific gravity (initial wood volume)”) was calculated using the final dry weight (without soil) and initial volume for each disk (Ulyshen and Wagner 2013). Initial volume was calculated using the average disk thickness and the average wood diameter measured at the beginning of the study for each 1-m bolt. We multiplied initial wood volume by initial specific gravity to estimate the initial mass for each disk. This was used to calculate percent mass loss. We were also interested in determin-

ing how the specific gravity (designated herein as “specific gravity (final wood volume)”) of the remaining wood (by ignoring wood missing due to insect activity) differed between the protected and unprotected bolts. To accomplish this, we submerged the middle disk from each unprotected and fully protected bolt in a tared pan of water on a scale. After allowing 30 minutes for the air trapped within the wood to be displaced by water, the weight (=volume) was recorded.

After the disks were dried, digital images of the top and bottom surfaces were taken next to a ruler for calibration. The images were enhanced (e.g., backgrounds whitened) and areas of insect damaged to the wood surface were delineated (e.g., colored white) using Photoshop 7.0 (Adobe

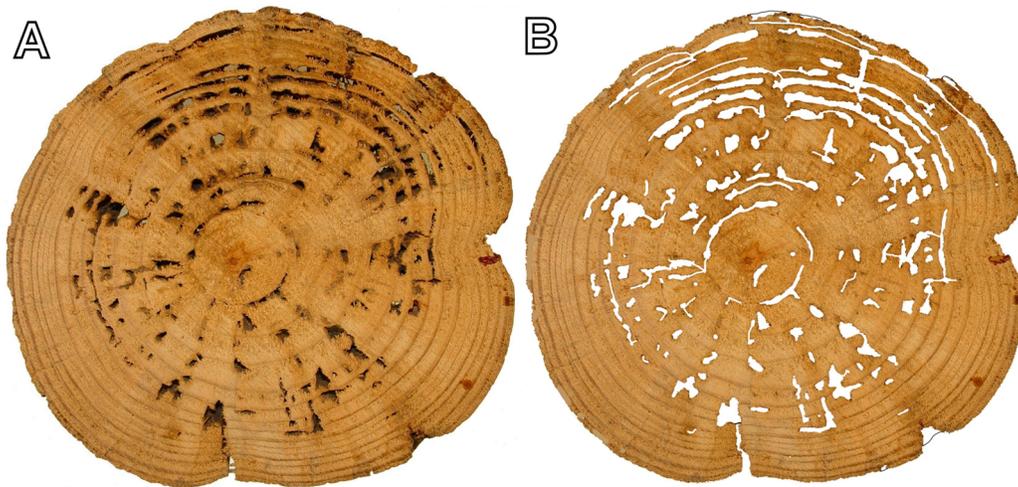


Fig. 2. Insect damage visible on dried disks (A) was colored white (B) and quantified using computer software to estimate percentage of wood volume consumed (see text). Note that much of the damage was limited to the lighter-colored “spring wood” whereas the darker and denser “summer wood” remained relatively intact.

Systems, San Jose, CA) (Fig. 2). SigmaScan Pro 5.0 (Systat Software, Point Richmond, CA) was used to measure the surface areas of intact wood and the wood damaged by termites or beetles and the min/max diameters of the top and bottom surfaces of each disk. Because it became increasingly difficult to distinguish termite galleries from other kinds of insect damage over time, it was not possible to separate the wood volumes consumed by termites and beetles for the unprotected treatment. Volumetric measures of insect damage ended with the 52-month sample after which it became too difficult to accurately discern damage.

Data analysis

The effects of insects on wood decay were investigated by comparing wood volume consumed, specific gravity and mass loss between treatments and over time. How the exclusion treatment may have affected wood water content was also of interest as this has the potential to affect microbial activity. We also examined the relationship between water content and wood volume consumed by insects in unprotected bolts. We were also interested in looking at how the cross-sectional area of the bolts may have varied between treatments (e.g., whether insect activity accelerates log collapse) and over time. While the main analysis focuses on differ-

ences among-bolts (“among-bolt analysis”), our sampling design also provides a unique opportunity to examine how insect activity (wood consumption and termite-imported soil) and water content vary with distance from the ends to the centers of bolts (“within-bolt analysis”).

For among-bolt analyses, measurements made on the nine disks comprising each bolt were summed (thickness, dry weight) or averaged (water content, percent damage, etc.) to obtain composite values for the entire experimental unit. The PROC GLM procedure of SAS (SAS Institute 1999) was used to conduct analyses of variance on a dataset from which the partially protected treatment had been excluded (because it was not properly randomized). The dataset was further limited to the first 44 months, after which the fully protected treatment was discontinued. The response variables were specific gravity, mass loss, water content (based on both wet and dry weights) and change in cross-sectional area (Table 1) with the model parameters being treatment, time, treatment \times time, initial wood specific gravity (covariate) and initial wood diameter (covariate). Time was partitioned into $time_{lin}$ (time linear) and $time_{lof}$ (time lack-of-fit to linear, i.e., the variation among time effects that is not explained by linear regression) to distinguish between linear and non-linear effects of time on the response variables (Steel et al. 1997). Data

Table 1. Main response variables used in the analysis.

Variable	Calculation	Treatment			Sample coverage (months)	Comments
		Partially protected†	Fully protected‡	Unprotected		
Specific gravity						
Initial wood volume	(final oven-dried wood weight§)/(estimated initial wet wood volume)	x	x	x	4–60	
Final wood volume	(final oven-dried wood weight§)/(final water-displaced oven-dried wood volume)		x	x	4–32	measured from center disks only
Mass loss (%)	[(estimated initial oven-dried wood weight) – (final oven-dried wood weight§)/(estimated initial oven-dried wood weight)] × 100	x	x	x	4–60	
Volume consumed (%)	Percentage of oven-dried disk area with visible insect damage	x	x	x	4–52	measurements made with image software
Water content (%)						
Dry weight basis	((wet weight – dry weight)/(dry weight)) × 100	x	x	x	4–60	weights included soil, when present
Wet weight basis	((wet weight – dry weight)/(wet weight)) × 100	x	x	x	4–60	weights included soil, when present
Soil content (%)	[(soil weight)/(final oven-dried wood weight with soil)] × 100			x	36–60	soil isolated by burning wood
Change in cross sectional area (%)	[(estimated initial wet wood cross-sectional area) – (final wet wood cross-sectional area)]/(estimated initial wet wood cross-sectional area) × 100	x	x	x	4–60	

† Treatment ended at 24 months.
 ‡ Treatment ended at 44 months.
 § Final weight after correcting for soil.

transformations were applied prior to analysis when necessary to improve normality (see below) but only untransformed means and standard errors are presented in figures. When found to be non-significant the covariates were removed from the final model.

For within-bolt analyses, we were interested in examining how volume consumed by insects, water content and soil content varied with distance from the ends to the centers of the unprotected bolts (the other treatments were not included). The approximate distances from bolt ends were 10, 20, 30, 40 and 50 cm for disks one and nine, two and eight, three and seven, four and six and five, respectively. For each bolt, the response variables of interest were then averaged for disks corresponding to each distance (only a single disk, disk five, provided data for the central 50 cm distance). A split plot analysis of variance was performed using PROC GLM with time as

the whole plot factor and distance as the subplot factor. A TEST statement was included to test the main effect of time against whole plot error based on variation among means for bolts nested within sampling times, denoted bolts(time). Time and distance × time were tested against sub-plot error, or distance × bolt(time), the default error in GLM. We also used contrast and estimate statements to test for linear trends with distance.

Transformations made to the data prior to analyses are listed below. Initial wood area, initial diameter, initial specific gravity, dry wood weight without soil, final wood area and final specific gravity (initial wood volume) were log-transformed whereas initial water content, final water content (wet weight basis), soil content and volume consumed were arcsine-transformed. Final water content (dry weight basis) was fourth-root-transformed.

RESULTS

Consumption by insects

Although beetle galleries that varied widely in diameter and extent were commonly observed in the partially protected bolts (Fig. 3), much larger volumes of wood were consumed in unprotected bolts colonized by termites. For example, after two years, partially protected bolts had lost only about one sixth as much wood volume as their unprotected counterparts (1.9% vs. 11.4%, respectively; Fig. 4A). The volume of wood consumed by termites and other insects increased rapidly after the first year but gradually leveled off to between 15 and 20% (Fig. 4A). For bolts belonging to the unprotected treatment, distance from the ends of the bolts had a significant and linear effect on volume consumed by insects (Table 2), with the volume consumed decreasing with distance from the ends ($t = -6.57$, $P < 0.0001$).

Mass loss

Percent mass loss increased steadily (Fig. 4B) and significantly (Table 3) over time but there were no differences among treatments. At the end of the experiment, after 60 months, about 60% of the original mass had been lost (Fig. 4B) from unprotected bolts. There was a significant treatment \times time_{eof} interaction (Table 3) as can be seen in Fig. 4B, i.e., mass loss varied more erratically over time for fully protected bolts than for unprotected bolts.

Specific gravity

From an average initial (i.e., between-bolt samples taken at the beginning of the study) value of 0.4 ± 0.003 (mean \pm SE; range: 0.33–0.52), specific gravity (initial wood volume) decreased gradually (Fig. 4C) and significantly (Table 3) over time. There were no differences in specific gravity (initial wood volume) among treatments and initial wood specific gravity was a significant covariate in the model (Table 3). As for mass loss (see above), there was a significant treatment \times time_{eof} interaction (Table 3) as can be seen in Fig. 4C, i.e., specific gravity (initial wood volume) varied more erratically over time for fully protected bolts than for unprotected bolts.

When final wood volume was determined using the water-displacement technique (i.e.,



Fig. 3. An example of damage caused by beetles in a partially protected bolt.

whereby wood consumed by insects was excluded), specific gravity (final wood volume) decreased steadily and significantly over time ($F_{1,60} = 60.0$, $P < 0.0001$; Fig. 4D). The specific gravity (final wood volume) of wood from the unprotected treatment was significantly higher than that from the fully protected treatment ($F_{1,60} = 7.3$, $P < 0.01$; Fig. 4D).

Decay rate constant

The average specific gravity for the ten unprotected bolts sampled at the end of the study (i.e., after 60 months of decay) was 0.17. The estimated initial specific gravity for the same ten bolts was 0.42. The decay rate constant based on these data is 0.015 for months or 0.181 for years (formulas from Stokland et al. 2012). The half-life based on this value is about 46 months or 3.8 years, consistent with what is shown in Fig. 4.

Water content

For the first two years, wood water content (in terms of both dry and wet weights) remained about the same but increased steadily thereafter (Fig. 5A, B). Moreover, there was a significant interaction between treatment and time_{lin} (Table 3, Fig. 5A, B). Whereas for the first 20 months fully protected bolts had a higher water content than unprotected bolts, the opposite pattern was observed consistently after 24 months, i.e., the lines crossed at 24 months (Fig. 5A, B). For bolts

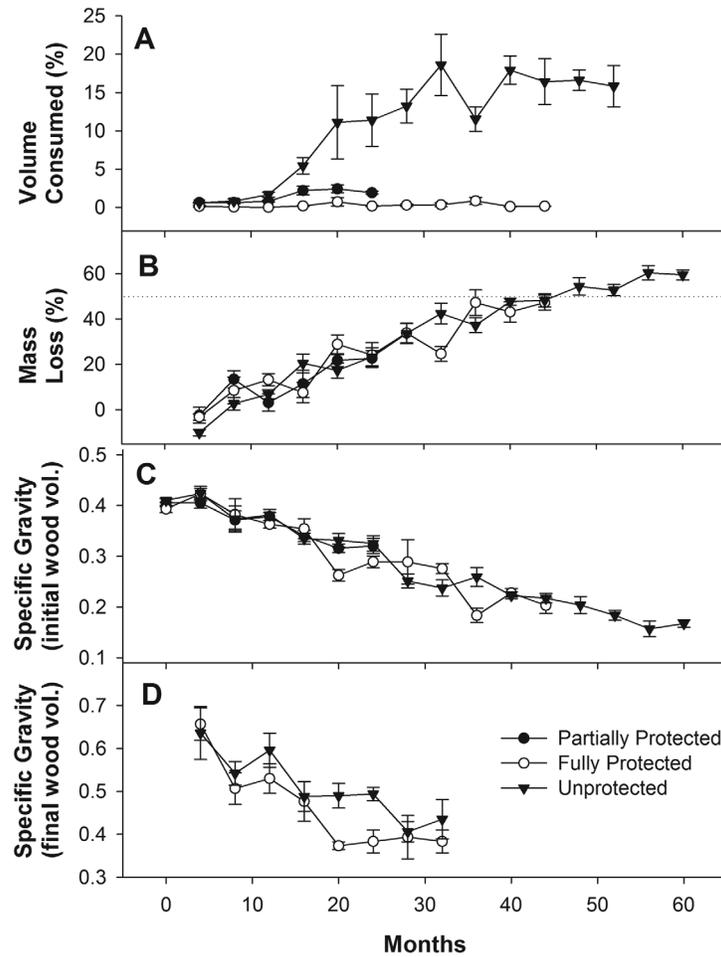


Fig. 4. Wood volume consumed by insects (A), mass loss (B), specific gravity based on the initial wood volume (C) and specific gravity based on final wood volume (D) (mean ± SE). The dotted line in panel B represents 50% mass loss.

belonging to the unprotected treatment, distance from the ends of the bolts had a significant and linear effect on water content (Table 2), with water content increasing with distance from the ends ($t = 5.79, P < 0.0001$).

In a separate analysis focused on unprotected bolts only, water content (dry weight based) varied significantly with time ($F_{1,63} = 6.52, P = 0.01$) and with volume of wood consumed by insects ($F_{1,63} = 21.74, P < 0.0001$). The regression

Table 2. ANOVA results for within-bolt comparisons (unprotected treatment only).

Variable	Volume consumed (%)		Water content (%)		Soil content (%)	
	F	df	F	df	F	df
Distance	11.09**	4, 220	9.95**	4, 220	7.19**	4, 92
Linear distance	43.17**	1, 220	33.52**	1, 220	25.82**	1, 92
Time	13.75**	12, 55	19.16**	12, 55	1.13	4, 23
Distance × Time	1.38	48, 220	1.14	48, 220	0.64	16, 92
Bolt(time)	59.65**	55, 220	23.49**	55, 220	71.19**	23, 92

Notes: Results for water content are shown on a wet weight basis only. Asterisks denote significance: * $P < 0.05$; ** $P < 0.01$.

Table 3. ANOVA results for among-bolt comparisons (for the first 44 months and excluding partially protected bolts, see *Methods*).

Variable	Specific gravity (initial wood volume)		Mass loss (%)		Water content (%) (dry weight basis)		Water content (%) (wet weight basis)		Change in cross sectional area (%)	
	F	df	F	df	F	df	F	df	F	df
Treatment	0.55	1, 65	0.21	1, 65	0.01	1, 66	0.00	1, 66	0.23	1, 66
Time _{lin}	450.74**	1, 65	526.48**	1, 65	50.65**	1, 66	46.03**	1, 66	2.31	1, 66
Time _{lof}	1.50	9, 65	1.23	9, 65	11.93**	9, 66	12.86**	9, 66	0.78	9, 66
Treatment × Time _{lin}	0.26	1, 65	2.85	1, 65	16.16**	1, 66	17.20**	1, 66	3.86	1, 66
Treatment × Time _{lof}	3.46*	9, 65	3.24*	9, 65	1.47	9, 66	1.55	9, 66	1.51	9, 66
Initial specific gravity	18.34**	1, 65	8.09*	1, 65	ns		ns		ns	
Initial diameter	ns		ns		ns		ns		ns	

Notes: Time was partitioned into time_{lin} (time linear) and time_{lof} (time lack-of-fit to linear). When non-significant (ns) the covariates (initial wood specific gravity and diameter) were removed from the model. Asterisks denote significance: * $P < 0.05$; ** $P < 0.01$.

coefficient for volume consumed was -2.66 ($t = -4.66$, $P < 0.0001$), indicating that water content decreases as wood consumption by insects increases. There was also a significant time × consumption interaction ($F_{1,63} = 6.87$, $P = 0.01$). The nature of the interaction is unclear, however (Appendix B).

Soil content

The soil content of unprotected bolts increased steadily from 36 months (i.e., the first sample for which we collected such data) to the end of the study (Fig. 5C). After 60 months, an average of $19.4\% \pm 5.6\%$ of oven-dried wood weight consisted of soil. Distance from the ends of the bolts had a significant and linear effect on soil content (Table 2), with soil content decreasing with distance from the ends ($t = -5.08$, $P < 0.0001$). The effect of distance on soil content was still significant after adding volume consumed to the model (distance sum of squares was reduced by about 60%).

DISCUSSION

Our results show that termites consume a much larger volume of wood relative to all other insects combined during the first several years of pine decomposition in southeastern U.S. forests. After two years, for example, partially protected bolts had lost only about one sixth as much wood volume as their unprotected counterparts (1.9% vs 11.4%, respectively). Considering the large amount of wood consumed by termites in the unprotected bolts (~15–20% after three years), it is surprising there were no differences in mass

loss or specific gravity (initial wood volume) among treatments (Fig. 4B, C). These findings may be due in part to the tendency of subterranean termites to feed preferentially on the softest, least dense wood; e.g., consuming spring wood while leaving the denser rings of summer wood relatively intact (Fig. 2). This likely explains why the specific gravity (final wood volume) of the remaining wood was higher in bolts exposed to termites compared to their protected counterparts (Fig. 4D). Because the wood consumed by termites tends to be the most easily degraded, it seems plausible that fungi may degrade equivalent amounts of wood—but cause less visible damage—in the absence of termites. Our results further suggest either an inhibition of microbial activity by insects (i.e., if their effect was neutral or stimulatory we would have expected a synergistic effect on decay) or an enhancement of microbial activity by the exclusion methods used in the protected treatments. As discussed below, both possibilities have some merit.

Like most wood-feeding arthropods (Swift and Boddy 1984), termites are well known to prefer wood partially degraded by certain types of fungi over pristine wood (Hendee 1935, Kooroor 1964, Becker 1965, Smythe et al. 1971, Gentry and Whitford 1982). Upon colonization, however, it is not clear whether the activities of subterranean termites promote or retard further fungal growth. Because termites are known for their antimicrobial secretions and behaviors (Rosengaus et al. 1998, Rosengaus et al. 2000, Hamilton et al. 2011, Bulmer et al. 2012), however, an inhibitory effect of termites on wood decomposition by fungi is plausible. Ants are also known

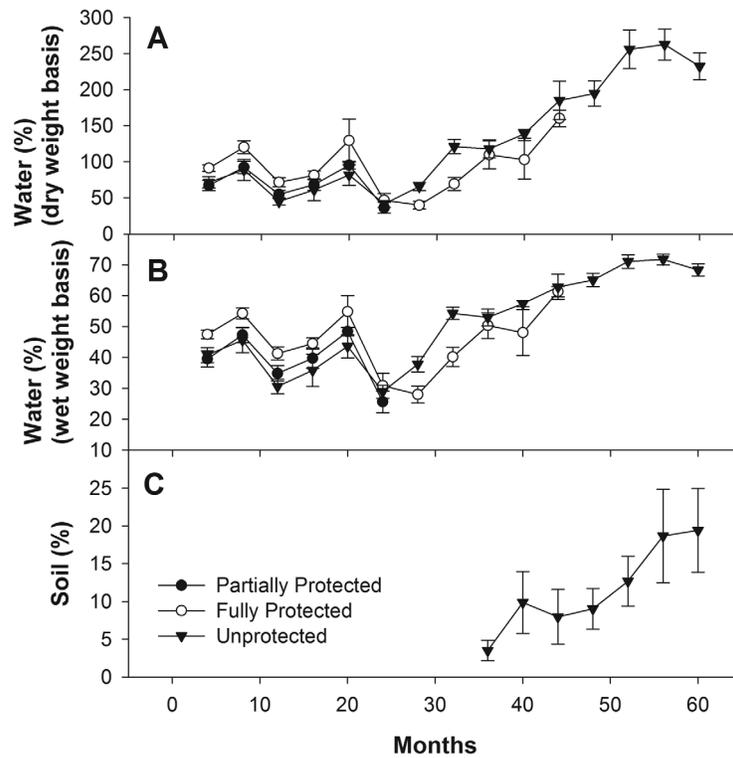


Fig. 5. Water content based on dry and wet wood weights over time (A and B, respectively) and soil content (C) (mean \pm SE).

to secrete antimicrobial compounds and have been shown to inhibit fungal growth and decomposition in wood (Warren and Bradford 2012). Because decaying logs in the southeastern United States are almost always colonized by termites, ants or both groups simultaneously (M. D. Ulyshen, unpublished data), logs exposed to insect colonization may be characterized by depressed microbial activity.

Both exclusion methods used in our study had the potential to alter microbial activity. The cypermethrin used to treat the soil under both partially and fully protected bolts, for instance, may have represented a source of carbon and nitrogen for both fungi (Chen et al. 2011) and bacteria (Tallur et al. 2008). In Canada, Tu (1991) found both technical and formulated applications of cypermethrin to significantly stimulate fungal growth in soil, suggesting the compound may have accelerated the degradation of wood by microbes in the current study.

Additionally, the mesh cages used in the fully protected treatment may have affected microbial

activity by altering the moisture content of the enclosed bolts relative to those without cages. We observed a higher moisture content in fully protected (i.e., caged) bolts than in unprotected bolts until about two years after which the pattern reversed and caged bolts had a lower moisture content (Fig. 5A, B). Because moisture content was higher in caged bolts after just four months (i.e., before much insect activity), it seems probable that the cages may have been responsible for this difference. Support for this comes from litter bag studies (Lousier and Parkinson 1976) and, most notably, from Leach et al. (1937) who found the moisture content of caged logs to be slightly higher than that of uncaged logs in Minnesota. Microbial decay agents are well-known to be sensitive to the moisture content of their substrate. As reviewed by Käärrik (1974), research from Europe has shown that wood having a moisture content (dry weight basis) of 60–120% decays rapidly whereas wood with a moisture content below 30% or above 120% is not attacked by most

basidiomycete fungi. It is not clear how important fluctuations within the optimal water content range (i.e., 60–120%) are for most wood-decaying fungi. It is evident from Fig. 5 that most bolts, regardless of treatment, stayed within this range for the first three years of the study. Because fully protected (i.e., caged) bolts tended to have a higher moisture content than unprotected bolts for the first two years, however, we cannot exclude the possibility that the differences in water content between treatments were enough to somewhat influence decay rates.

Although few efforts have been made to relate wood water content to insect activity, this represents another potential explanation for differences in water content between protected and unprotected bolts. We found a negative correlation between water content and the volume of wood consumed by termites (see *Results* and Appendix B). Because water content decreases with increasing wood specific gravity (results not shown), this can likely be attributed to the wood left behind by termites in unprotected bolts being higher in specific gravity than the wood remaining in the protected bolts (Fig. 4D). Although water content was higher in fully protected bolts until 24 months, the opposite pattern was observed thereafter despite continued termite activity. This suggests additional factors—not explored in the current study—may also have been involved. Dissimilar rates of bark loss between treatments may have affected water content, for example.

One advantage of our sampling design is that it allows us to investigate how certain measures vary with distance from the bolt ends. For instance, we found that water content decreased linearly from the centers to the ends of the bolts (Table 2), suggesting that the ends dried out more quickly than the bolt centers. This could also be due in part to the fact that termites were more active near the bolt ends considering the negative relationship between termite damage and water content. Because the cut ends were not sealed, the bolts overall may have been drier than they otherwise would have been (e.g., in intact fallen trees), as observed by Leach et al. (1937). The unsealed bolt ends may also have limited our ability to detect an effect of beetles on decay rates. For example, Leach et al. (1937) reported a stronger correlation between the number of

wood-boring insects (especially *Monochamus* spp.) and heartwood decay in logs that had sealed ends compared to those with unsealed ends in Minnesota. This was due to the relative ease by which fungi entered the logs from the unsealed ends. Future research may therefore benefit from including a treatment with sealed log ends.

Both the volume of wood consumed and the weight of soil imported by termites increased linearly from the centers to the ends of the bolts. The tendency of termites to carry soil into wood has been widely observed (Greaves 1962, Ocloo 1973, Abe 1980, Grove 2007) but we are unaware of any previous effort to quantify this behavior in the field (but see Mobley et al. (2013)). We found that after just five years approximately 20% of the dry wood weight consists of termite soil. Why termites put so much energy into moving soil into wood remains uncertain (Howse 1966, Stuart 1967, Li and Su 2008, Ulyshen and Shelton 2012). Adding volume consumed to our model only reduced distance sum of squares by about 60%, however, suggesting soil content is not simply a function of termite activity.

The decay rate calculated from our results was 0.181, corresponding to a half-life of about 3.8 years. This is a higher rate than reported for pine elsewhere in the southeastern United States (Barber and Van Lear 1984, Eaton and Sanchez 2009, Hanula et al. 2012, Mobley et al. 2013). Although differences in site conditions and bolt lengths are likely important variables, this discrepancy is probably due in part to our use of initial volume (Ulyshen and Wagner 2013), as opposed to final water displaced volume when calculating specific gravity. While commonly used for pristine wood (Williamson and Wiemann 2010), the water displacement method is less suitable for decay studies because it ignores missing wood, e.g., from insect activity. We therefore encourage future researchers to use initial volumes when calculating specific gravity, decay rate constants or other such metrics.

This study represents one of the first experimental efforts to quantify the contributions of saproxylic arthropods to wood decomposition. We unexpectedly found that even though insects (especially termites) consumed large volumes of wood (i.e., ~15–20%), they did not act to accelerate mass loss beyond what is achieved

by microbial decomposers. More research is needed to test this in the southeastern United States and beyond, however, especially given the uncertainties inherent to exclusion studies.

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LITERATURE CITED

- Abe, T. 1978. The role of termites in the breakdown of dead wood in the forest floor of Pasoh study area. *Malayan Nature Journal* 30:391–404.
- Abe, T. 1980. Studies on the distribution and ecological role of termites in a lowland rain forest of west Malaysia (4) The role of termites in the process of wood decomposition in Pasoh forest reserve. *Revue d'écologie et de biologie du sol* 17:23–40.
- Angers, V. A., P. Drapeau, and Y. Bergeron. 2012. Mineralization rates and factors influencing snag decay in four North American boreal tree species. *Canadian Journal of Forest Research* 42:157–166.
- Barber, B. L., and D. H. Van Lear. 1984. Weight loss and nutrient dynamics in decomposing woody loblolly pine logging slash. *Soil Science Society of America Journal* 48:906–910.
- Becker, G. 1965. Versuche über den einfluss von braunfaulepilzen auf wahl und ausnutzung der holznahrung durch termiten. *Material und Organismen* 1:95–156.
- Blackman, M. W., and H. H. Stage. 1924. On the succession of insects living in the bark and wood of dying, dead and decaying hickory. Technical Publication Number. 17. New York State College of Forestry.
- Bulmer, M. S., D. Denier, J. Velenovsky, and C. Hamilton. 2012. A common antifungal defense strategy in *Cryptocercus* woodroaches and termites. *Insectes Sociaux* 59:469–478.
- Buxton, R. D. 1981. Termites and the turnover of dead wood in an arid tropical environment. *Oecologia* 51:379–384.
- Chen, S., Q. Hu, M. Hu, J. Luo, Q. Weng, and K. Lai. 2011. Isolation and characterization of a fungus able to degrade pyrethroids and 3-phenoxybenzaldehyde. *Bioresource Technology* 102:8110–8116.
- Collins, N. M. 1981. The role of termites in the decomposition of wood and leaf litter in the southern Guinea savanna of Nigeria. *Oecologia* 51:389–399.
- Cornwell, W. K., J. H. C. Cornelissen, S. D. Allison, J. Bauhus, P. Eggleton, C. M. Preston, F. A. Scarff, J. T. Weedon, C. Wirth, and A. E. Zanne. 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? *Global Change Biology* 15:2431–2449.
- Dowding, P. 1984. The evolution of insect-fungus relationships in the primary invasion of forest timber. Pages 133–153 in J. M. Anderson, A. D. M. Rayner, and D. W. H. Walton, editors. *Invertebrate-microbial interactions*. Cambridge University Press, Cambridge, UK.
- Eaton, R. J., and F. G. Sanchez. 2009. Quantitative and qualitative measures of decomposition: Is there a link? *Southern Journal of Applied Forestry* 33:137–141.
- Edmonds, R. L., and A. Eglitis. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. *Canadian Journal of Forest Research* 19:853–859.
- Gentry, J. B., and W. G. Whitford. 1982. The relationship between wood litter infall and relative abundance and feeding activity of subterranean termites *Reticulitermes* spp. in three southeastern coastal plain habitats. *Oecologia* 54:63–67.
- Greaves, T. 1962. Studies of foraging galleries and the invasion of living trees by *Coptotermes acinaciformis* and *C. brunneus* (Isoptera). *Australian Journal of Zoology* 10:630–651.
- Grove, S. J. 2007. Mudguts. *Tasmanian Naturalist* 129:2–7.
- Hamilton, C., F. Lay, and M. S. Bulmer. 2011. Subterranean termite prophylactic secretions and external antifungal defenses. *Journal of Insect Physiology* 57:1259–1266.
- Hanula, J. L. 1996. Relationships of wood-feeding insects and coarse woody debris. Pages 55–81 in J. W. McMinn and D. A. Crossley, Jr., editors. *Biodiversity and coarse woody debris in southern forests*. General Technical Report SE-94. USDA Forest Service, Southern Research Station.
- Hanula, J. L., M. D. Ulyshen, and D. D. Wade. 2012. Impacts of prescribed fire frequency on coarse woody debris volume, decomposition and termite activity in the longleaf pine flatwoods of Florida. *Forests* 3:317–331.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate

- ecosystems. *Advances in Ecological Research* 15:133–302.
- Hendee, E. C. 1935. The role of fungi in the diet of the common damp-wood termite, *Zootermopsis angusticollis*. *Hilgardia* 9:499–525.
- Howse, P. E. 1966. Air movement and termite behavior. *Nature* 210:967–968.
- Käärik, A. A. 1974. Decomposition of wood. Pages 129–174 in C. H. Dickinson and G. J. F. Pugh, editors. *Biology of plant litter decomposition*. Volume 1. Academic Press, London, UK.
- Kovoor, J. 1964. Modifications chimiques provoquées par un termitide *Microcerotermes edentatus* dans du bois de peuplier sain ou partiellement dégradé par des champignons. *Bull. Biol. France Belg.* 98:491–509.
- Leach, J. G., L. W. Orr, and C. Christensen. 1937. Further studies on the interrelationship of insects and fungi in the deterioration of felled Norway pine logs. *Journal of Agricultural Research* 55:129–140.
- Lee, K. E., and T. G. Wood. 1971. *Termites and soils*. Academic Press, London, UK.
- Li, H.-F., and N.-Y. Su. 2008. Sand displacement during tunnel excavation by the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Annals of the Entomological Society of America* 101:456–462.
- Lim, S. Y., and B. T. Forschler. 2012. *Reticulitermes nelsonae*, a new species of subterranean termite (Rhinotermitidae) from the southeastern United States. *Insects* 3:62–90.
- Longman, K. A., and J. Jenik. 1987. *Tropical forest and its environment*. Second edition. Longman Scientific & Technical.
- Lousier, J. D., and D. Parkinson. 1976. Litter decomposition in a cool temperate deciduous forest. *Canadian Journal of Botany* 54:419–436.
- Mobley, M. L., D. Richter, and P. R. Hein. 2013. Accumulation and decay of woody detritus in a humid subtropical secondary pine forest. *Canadian Journal of Forest Research* 43:109–118.
- Müller, M. M., M. Varama, J. Heinonen, and A.-M. Hallaksela. 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. *Forest Ecology and Management* 166:165–181.
- Ocloo, J. K. 1973. The estimation of damage by the larger macrotermitinae (Isoptera, Insecta) using volume measurement. *Ghana Journal of Science* 13:92–96.
- Rosengaus, R. B., M. R. Guldin, and J. F. A. Traniello. 1998. Inhibitory effect of termite fecal pellets on fungal spore germination. *Journal of Chemical Ecology* 24:1697–1706.
- Rosengaus, R. B., M. L. Lefebvre, and J. F. A. Traniello. 2000. Inhibition of fungal spore germination by *Nasutitermes*: Evidence for a possible antiseptic role of soldier defense secretions. *Journal of Chemical Ecology* 26:21–39.
- SAS Institute. 1999. SAS system for windows. Version 8. SAS Institute, Cary, North Carolina, USA.
- Schultz, R. P. 1997. Loblolly pine: The ecology and culture of loblolly pine (*Pinus taeda* L.). USDA Forest Service Agricultural Handbook 713.
- Schuurman, G. 2005. Decomposition rates and termite assemblage composition in semiarid Africa. *Ecology* 86:1236–1249.
- Smythe, R. V., F. L. Carter, and C. C. Baxter. 1971. Influence of wood decay on feeding and survival of the eastern subterranean termite, *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). *Annals of the Entomological Society of America* 64:59–62.
- Steel, R. G., J. H. Torrie, and D. A. Dickey. 1997. *Principles and procedures of statistics: A biometrical approach*. Third edition. McGraw-Hill, New York, New York, USA.
- Stokland, J. N., J. Siitonen, and B. G. Jonsson. 2012. *Biodiversity in dead wood*. Cambridge University Press, Cambridge, UK.
- Stuart, A. M. 1967. Alarm, defense, and construction behavior relationships in termites (Isoptera). *Science* 156:1123–1125.
- Swift, M. J., and L. Boddy. 1984. Animal-microbial interactions in wood decomposition. Pages 89–131 in J. M. Anderson, A. D. M. Rayner, and D. W. H. Walton, editors. *Invertebrate-microbial interactions*. Cambridge University Press, Cambridge, UK.
- Tallur, P. N., V. B. Megadia, and H. Z. Ninnekar. 2008. Biodegradation of cypermethrin by *Micrococcus* sp. strain CPN 1. *Biodegradation* 19:77–82.
- Tu, C. M. 1991. Effect of some technical and formulated insecticides on microbial activities in soil. *Journal of Environmental Science and Health, B* 26:557–573.
- Turner, D. P., G. J. Koerper, M. E. Harmon, and J. J. Lee. 1995. A carbon budget for forests of the conterminous United States. *Ecological Applications* 5:421–436.
- Ulyshen, M. D. 2013. Strengthening the case for saproxylic arthropod conservation: a call for ecosystem services research. *Insect Conservation and Diversity* 6:393–395.
- Ulyshen, M. D., and J. L. Hanula. 2009. Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. *Forest Ecology and Management* 257:653–664.
- Ulyshen, M. D., and T. G. Shelton. 2012. Evidence of cue synergism in termite corpse response behavior. *Naturwissenschaften* 99:89–93.
- Ulyshen, M. D., and T. L. Wagner. 2013. Quantifying arthropod contributions to wood decay. *Methods in Ecology and Evolution* 4:345–352.
- Warren, R. J., and M. A. Bradford. 2012. Ant

colonization and coarse woody debris decomposition in temperate forests. *Insectes Sociaux* 59:215–221.

Williamson, G. B., and M. C. Wiemann. 2010. Measuring wood specific gravity...correctly. *American Journal of Botany* 97:519–524.

Wood, T. G. 1976. The role of termites (Isoptera) in decomposition processes. Pages 145–168 *in* J. M. Anderson and A. Macfadyen, editors. *The role of terrestrial and aquatic organisms in decomposition processes*. Blackwell Scientific, Oxford, UK.

Wood, T. G. 1978. Food and feeding habits of termites. Pages 55–80 *in* M. V. Brian, editor. *Production ecology of ants and termites*. Cambridge University Press, Cambridge, UK.

Wood, T. G., and W. A. Sands. 1978. The role of termites in ecosystems. Pages 245–292 *in* M. V. Brian, editor. *Production ecology of ants and termites*. Cambridge University Press, Cambridge, UK.

SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Number of bolts collected by treatment and sampling period.

Sample (months)	Treatment			Total
	Partially protected	Fully protected	Unprotected	
4	5	3	5	13
8	5	3	5	13
12	5	3	5	13
16	5	3	5	13
20	5	3	5	13
24	5	3	5	13
28	0	3	5	8
32	0	3	4	7
36	0	3	5	8
40	0	3	6	9
44	0	2	6	8
48	0	0	6	6
52	0	0	5	5
56	0	0	7	7
60	0	0	10	10
Total	30	32	84	146

APPENDIX B

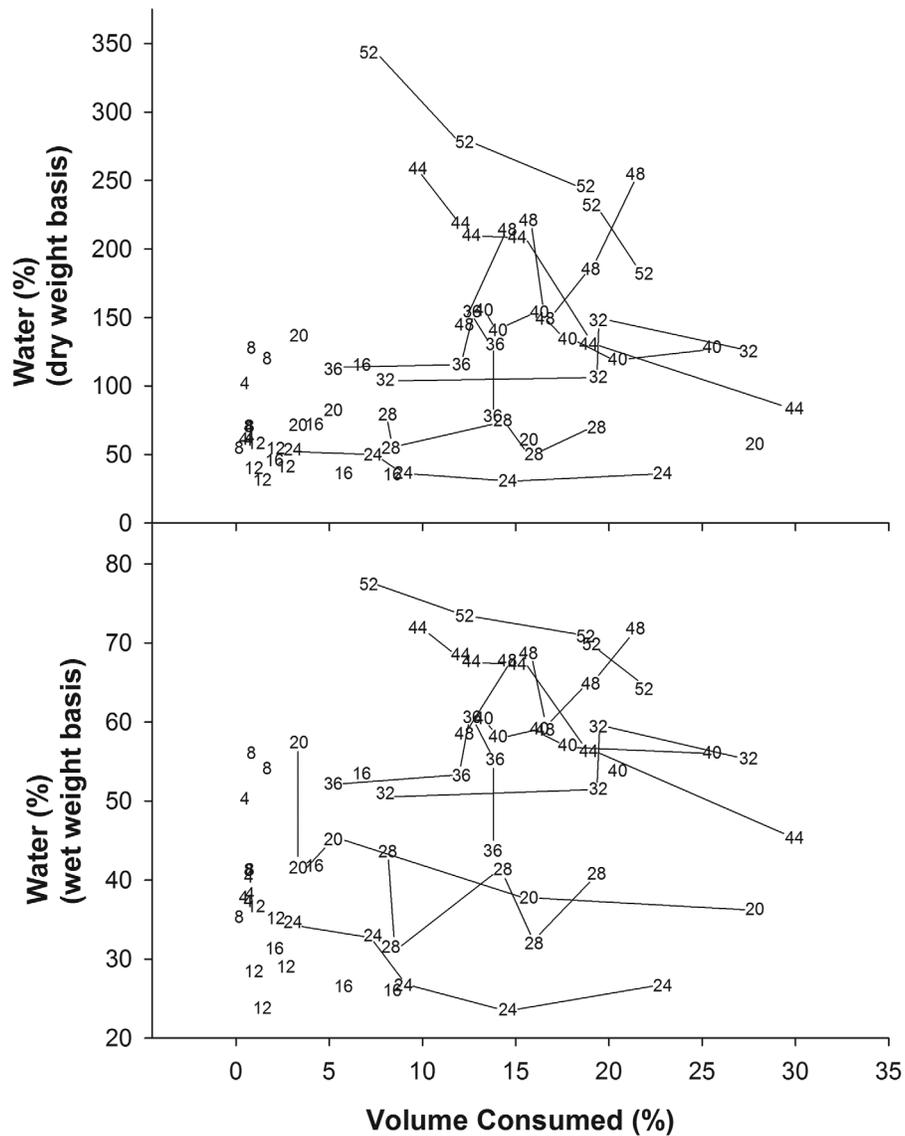


Fig. B1. Relationship between wood water content and volume consumed by insects (unprotected treatment only). Data points are indicated by sample period (month). Beginning at 24 months, lines were added to help visualize trends in the data for each sampling period separately. The top and bottom figures show water contents based on dry and wet weights, respectively.