

Below- and above-ground effects of deadwood and termites in plantation forests

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Abstract. Deadwood is an important legacy structure in managed forests, providing continuity in shelter and resource availability for many organisms and acting as a vehicle by which nutrients can be passed from one stand to the next following a harvest. Despite existing at the interface between below- and above-ground systems, however, much remains unknown about the role woody debris plays in linking these zones. Moreover, it remains untested whether the accelerative effects of wood-feeding insects on wood decomposition influence tree growth or nutritional status in forests. In this study, we added different quantities of pine logs to the bases of saplings in two-year-old loblolly pine (*Pinus taeda* L.) plantations in Mississippi, USA. We included a treatment in which subterranean termites (Blattodea: Rhinotermitidae: *Reticulitermes*) were excluded from logs to determine how these insects affect the release of nutrients from wood and, in turn, tree growth. After 51 months of decomposition, we quantified below-ground effects by measuring microbial biomass, plant-available forms of N, and ectomycorrhizal diversity associated with fine tree roots. Meanwhile, above-ground measurements focused on the elemental concentrations in decomposing wood either protected or unprotected from termites and tree metrics related to growth and nutrient status. We found additions of wood to significantly increase nitrate and potential net nitrification relative to reference treatments but detected no significant effects on tree growth, needle nitrogen concentrations, or ectomycorrhizal diversity. Soil nitrate and potential net nitrification were higher under protected vs. unprotected logs, and plant-available forms of N were mostly more abundant short distances away from both protected and unprotected logs than directly under them. The wood of logs protected from termites had significantly lower concentrations of most elements compared to that of unprotected logs, largely due to the large amounts of soil imported into unprotected logs by termites. Termite exclusion had no measurable effect on tree growth, nutritional status, or ectomycorrhizal diversity, however. Our findings indicate that deadwood and termites both contribute to the spatial heterogeneity of soil properties but may have limited short-term local effects on tree growth. Longer-term studies and studies on less fertile sites are needed.

Key words: coarse woody debris; ecosystem services; fertility; forest management; invertebrates; Isoptera; logging slash; mycorrhizae; productivity; saproxylic.

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INTRODUCTION

The challenge of ecological forestry is to balance the demand for timber products with the desire to protect natural processes and associated biodiversity (Seymour and Hunter 1999). Areas of overlap within which management decisions can potentially help satisfy both objectives are therefore of great practical interest. One such area concerns deadwood and the dual role it plays in supporting a large fraction of forest biodiversity (~20–30% of all forest animal species, for example, Stokland et al. 2012) and acting as a long-term source of nutrients (Laiho and Prescott 2004, Palviainen et al. 2010). Due to its large size and the recalcitrant nature of its main structural compounds (i.e., lignin and cellulose), deadwood decomposes slowly in most forests and accumulates over time. Managed forests typically contain less deadwood than unmanaged forests, however, due to the harvesting of trees prior to natural senescence as well as sanitation practices that remove woody debris created during timber operations. Over large areas and long periods of time, these reductions have threatened numerous species dependent on dead or dying wood in certain intensively managed landscapes (Speight 1989). Although the importance of deadwood to biodiversity is now widely accepted, we still do not fully understand the ecological importance of this substrate including the role it plays in long-term nutrient cycling and, ultimately, forest productivity. With a growing interest in removing woody debris for biofuel production (Eisenbies et al. 2009, Tilman et al. 2009, Paré and Thiffault 2016) as well as fuel reduction treatments to reduce wildfire risks (Graham et al. 2004, Agee and Skinner 2005), research is needed to develop a more holistic basis for any decision concerning these legacy structures (Franklin et al. 2007) in managed forests.

Although numerous studies have looked at the effects of deadwood on soil properties (Busse 1994, Hafner and Groffman 2005, Lodge et al. 2016, Zalamea et al. 2016) or tree growth (Sterba 1988, Zimmerman et al. 1995, Beard et al. 2005, Ares et al. 2007) separately, relatively few have explored the complex role it plays in linking below- and above-ground systems. Like any other aspect of terrestrial ecology, the ecology of deadwood, and its importance in managed forests,

cannot be fully understood without considering both systems simultaneously (Bardgett and Wardle 2010). Dead logs, branches, and stumps on the forest floor are sites of intense biotic activity where above-ground and subterranean organisms interact to affect decomposition (Rayner and Boddy 1988, Ulyshen 2016). The nutrient content of living biomass within decaying wood far exceeds what is provided by the wood itself (Merrill and Cowling 1966, Baker 1969, Higashi et al. 1992), and this is largely made possible by the mycelial cords of decay fungi that act to translocate nutrients into wood from the soil (Clinton et al. 2009, Filipiak et al. 2016). Wood is therefore commonly thought to act as a sink of nutrients early in the decomposition process although evidence for this is mixed (Holub et al. 2001, Creed et al. 2004, Johnson et al. 2014). Insects have been proposed to play an important role in releasing nutrients immobilized by fungi in decomposing wood, thereby accelerating the nutrient sink-source transition (Swift 1977, Boddy and Watkinson 1995, Takamura and Kirton 1999), but insect biomass may alternatively act as just another sink in which nutrients are first immobilized and then disseminated widely by dispersing individuals. This has been predicted for social insects in particular (Hadley 1972) including termites which are famous for producing large numbers of nutrient-rich winged reproductive individuals that disperse over large areas (Wood and Sands 1978).

Whether locally or over large areas, the nutrients contained within deadwood are eventually returned to the soil where they may become immobilized within the biomass of soil microbes, invertebrates, or living plants. Soil microbes and plants interact in complex ways including intense competition and symbiosis (Van Der Heijden et al. 2008). The latter include mycorrhizal fungi associated with the roots of many plants that provide limiting nutrients in exchange for carbon. Ectomycorrhizae are common among plants in temperate and boreal forests where they forage for nutrients using extensive hyphal networks and extracellular enzymes and have been shown to source a large fraction of plant nutrients (Van Der Heijden et al. 2008). Interactions among deadwood, ectomycorrhizae, and plants remain poorly understood. Plants are known to sometimes extend roots into deadwood, however, and ectomycorrhizal fungi

become more abundant in deadwood as decomposition proceeds (Baldrian 2017). In addition to being a source of nutrients, deadwood is thought to protect mycorrhizal diversity from disturbance and extreme climatic conditions (Vogt et al. 1995, Tedersoo et al. 2003).

Forests of the southern United States are among the most productive and diverse in North America and collectively produce more industrial timber than any other region of the world (Fox et al. 2007). A fast-growing species native to the region, loblolly pine (*Pinus taeda* L.) has become the most important timber species in southern states and has been planted in many other countries as well. Although rotations of <20 yr are not uncommon, growth rates of loblolly pine have been shown to vary greatly depending on site conditions and management intensity (Borders and Bailey 2001). Efforts to maximize growth commonly involve intensive site preparation (including the removal of competing woody vegetation and woody debris), fertilization (N and/or P, as needed), and herbicide applications (Schultz 1997, Borders and Bailey 2001, Carter and Foster 2006, Fox et al. 2007). Removing woody debris prior to re-planting is common, but this overlooks the many potential benefits these legacy structures may provide including the release of biologically available nitrogen and other nutrients through decomposition (Vitousek and Matson 1985), the importance of deadwood to forest biodiversity, and the role wood-dwelling invertebrates may play in accelerating nutrient cycles. Native subterranean termites (Rhinotermitidae) belonging to the genus *Reticulitermes* are the most important wood-feeding insects in southeastern U.S. loblolly pine forests where they have been shown to consume up to a fifth of the wood volume (Ulyshen et al. 2014), accelerate wood mass loss (Ulyshen 2014, Stoklosa et al. 2016, Ulyshen et al. 2016b, Zhang et al. 2016), and significantly alter microbial community composition within deadwood (Ulyshen et al. 2016a). The movement of these insects between the wood and soil, including their importation of large amounts of soil into wood (Ulyshen et al. 2014), raises questions about how they impact soil properties and microbial activity below woody debris. By disrupting fungal networks in decomposing wood and by promoting the fixation of atmospheric nitrogen

by both free-living and endosymbiotic prokaryotes, termites may have a fertilizing effect in forests (Ulyshen 2015), with potentially important below- and above-ground implications.

In the current study, we investigated various below- and above-ground impacts of deadwood additions and termite exclusion after more than four years of decomposition in young loblolly pine plantations in Mississippi, USA. Final measurements were collected after 51 months when, based on previous research conducted in the same area, the experimental logs should have been more than half-decomposed (Ulyshen et al. 2014). Below-ground measurements focused on soil properties, plant-available forms of N, and ectomycorrhizal diversity associated with fine tree roots. Above-ground measurements focused on the elemental concentrations in decomposing wood either protected or unprotected from termites and tree metrics related to growth and nutrient status. We predicted that additions of deadwood around the bases of trees would increase plant-available N in the underlying soil, increase ectomycorrhizal diversity associated with tree roots, and stimulate tree growth. We also predicted that termites would accelerate the release of nutrients from wood relative to logs protected from these insects and that this would result in substantially faster growth in trees receiving logs unprotected from termites compared to those receiving protected logs.

METHODS

Study location and site quality

This experiment took place on the John W. Starr Memorial Forest in Oktibbeha and Winston counties, Mississippi (Fig. 1, map). The climate of the region is considered humid subtropical, with annual precipitation and temperature averaging 140 cm and 16.9°C, respectively (usclimatedata.com). The experiment was repeated in three loblolly pine plantations (Fig. 1A) of about 24, 15, and 26 ha in size and separated from one another by ~1–8 km. Coordinates for locations 1, 2, and 3 are 33°16'45.99" N 88°54'33.47" W, 33°20'50.96" N 88°52'17.58" W, and 33°19'58.02" N 88°51'42.72" W, respectively. Soils at location 1 were a combination of sandy loam and silty clay loam, whereas silt loam dominated at location 2 and location 3 was characterized by a combination of silt loam

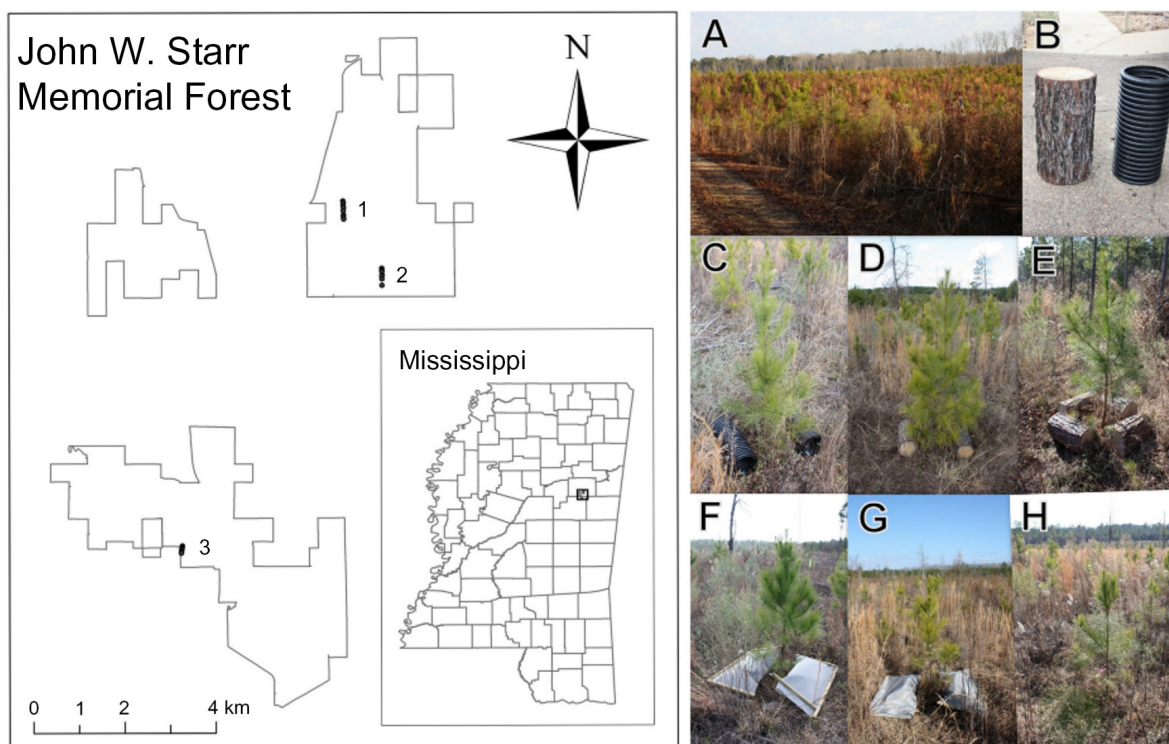


Fig. 1. Map of study locations (left) and pictures of treatments (right). On the map, the numbers 1–3 refer to the three loblolly pine plantations. (A) One plantation at the beginning of the study; (B) log and pipe shown together; (C) two-unprotected-pipes; (D) two-unprotected-logs; (E) four-unprotected-logs; (F) two-protected-pipes; (G) two-protected-logs; and (H) reference.

and silty clay loam (websoilsurvey.nrcs.usda.gov). All sites were planted in February 2009 using bare root Coastal 2nd Generation loblolly pine at 1347 trees per ha (2.4×3 m spacing). Two methods were used to determine whether there were any N or P deficiencies, the two most limiting elements in southeastern U.S. pine plantations (Fox et al. 2007), at any of our sites. Needle nitrogen concentrations were measured from all of our study trees at the beginning of the study, and soil phosphorus concentrations were measured from soil samples collected at the base of our control trees three years after our study began (i.e., 5 yr after the trees were planted). We found initial needle N (%) to be 1.42 ± 0.03 , 1.30 ± 0.05 , and 1.29 ± 0.03 for locations 1, 2, and 3, respectively, all well above the critical range of 1.1% reported for loblolly pine by Moorhead (1998). By contrast, we found soil P concentrations at all three locations to be below the critical range of 4–6 ppm (Appendix S2: Table S1) reported for other managed pine species in the

southeastern United States by Moorhead (1998). Taken together, these findings suggest that all three locations were deficient in P but not initially deficient in N.

Experimental design

The experiment comprised a randomized block design at each of the three locations (plantations), with eight replicate blocks per location and six treatments per block within each location. The blocks were established within 50 m of a road to facilitate access. Six trees were selected near the center of each block and randomly assigned to one of six treatments, involving 144 trees in total (Table 1). Treatments were designed to achieve two primary objectives. First, we sought to determine how additions of deadwood affect tree growth, soil properties, and ectomycorrhizal diversity. This involved adding either zero, two, or four freshly cut loblolly pine logs (0.5 m in length; see following section *Experimental logs* for more information) next to each

Table 1. Mean $\pm$ SE ($n = 24$) estimated total initial volumes, dry weights, nitrogen contents, and phosphorus contents of logs (pooled by study tree and including wood and bark) by treatment.

Treatment	Log additions				Measurements			
	Vol. (m ³)	Dry wt. (kg)	N (g)	P (g)	Tree	Soil	Mycorr	Wood
Reference	NA	NA	NA	NA	x	x	x	
Two-unprotected-logs	0.05 $\pm$ 0.00	20.08 $\pm$ 0.82	33.06 $\pm$ 1.37	4.72 $\pm$ 0.19	x	x	x	x
Four-unprotected-logs	0.13 $\pm$ 0.00	49.84 $\pm$ 1.28	82.27 $\pm$ 2.13	11.75 $\pm$ 0.30	x	x		
Two-unprotected-pipes	NA	NA	NA	NA	x		x	
Two-protected-logs	0.05 $\pm$ 0.00	19.75 $\pm$ 0.68	32.51 $\pm$ 1.14	4.64 $\pm$ 0.16	x	x	x	x
Two-protected-pipes	NA	NA	NA	NA	x			

Notes: Metrics are not applicable (NA) to the reference or pipe treatments. Treatments marked by an x were included in comparisons of tree, soil, mycorrhizae, and wood measurements.

experimental tree (i.e., the “reference,” “two-unprotected-logs,” and “four-unprotected-logs” treatments, respectively). For the two-unprotected-logs treatment, the logs were placed parallel to one another on either side of each tree and separated by ~ 0.5 m as measured from the sides of the logs (Fig. 1D). For the four-unprotected-logs treatment, the logs were arranged in the shape of a square surrounding each tree (Fig. 1E). The distance between logs in this treatment was also 0.5 m. Because competing vegetation is known to significantly reduce tree growth in loblolly pine plantations (Martin and Shiver 2002), we also included a treatment consisting of “two-unprotected-pipes” to test the idea that additions of wood may stimulate tree growth by reducing competition from other plants as shown in other systems (Harrington et al. 2013, Trotter-Picard et al. 2014). The pipes were made from black single-wall corrugated plastic conduit and were cut to the same 0.5 m length and were of similar diameter (24 cm) to the logs used in the two-unprotected-logs treatment (Fig. 1B). Stainless steel stakes were used to hold the pipes in place and in the same configuration as the two-unprotected-logs treatment. Our second objective was to test how the exclusion of subterranean termites would affect our various response variables. This was accomplished by enclosing two logs of similar dimensions to those in the two-unprotected-logs treatment within stainless steel mesh bags with 0.38-mm openings (Fig. 1G). The bags were completely enclosed and were identical to those used to successfully exclude termites in a previous study (Ulyshen 2014). The bags were placed, so the between-log distance matched that of the unprotected logs treatments. Our sixth treatment consisted of “two-protected-

pipes” to pair with the two-protected-logs treatment, thus further addressing the possibility of a competition-reduction effect (Fig. 1F).

Experimental logs

In November 2011, twelve loblolly pine trees (approximately 40 yr old based on growth rings) were felled in a single stand near our study sites. In total, 192 log sections were collected (0.5 m long and 26.5 ± 0.3 cm diameter). Thirteen basal logs too large (≥ 32.5 cm diameter) to fit within the mesh cages were immediately assigned to the four-unprotected-logs treatment. These logs were then randomly assigned to particular locations and experimental trees within this treatment. All other log assignments were entirely random with respect to location, treatment, and tree. The dry weights of bark and wood were estimated for each log using equations developed from unpublished data collected in a previous study (Appendix S1: Fig. S1). Total volume, estimated dry weight, and estimated N content were calculated for logs at all trees receiving logs. Importantly, as shown in Table 1, these variables did not differ between the two-protected-logs and two-unprotected-logs treatments. Because the logs used in the four-unprotected-logs treatment were often larger than those used in the two-unprotected-logs treatment, there was more than a twofold difference in the total volume of logs between the treatments involving two and four logs (Table 1).

Soil parameters and soil/root sample preparation

Soil samples were collected after three years to compare macronutrients (P, Ca, K, Mg, Mn, and Zn) among treatments and locations (Appendix S2) and at the end of the study, after 51 months, for a final assessment of soil

parameters and ectomycorrhizal diversity. For the final sampling, soil cores were collected to a depth of 20 cm on four sides of each tree along two perpendicular axes. This was done on four of the eight blocks at each location due to limited laboratory capacities. The placement of logs or pipes determined the direction of the sampling axes as cores were removed directly “under” the centers of these treatments (i.e., ~35–40 cm from the tree). Keeping this distance constant, we also collected cores from the corresponding “away” positions along the perpendicular axis, where applicable. For trees assigned to the four-unprotected-logs treatment and the reference treatment, the four sample positions were all classified as under or away, respectively. Soil samples were transported in coolers and then stored at 4°C. The four samples from each tree were randomly divided into two sets, with one set being for analysis of microbial biomass and other soil parameters and the other for mycorrhizal analysis.

Due to practical limitations, our final soil analysis was limited to the following treatments: two-unprotected-logs, two-protected-logs, four-unprotected-logs, and reference. We analyzed two cores (0–20 cm depth) from each treatment, including both under and away positions for the two-unprotected-logs and two-protected-logs treatments, for a total of 96 samples. After collection, samples were sieved (4 cm), homogenized, and stored at 4°C until analysis. For soil analyses, we determined 100% water-holding capacity (WHC), substrate-induced respiration biomass, mineralizable C, potential net N mineralization, potential net nitrification, extractable ammonium (NH_4^+), extractable nitrate (NO_3^-), microbial biomass C and N, and dissolved organic C and N. 100% WHC (after wetting to field capacity) was determined by drying soil at 105°C for 24 h.

Substrate-induced respiration biomass, an indicator of active microbial biomass (Fierer et al. 2003), was determined following Strickland et al. (2010). Briefly, we amended 4 g dry weight equivalent soil with 8 mL solutions of autolyzed yeast. Autolyzed yeast was used rather than glucose because it represents a stoichiometrically balanced substrate, allowing for maximum standing microbial respiration. The autolyzed yeast may also mimic microbial necromass, a determinant of microbial respiration under field conditions (Kaiser et al. 2014). After a 1-h pre-incubation with

shaking, the soil slurries (i.e., soil and solution combinations) were incubated for 4 h at 20°C. After incubation, respiration for each amendment was determined on an infrared gas analyzer (IRGA, Model LI-7000; Li-Cor Biosciences, Lincoln, Nebraska, USA) using a static incubation technique. Total microbial biomass C and N were determined as the flush of DOC (i.e., dissolved organic carbon) or total N, respectively, following fumigation with chloroform.

DOC and total N in soil solution were determined by first shaking soils for 4 h with 0.5 mol/L K_2SO_4 (Fierer and Schimel 2003). After shaking, the soil solution was filtered; then, total organic carbon (TOC) and total N (TN) concentrations were determined using a TOC/TN analyzer (Model Vario TOC Select; Elementar, Langensfeld, Germany). Dissolved organic N (DON) was quantified after accounting for inorganic N concentrations, determined using the initial N mineralization samples (see paragraph on determination of N mineralization and nitrification below). While DOC is often considered a labile soil C pool, it can be composed of both simple and complex C compounds (Strickland et al. 2010). For this reason, we also determined the mineralizable C pool which is expected to be indicative of the most labile soil C.

Mineralizable C, an estimate of labile soil C, was determined by measuring total CO_2 emissions over the course of a 30-d incubation (Fierer et al. 2005). Soils were maintained at 65% water-holding capacity and 20°C with respiration across this time period determined using the static incubation procedure described for catabolic profiles. Total mineralizable C was estimated by integrating CO_2 production across time.

Potential net N mineralization and potential net nitrification were determined following Fraterrigo et al. (2005). Briefly, NH_4^+ and NO_3^- were determined on an initial 10-g soil sample after extraction with 50 mL of 2 mol/L KCl using a Lachat analyzer (Model QuikChem 8500; FIA System, Loveland, Colorado, USA). A second 10-g soil sample was incubated at 65% water-holding capacity and 20°C for 28 d. After the 28-d incubation, NH_4^+ and NO_3^- concentrations were again determined. Potential nitrification and mineralization were calculated as the change in NO_3^- concentration and the change in NH_4^+ and NO_3^- concentrations, respectively, across the 28-d incubation (Keiser et al. 2016).

Identification of ectomycorrhizal fungi

For our analysis of ectomycorrhizal diversity, we limited our analysis to the following treatments: two-unprotected-logs, two-protected-logs, two-unprotected-pipes, and reference. For the first three of these treatments, only samples from the under position were included, for a total of 48 samples. Fine roots ≤ 2 mm in diameter were removed from each sample by carefully picking apart the soil by hand or by gently rinsing it with water. We then identified root tips showing evidence of a fungal mantle or sheath which is typically construed as evidence of an ectomycorrhiza. As detailed in Appendix S3, small masses excised from these root tips were processed to identify mycorrhizae using DNA barcoding methods.

Deadwood elemental concentrations

A disk (~5–7 cm thick) was cut from the center of one randomly chosen log from each of the two-unprotected-logs and two-protected-logs treatments. In total, 21 and 24 disks were collected from the unprotected and protected treatments, respectively (disks from three unprotected logs were not collected due to vandalism). Disks were placed in large ziplock bags and stored at 4°C until processing. Each disk was dissected to remove any insects, and we recorded presence/absence data for termite and wood-boring beetle activity (including evidence of previous activity). After removing all insects, the wood samples were dried at 65°C until no further mass loss was observed and were then ground into a powder using a Wiley mill. The ground samples were sent to the Soil, Plant and Water Laboratory at University of Georgia to determine elemental concentrations, including N, Ca, K, Mg, P, S, Al, B, Cd, Cr, Cu, Fe, Mn, Mo, Na, Ni, Pb, and Zn. Two subsamples from each ground and homogenized disk sample were placed in a muffle furnace and combusted at 500°C for four hours until only soil and ash remained. The purpose of this was to determine, based on the average of the two subsamples, what fraction of dry wood weight consisted of termite-imported soil (and ash although this was a negligible component for most disks from unprotected logs).

Tree growth and nutrient status

Initial measurements that were made on the 144 study trees included trunk diameter at 0.5 m

above the ground to the nearest 0.01 cm, height to the nearest cm, and needle nitrogen content. Nitrogen content was determined by collecting a total of ten leaf fascicles from each tree (removed from multiple positions), dried at 102°C for 24 h, and ground into powder using a Wiley mill. These samples were analyzed using a PerkinElmer Series II 2400 CN analyzer (PerkinElmer, Inc., Waltham, Massachusetts, USA), with autosampler, at the University of Georgia's Chemical Analysis Laboratory. We also developed a competition index for each tree based on how many woody stems were present nearby. This was calculated using the formula $\sum_{i=1}^n d_i^{-1}$, where d is the distance between the study tree and a competitor tree for n trees. Measured one year after the study began, competitor trees were defined as living trees (including other pines and hardwoods) with a basal stem diameter >2.5 cm that were growing within a 2.5 m radius of the study tree. There were no competitor trees within 2.5 m for two of the study trees, so in those cases we used the distance to the nearest tree. Overall, the number of competitor trees included in this calculation ranged from 1 to 5 and the competition index ranged from 0.18 to 3.99. Final tree data were collected in late February 2016, after 51 months. All study trees were felled at 0.5 m, and a disk was collected at this height to measure cross-sectional stem area (the face corresponding to 0.5 m was marked). The height of each tree, including the stump and removed disk, was measured to the nearest cm. Needles were collected from the terminal branch for nutrient analysis. Upon returning to the laboratory, we photographed each of the disks and used ImageJ (Rasband 1997) to measure the cross-sectional area (i.e., not including phloem or bark).

Data analysis

The Proc Mixed procedure of SAS (SAS Institute 1999) was used to determine whether the three final tree measurements (cross-sectional stem area, height, and needle nitrogen concentration) varied among treatments with location, block within location, and treatment by location treated as random effects. Initial models also included three uncorrelated covariates (initial tree diameter, initial needle nitrogen concentration, and competition), but covariates were eliminated one at a time when non-significant. Three estimate statements were used with these models to (1) compare treatments

with termites (two-unprotected-logs and four-unprotected-logs) to those without termites (all other treatments), (2) compare the two-unprotected-logs and two-protected-logs treatments, and (3) test for a linear trend in response to increasing amount of unprotected wood added (i.e., reference vs. four-unprotected-logs). Denominator degrees of freedom (DF) were calculated using the Kenward-Roger method (SAS Institute 1999).

The Mixed procedure of SAS was also used to compare soil parameters among treatments and between sample positions (i.e., under vs. away). As above, location, block within location, and treatment by location were treated as random effects. In addition, because sample position represented a sub-plot factor, treatment by block in location was included as a random effect to account for “whole-plot error” leaving “within-plot” error as the residual. The whole-plot error term was eliminated from the model when estimated to be zero. Denominator DF were calculated using the Kenward-Roger method (SAS Institute 1999). When a main effect (i.e., treatment or sample) was significant, levels within that factor were compared using Fisher’s protected least significant difference (Day and Quinn 1989). These comparisons consisted of (1) the six pairwise comparisons between treatments after averaging across sample positions (i.e., under and away) and (2) comparisons between under vs. away samples separately for each of the two-unprotected- and two-protected-logs treatments. Extractable NH_4^+ , extractable NO_3^- , potential net N mineralization, and potential net nitrification were log-transformed prior to analysis (the latter two variables were adjusted by adding a constant to avoid negative or zero values prior to applying the log transformation).

We analyzed ectomycorrhizal colonization across treatments using generalized linear mixed models via the lme4 package (Bates et al. 2012) for R 3.3.2 (R Core Team 2016). Presence/absence of mycorrhizal colonization, as confirmed via identification of mycorrhizal fungal DNA barcodes or RFLP patterns, was used as the binomial response variable, with treatment as the fixed factor and location as the sole random factor. We also assessed mycorrhizal diversity across treatments using contingency table analysis.

For the comparison of log elemental concentrations between protected and unprotected logs,

we used the Mixed procedure of SAS, with treatment viewed as fixed and location, block within location, and the location $\times$ treatment interaction as random effects. To examine the possible effect of termite-imported soil on elemental concentrations of logs, this mixed model also included soil content (log-transformed) as a linear predictor for elemental concentrations, only in the unprotected logs treatment. Soil content was not included as a predictor of elemental concentrations for the protected logs because importation of soil by termites did not occur for this treatment. The null hypothesis that there was no relationship between termite-imported soil and elemental concentrations was examined by testing that slope = 0 for the soil predictor in the unprotected logs treatment. To determine whether treatment differences were due primarily to the presence of termite-imported soil in unprotected logs, we compared sequential, or Type 1, and partial, or Type III, tests to look at the treatment effect before and after accounting for soil. Under the fitted model, Type I F tests compare treatment means that are not adjusted for soil amounts, while the Type III F tests are equivalent to comparing the unadjusted mean for protected logs to the predicted mean for unprotected logs adjusted to a value of $\ln_{\text{soil}} = 0$ (i.e., soil = 1%). Concentrations of Al, Cr, Fe, Mo, Ni, and Pb were log-transformed, and one outlier was dropped for Zn prior to analysis. Denominator DF were calculated using the Kenward-Roger method (SAS Institute 1999). For the final analysis of measurements from logs, we used PC-ORD (McCune and Mefford 2011) to conduct principal components analysis (PCA) on the same dataset (with log-transformed concentrations for Al, Cr, Fe, Mo, Ni, and Pb). A correlation matrix was used, and the data were relativized by maximum before analysis. We also excluded data from one log due to the presence of an outlier for Zn. Correlations between each element and the first two principal components were calculated.

We also estimated changes in N and P contents in the wood of protected vs. unprotected logs over the 51-month study period. To estimate the initial N and P contents, we used the estimated initial dry mass of wood (i.e., not including bark) and published values for N and P concentrations of loblolly pine wood (see Appendix S1: Fig. S1). To estimate the final dry mass of the wood of

logs surrounding each tree, we used the decay rate constants (from the single exponential model) calculated for loblolly pine logs protected (using the same method in the current study) or unprotected from termites for 31 months in the same general study area (Ulyshen 2014). These constants were 0.01649 and 0.02009 for protected and unprotected logs, respectively. We used 51 months in the equation to estimate mass remaining and multiplied this value by our final N and P concentrations to determine the contents of these elements. We compared the change in content of these two elements between protected and unprotected logs using Proc Mixed in which location, block within location, and treatment by location were treated as random effects.

RESULTS

Soil parameters and ectomycorrhizal diversity

Our final soil analysis, after 51 months, showed nitrate and potential net nitrification (averaged across sample locations, means $\pm$ SE, $n = 12$) to be significantly higher for the four-unprotected-logs (3.41 ± 0.86 and 4.30 ± 1.16 , respectively) and two-protected-logs treatments (4.40 ± 1.02 and 3.98 ± 1.13 , respectively) than for the reference (0.76 ± 0.01 and 0.10 ± 0.07 , respectively) or two-unprotected-logs (0.97 ± 0.09 and 0.31 ± 0.11 , respectively) treatment (Fig. 2). Substrate-induced respiration biomass was significantly higher for the reference treatment (0.74 ± 0.08) than for the four-unprotected-logs treatment (0.62 ± 0.08 ; Fig. 2). There were also significant differences between soil samples taken directly under or away from unprotected or protected logs. Ammonium was higher away from unprotected logs (8.19 ± 1.21) than under them (3.97 ± 0.81) but showed the opposite pattern for protected logs (5.94 ± 1.34 and 9.35 ± 0.84 , respectively; Fig. 2). Nitrate was higher away from protected logs (6.56 ± 1.75) than under them (2.24 ± 0.50), as was potential net N mineralization (3.89 ± 0.99 and 0.43 ± 0.55 , respectively). Potential net nitrification was significantly higher away from both unprotected (0.59 ± 0.23) and protected logs (5.69 ± 1.57) than under them (0.02 ± 0.02 and 2.26 ± 0.85 , respectively; Fig. 2). Finally, dissolved organic carbon was significantly higher under than away from both unprotected (0.12 ± 0.01 and 0.09 ± 0.01 , respectively) and

protected logs (0.11 ± 0.02 and 0.07 ± 0.01 , respectively). There were no significant differences for all other soil parameters (100% WHC, pH, mineralizable C, microbial N, microbial C, microbial C:N, and DON; see Fig. 2). Our comparison of soil nutrients (P, Ca, K, Mg, Mn, and Zn) after three years detected no differences among treatments (data are provided in Appendix S2).

Ectomycorrhizal fungi identified as symbiotic with *Pinus taeda* included members of the Amanitaceae, Bankeraceae, Rhizopogonaceae, Russulaceae, Suillaceae, and Thelephoraceae (Appendix S3). We detected no differences in mycorrhizal colonization among treatments (likelihood ratio test of presence/absence of mycorrhizal fungi in mixed model without treatment against mixed model with treatment: $\chi^2_3 = 3.317$; $P = 0.345$).

Log elemental concentrations and content change of N and P

Whereas 90% of the disks collected from unprotected logs had evidence of previous or current termite activity, termites appeared to be completely excluded from the protected logs, as intended. By contrast, 49% of all disks had evidence of wood-feeding beetle activity, including 43% and 54% of disks from unprotected and protected logs, respectively. While a variety of wood-boring beetles were found in the disks (including members of Cerambycidae, Buprestidae, and Passalidae), cerambycids were the most frequently encountered beetles in both unprotected and protected logs. Larvae collected from three of the protected logs were identified, after completing development, as *Typocerus zebra* (Olivier). The presence of *T. zebra* in protected logs indicates these beetles were able to successfully oviposit through the mesh. Of the nine disks from unprotected logs with wood-borer activity, the activity levels for two were visually rated as extensive, three as intermediate, and four as minimal. Similarly, of the 13 disks from protected logs with wood-borer activity, two were rated as extensive, four as intermediate, and seven as minimal. Based on subsamples combusted in a muffle furnace, $22.4\% \pm 3.0\%$ (range: 0.6–71.2%) of final dry wood weight from unprotected logs consisted of non-organic material. This can be mostly attributed to termite-imported soil (Ulyshen and Wagner

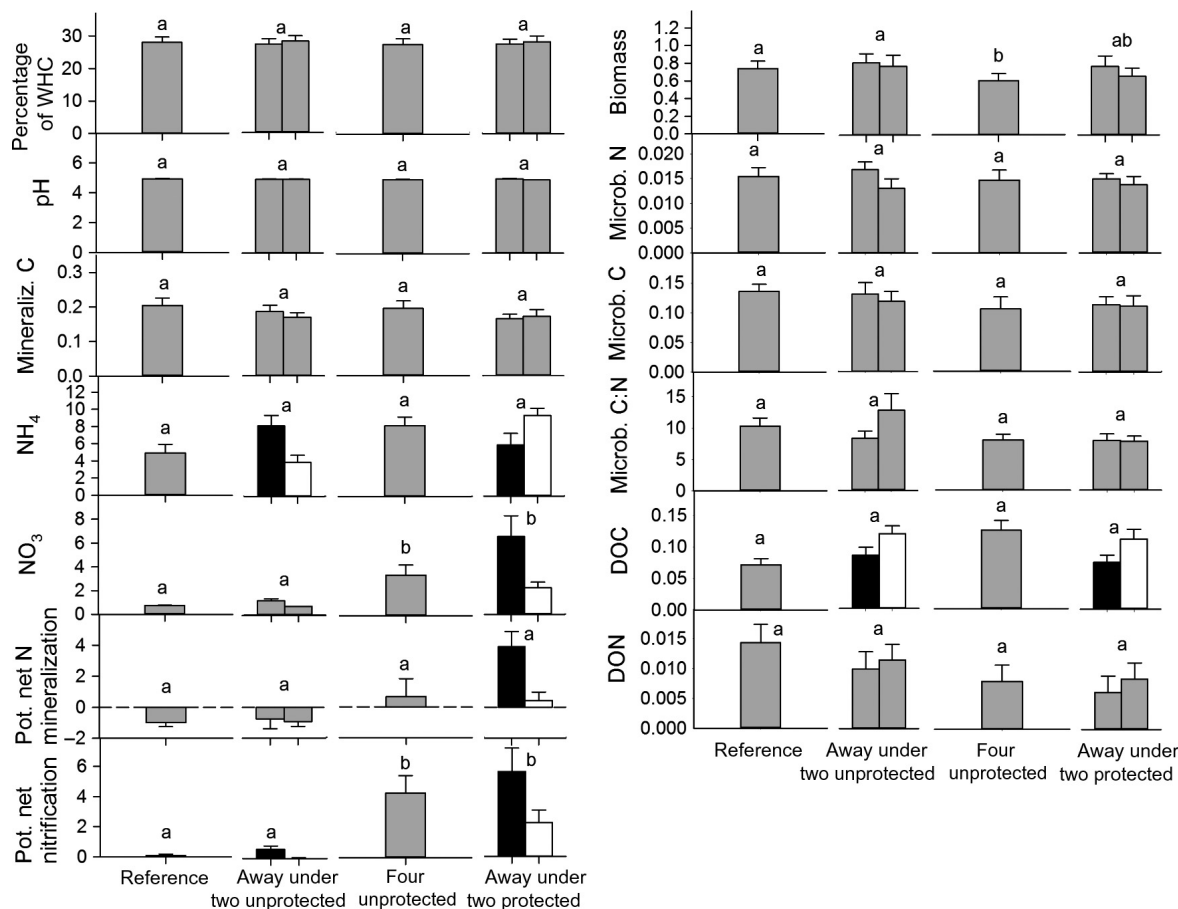


Fig. 2. Mean $\pm$ SE soil parameters for the different treatments and sample locations. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here. Bars with different letters above them are significantly different, with data averaged across the away and under samples for the two-unprotected-logs and two-protected-logs treatments (means not shown). For these two treatments, significant differences between the away and under samples are indicated by black and white bars, whereas bars with non-significant differences are shaded gray. WHC = water holding capacity; DOC = dissolved organic carbon; DON = dissolved organic nitrogen.

2013) considering the mean value of ash remaining from protected logs was only $0.8\% \pm 0.03\%$.

Ignoring soil content, ANOVA Type I F tests detected significant differences between treatments for P, N, S, Al, B, Cr, Cu, Fe, Mo, Ni, and Pb (Appendix S4: Table S1). Mean values were higher in unprotected vs. protected logs for all of these elements (Appendix S4: Table S2). Our test of slopes indicated significant positive relationships between soil content in unprotected logs and the concentrations of Mg, P, Al, B, Fe, and Pb, suggesting imported soil may have driven treatment differences for some of these elements (Appendix S4: Table S3). Comparisons between

the Type I and Type III F values (which measure strength of the treatment effect before and after accounting for the soil content of unprotected logs, respectively) indicate that the difference in elemental concentrations between treatments disappears for most elements when soil is accounted for, the exceptions being Cr, Fe, Mo, and Ni (Appendix S4: Table S1). In our PCA, the first two components, pc1 and pc2, explained 48.8% and 19.4% of the variation, respectively, with the two treatments clearly separating along pc1 (Fig. 3). The twelve elements correlating most strongly (Pearson's $r > 0.7$) with principal component 1 were, in decreasing order, Al, Fe, P, Cr, Ni, Cu,

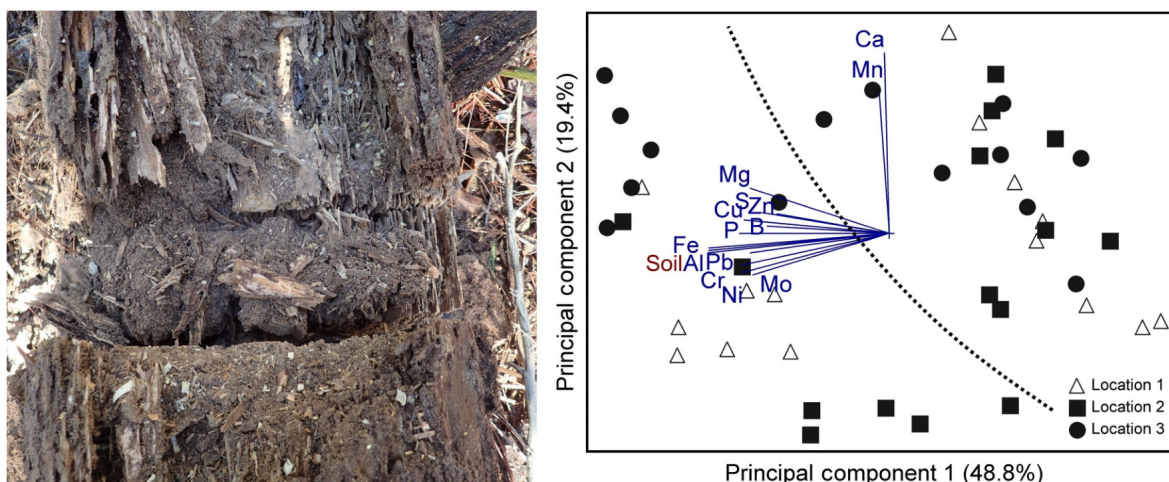


Fig. 3. Example of a disk cut from the center of an unprotected log with extensive termite damage and imported soil (left) and ordination from principal components analysis (PCA; right). The symbols in the ordination represent individual logs, and the different symbol shapes correspond to the three locations (plantations). The dotted line separates unprotected logs (left) from protected logs (right). Note that only elemental concentrations were included in the PCA and vectors are shown for those for which R^2 was ≥ 0.5 . The correlation between soil and the x-axis is shown for illustrative purposes only (i.e., soil was not used to develop the principal components).

Pb, Mg, Mo, S, B, and Zn (Fig. 3; Appendix S4: Table S4). Although not included in the PCA, soil also correlated strongly ($r = -0.90$) with principal component 1. Only two elements, Ca and Mn, correlated as strongly with principal component 2 (Fig. 3; Appendix S4: Table S4).

By the end of the study, the N and P contents of logs had reduced by more than 50% in both the two-protected-logs and two-unprotected-logs treatments (Fig. 4). The former treatment experienced larger reductions in both elements, but these differences were not significantly different

($F_{1,2} = 5.36$, $P = 0.15$; and $F_{1,2} = 14.49$, $P = 0.06$, for percent change in N and P contents, respectively). There were net N losses of 16.4 ± 0.9 g and 15.3 ± 1.4 g from the wood of logs assigned to the two-protected-logs and two-unprotected-logs treatments, respectively, that is, ~ 1 g difference between treatments. The respective values for net P losses were 2.9 ± 0.1 g and 2.7 ± 0.1 g. Assuming final elemental concentrations for logs assigned to the four-unprotected-logs treatment were the same as those assigned to the two-unprotected-logs treatment, the net N and P losses from these logs amounted to 35.4 ± 2.0 g and 6.6 ± 0.2 g, respectively.

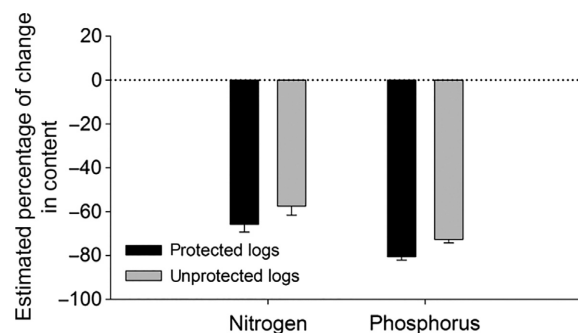


Fig. 4. Changes in N (Nitrogen) and P (Phosphorus) contents of logs after 51 months of decomposition were larger in logs protected vs. unprotected from termite activity.

Tree growth and nutrient status

For the final tree measurements, there were no significant differences among treatments for cross-sectional stem area, tree height, or needle nitrogen concentration (Appendix S5: Table S1, Fig. S1). Contrasts indicate that increasing amounts of unprotected logs had no effect on these response variables. The presence of termite activity also did not matter, and there were no differences between treatments receiving two-unprotected-logs vs. two-protected-logs (Appendix S5: Table S1). Initial diameter and competition were significant covariates for final cross-sectional stem area, and initial

diameter was also significant for final tree height (Appendix S5: Table S1).

DISCUSSION

The main objectives of this study were to explore the role deadwood plays in linking below- and above-ground systems and to specifically test whether subterranean termites accelerate the release of nutrients from decomposing logs and stimulate tree growth. Final soil, tree, and wood measurements were made after 51 months when the added logs were more than half-decomposed. As discussed below, our findings indicate that deadwood and termites both contribute to the spatial heterogeneity of soil properties but may have limited short-term local effects on tree growth.

Effects of deadwood and termites on soil parameters and tree metrics

We found soil properties to differ in relation to the number of logs added as well as to whether the logs were protected from termites or not. Among treatments receiving unprotected logs, the addition of four but not two logs resulted in greater nitrate and potential net nitrification compared to the reference condition where no logs were added. These results are consistent with the expectation that coarse woody debris increases plant-available N in the soil but suggest that large amounts of wood may be needed to register an effect. Among treatments receiving two logs, those protected from termites resulted in significantly greater soil nitrate and potential net nitrification than those left unprotected. These findings suggest that termites may act to reduce, rather than increase, plant-available N in the soil beneath decomposing logs. One possible explanation of this may be that termites immobilize N within their tissues, which later gets disseminated over large distances with dispersing reproductive individuals (Wood and Sands 1978). Indeed, termites are known to tightly conserve nutrients within their colonies through trophallaxis and cannibalism (Wood 1976, Lee 1983). The fact that soil parameters did not differ between the four-unprotected-logs treatment and the two-protected-logs treatment suggests that additional inputs of logs can overcome the negative influence of termites on N availability in the soil.

Our comparison of soil properties under and away from unprotected and protected logs yielded some interesting insights into the local-scale effects of deadwood and termites. For unprotected logs, ammonium and potential net nitrification were significantly higher away from logs than under them (Fig. 2). Potential net nitrification was also significantly higher away vs. under protected logs, as were nitrate and potential net nitrification, but the opposite pattern was observed for ammonium. The inconsistent pattern for ammonium observed between unprotected and protected logs is likely due to higher rates of nitrification at the away positions for protected logs; that is, ammonium is lower because it is being oxidized to nitrate. Overall, our findings suggest that plant-available forms of nitrogen tend to be less abundant under logs than away from them. Few previous studies have looked at this question although Zalamea et al. (2016) reported similar patterns in Puerto Rico, finding soil under decaying logs to have lower nitrate than soil 50 cm away from logs, for example. We detected lower levels of nitrate, potential net nitrification, and potential net N mineralization in reference treatment soil (no logs added) compared to soil away from protected logs (Fig. 2). These results indicate that the influence of deadwood on soil properties extends beyond the underlying soil. Although it is not clear whether these patterns are the result of N moving away from or toward the logs, the fact that N content had reduced by more than 50% by the end of the study (Fig. 4) shows that logs at this stage of decomposition act as a net source rather than a sink of N.

Despite differences in plant-available N among treatments, we found additions of unprotected or protected logs to have no effect on tree growth or needle N concentrations after 51 months. This is not surprising considering none of our sites was nitrogen-limited. Stronger productivity effects may have been seen on less fertile sites as has been shown in other studies (Sterba 1988, Thiffault et al. 2011, Egnell 2017). In Austria, for example, Sterba (1988) showed that retaining slash created by thinning increased foliar nitrogen and phosphorus concentrations and increased tree growth relative to plots in which slash was removed, but these effects were strongest at a site initially deficient in N. We may have also seen

stronger effects over longer periods of time as even under conditions of N-limitation, plants have been shown to compete effectively with microbes for N (Schimel and Bennett 2004).

Effects of termites on nutrient dynamics in decomposing wood

The concentrations of most elements, including nitrogen and phosphorus, were significantly higher in wood samples collected from unprotected vs. protected logs at the end of the study (Appendix S4: Tables S1, S2). These patterns cannot be attributed to the presence of insect biomass in unprotected logs as the disks were carefully dissected to remove all invertebrates prior to sample homogenization and analysis. Because termites are known to accelerate decomposition, the greater loss of carbon from unprotected logs is one possible explanation for these differences. Our comparisons of N and P contents between unprotected and protected logs provide only limited support for this idea, however (Fig. 4). Another contributing factor may be the soil imported into unprotected logs by termites. Indeed, we found strong positive correlations between soil content and the concentrations of many elements, and the treatment effect disappeared for most elements, including N and P, after accounting for the soil content of unprotected logs (Appendix S4: Table S3). This was not the case for all elements, however (e.g., Cr, Fe, Mo, and Ni). One possible explanation for these patterns concerns the production and deposition of frass by termites. The surfaces of *Reticulitermes* galleries are coated with layers of frass, and this material has been shown to contain higher concentrations of most elements than wood (Chen and Forschler 2016). Moreover, the frass-coated gallery material of subterranean termites has been shown to support large populations of bacteria (Chouvenec et al. 2011, Ulyshen et al. 2016a) which are believed to provide protection from fungal pathogens (Chouvenec et al. 2013). This bacterial biomass may result in higher concentrations of some elements compared to wood not colonized by termites. It should be noted that insects other than termites were likely excluded from protected logs and may have contributed to the differences we detected between treatments. Because termites are by far the most important wood-feeding insects in our study area (Ulyshen

et al. 2014), however, they probably exerted the strongest effects on both wood and soil properties. The presence of wood-boring beetles in many of our unprotected logs was unexpected, but we doubt this had much effect on our results given that the same beetle activity was observed in many of the unprotected logs as well.

Effects of competing vegetation

Growth rates of loblolly pine are known to be constrained by competing vegetation including both woody and herbaceous plants (Miller et al. 1991). It is therefore not surprising that our competition index, which reflected the number and proximity of other woody stems, was a significant covariate in our models of cross-sectional stem area. We included artificial log treatments in our assessment of tree responses to determine whether woody debris may benefit tree growth by reducing competition from other plants, similar to what Harrington et al. (2013) showed for Douglas fir seedlings. We found no evidence for this, possibly because grasses and other plants quickly grew up around and over these additions. It is possible that competing vegetation quickly immobilized nutrients released from decomposing logs, however, limiting the perceived impact these additions had on soil fertility and overall plant productivity. Future research addressing this possibility would be of interest, especially if it extended to the point of canopy closure when herbaceous vegetation becomes suppressed and the trees have a strong demand for nutrients.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

What to do with woody debris created during a logging operation remains an important question for forest managers, especially today with growing demand for woody biofuels (Eisenbies et al. 2009, Tilman et al. 2009) and concerns about wildfire risk (Graham et al. 2004, Agee and Skinner 2005). Although many studies have shown that leaving behind foliage and small branches significantly improves growth rates in subsequent stands, the results from studies exploring the extent to which coarse woody material impacts tree growth are more mixed. This question is complicated by the negative relationship between wood diameter and decay rate,

meaning that any effect of coarse woody debris on tree growth may be slower to materialize compared to the effects of foliage and branches. In addition, coarse wood is characterized by lower nutrient concentrations and may thus act to temporarily reduce rather than increase nutrient availability for living plants. Although a subject of long-standing speculation, the sink–source dynamics of deadwood remain poorly resolved and no previous study, to our knowledge, has attempted to simultaneously assess the impacts of naturally occurring coarse woody debris on below-ground soil properties and above-ground plant responses. In addition to this primary objective, we went a step further to look specifically at the role termites play in the nutrient dynamics of decomposing wood.

Our additions of deadwood resulted in increases in nitrate and nitrification in the underlying soil but had no effect on the growth or nutrient status of trees after a period of 51 months. Whether or not termites were excluded from logs also had significant effects on plant-available forms of nitrogen but, contrary to expectations, termites acted to delay rather than accelerate the release of nutrients from decomposing wood and had no short-term local effect on tree growth. These findings contrast with those from some agricultural systems where termites have been shown to improve soil fertility and crop yields (Burnett 1948, Evans et al. 2011). Although logs were more than half-decomposed after 51 months when the final data were collected in this study (Ulyshen et al. 2014), nitrogen may not have been limiting to the stand within this period of time. The soil N supply in planted loblolly pine plantations is thought to far exceed demand for the first several years of stand development, but severe deficiencies develop as tree size increases, with demand exceeding supply around the time of canopy closure (Fox et al. 2007). If this happens after about five years, as hypothesized by Fox et al. (2007), it may be unsurprising that our experimental manipulations had no detectable effects on tree growth or nutrient status at the end of this study, that is, six years after planting. Longer studies are therefore needed to fully understand the value of deadwood and termites to soil fertility and productivity in southeastern U.S. forests.

The evidence currently available from this and previous studies (Ulyshen et al. 2012) indicates

that coarse woody debris has little or no short-term benefits to productivity in the managed pine forests of the southeastern United States. Laiho and Prescott (2004) reached the same conclusion from the perspective of northern coniferous forests and suggested that other benefits of coarse woody debris (e.g., importance to forest biodiversity; see Stokland et al. 2012) be considered when developing guidelines for deadwood retention. However, we do find some indication that adding more coarse woody debris can improve soil fertility, which has the potential to stimulate plant productivity in the long term.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1910/full>