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Belowground community turnover accelerates the decomposition of standing dead wood

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Abstract. Standing dead trees (snags) decompose more slowly than downed dead wood and provide critical habitat for many species. The rate at which snags fall therefore influences forest carbon dynamics and biodiversity. Fall rates correlate strongly with mean annual temperature, presumably because warmer climates facilitate faster wood decomposition and hence degradation of the structural stability of standing wood. These faster decomposition rates coincide with turnover from fungal-dominated wood decomposer communities in cooler forests to codomination by fungi and termites in warmer regions. A key question for projecting forest dynamics is therefore whether temperature effects on wood decomposition arise primarily because warmer conditions facilitate faster decomposer metabolism, or are also influenced indirectly by belowground community turnover (e.g., termites exert additional influence beyond fungal-plus-bacterial mediated decomposition). To test between these possibilities, we simulate standing dead trees with untreated wooden posts and follow them in the field across 5 yr at 12 sites, before measuring buried, soil–air interface and aerial post sections to quantify wood decomposition and organism activities. High termite activities at the warmer sites are associated with rates of postfall that are three times higher than at the cooler sites. Termites primarily consume buried wood, with decomposition rates greatest where termite activities are highest. However, where higher microbial and termite activities co-occur, they appear to compensate for one another first, and then to slow decomposition rates at their highest activities, suggestive of interference competition. If the range of microbial and termite codomination of wood decomposer communities expands under climate warming, our data suggest that expansion will accelerate snag fall with consequent effects on forest carbon cycling and biodiversity in forests previously dominated by microbial decomposers.

Key words: basidiomycetes; coarse woody debris; downed dead wood; *Reticulitermes flavipes*; saproxylic insects; soil food webs; soil invertebrates; subterranean termites; wood-rot fungi.

INTRODUCTION

Dead wood in forests is an important carbon stock, comprising ~17% of the total wood carbon in the world's forests (Pan et al. 2011). Yet its persistence as a stock depends strongly on whether dead wood is standing or downed (Seibold et al. 2015, Venier et al. 2015). For example, standing dead trees (or snags) tend to decompose more slowly than downed wood, due in part to the relatively low moisture in the aboveground wood

of snags, which limits the activities of wood decomposers (Dix 1985, Onega and Eickmeier 1991, Petrillo et al. 2016, Hararuk et al. 2020). Further, snags provide unique and critical habitat for species such as cavity-nesting birds (Demarais et al. 2017, Sandström et al. 2019). Lower abundance and diversity of these species, such as in southern parts of eastern U.S. temperate forests, is associated with low snag abundance (Maynard et al. 2015).

The lower density of snags in the southern part of eastern U.S. temperate forests is likely observed, in part, because wood decomposition is accelerated by the warmer temperatures in that region. Notably, there is a strong negative relationship in temperate forest between

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mean annual temperature and the probability a snag remains standing (Oberle et al. 2018b). Plausibly, higher temperatures most influence decomposition rates of the snag at the air–soil interface, where the general abundance of both oxygen and moisture can facilitate high wood-rot fungal activities (Crowther et al. 2014). However, in hardwood temperate forest, decomposition of belowground wood is not expected to be limited by excessive moisture (Moroni et al. 2015), meaning belowground wood can decompose faster than surface-placed wood (Smyth et al. 2011, Oberle et al. 2018a). Either way, as the wood at the base of the snag decomposes and weakens, the likelihood of snag fall increases. However, in combination with higher fungal activities, the increased chance of snag fall in warmer regions of U.S. forests may also arise given the marked transition in belowground community composition, from a wood-decomposer community dominated by fungi, to one codominated by animals. Subterranean termites (soil and dead-wood nesting), which are found throughout U.S. temperate forests, can reach abundances in warmer regions that, along with ants, dominate litter and surface soil invertebrate communities (King et al. 2013). Hence, whereas wood-rot fungi are the dominant wood decomposers in cooler regions of temperate forest, it is expected that subterranean termites and wood-rot fungi together mediate wood decomposition in warmer, southern temperate regions (Ulyshen and Wagner 2013, Bradford et al. 2014).

Subterranean termites, albeit often represented by a single species (i.e., *Reticulitermes flavipes* (Kollar)), are present throughout the range of U.S. temperate forests, meaning that warming climate may facilitate fairly rapid increases in their abundance as they fill in habitat within their range (Maynard et al. 2015). It is unclear how such increases would influence snag abundance and longevity. Although the integral role that temperate termites play in decomposing snags has been recognized for more than 100 yr (Snyder 1915, Keen 1929), questions remain as to whether temperate termites simply substitute for fungi in the wood decomposition process or, alternatively, play a unique role in shaping wood decomposition rates (Ulyshen et al. 2014). Certainly, in tropical and subtropical Africa and Asia, there is broad representation of termite feeding and nesting groups, especially fungus-growing Macrotermitinae species that achieve enormous abundance and rapidly decompose wood in ground contact (Schuurman 2005, Griffiths et al. 2019, Law et al. 2019). Although fungus-growing species may be absent in other tropical systems, termite assemblages in these systems are also species rich, highly abundant, and functionally diverse, and mediate substantial decomposition of ground-contact wood (Bultman and Southwell 1976, Cornwell et al. 2009). In warm temperate forest, by contrast, it is unclear as to whether the typically one or few subterranean species present in most temperate-termite assemblages—particularly for wood belowground—cause decomposition beyond that mediated by fungi

(Gholz et al. 1991, Fasth et al. 2011). In fact, their role in wood decomposition, additional to that which wood-rot fungi mediate, is commonly assumed to be minimal compared to what is observed in tropical and subtropical systems (Cornwell et al. 2009). The lack of knowledge about how subterranean termites influence snag fall rates in temperate forest makes climate change influences on snag abundances across this system uncertain, along with the consequent effects on dead-wood carbon stocks and forest biodiversity.

To help disentangle questions about the relative roles of termites versus fungi in mediating wood decomposition in temperate forest, we investigated termite and fungal effects on the decomposition and fall rates of simulated snags (untreated-pine fence posts) at six sites each within a warm and a cool location of U.S. temperate forest. After 5 yr of field exposure, the 180 posts were sectioned into belowground (i.e., buried), soil–air interface, and aerial parts to investigate rate of wood decomposition and microbial (i.e., fungi + bacteria) and termite colonization. We hypothesized that termites would accelerate decomposition rates of the belowground and soil–air interface wood, expediting snag fall at the warm location. We found accelerated snag fall and the highest rates of decomposition when termites were abundant, where termites primarily decomposed buried wood and had a nonadditive relationship with microbial activities. Specifically, termites enhanced decomposition at lower microbial activities, as did fungi at lower termite activities. However, as termite and microbial activities increased in the same post, they appeared to first compensate and then inhibit the decomposition activities of the other group.

METHODS

Experimental design

We worked at two forested locations, ~160 km apart, where the change in elevation from the southern to northern location had a strong effect on mean climate and also termite abundance. The southern location is in the piedmont region of the southern Appalachians, specifically, Whitehall Forest is in Clarke County, Georgia, United States (33°53' N, 83°21' W; 122 cm mean annual precipitation, 17°C, 25.6°C, and 6.7°C mean annual, summer, and winter temperatures, respectively). The northern location, Coweeta Hydrologic Laboratory, is in the southern Appalachian Mountains. It is located in Macon County, North Carolina, United States (35°03' N, 83°25' W; 183 cm mean annual precipitation, 13°C, 21.6°C, and 1.7°C mean annual, summer and winter temperatures, respectively). We established six sites, within <1 to a few kilometers of each other, at each location, with three sites at each location across north- and three across south-facing slopes and with elevations ranging from 192 to 226 m above sea level (a.s.l.) (southern location) and 783–1,053 m a.s.l. (northern location).

All sites were located in relatively mature (~ 80 yr) *Quercus-Carya* (i.e., oak-hickory) dominated forests, with a mix of hardwood and softwood canopy species including *Pinus* species.

Wooden posts were sourced from locally grown *Pinus strobus* L. (eastern white pine), which were freshly milled to 121 cm long, with an $\sim 80\text{-cm}^2$ cross section but were otherwise untreated. At each site, a 140-m-long transect was established in July 2013 from the base of the slope at the site, spanning upward toward the ridge. Every 10 m, starting at 0 m on the transect, a post was driven into the soil to a depth of ~ 30 cm, leaving ~ 90 cm of the post aboveground in a vertical position. In total, we field placed 180 posts (2 locations \times 6 sites \times 15 posts).

Our design was intended to capture wide variation in microsite conditions by establishing posts across different elevations, aspects, and slope positions. We expected that variation in microclimate, and the post spacing, would lead to a wide range of termite colonization, spanning from no colonization to high colonization. Specifically, colonies of *Reticulitermes* spp. in eastern U.S. forests typically feed in multiple pieces of wood within a $\sim 10\text{-m}$ -diameter area around the subterranean nest, and are territorial, creating spacing among colonies. Our post spacing of 10 m within a transect was therefore intended to generate colonized and noncolonized posts, while avoiding the need to use termite-exclusion techniques (e.g., mesh cages, termiticide treatments) and their potential nontarget effects on fungal-mediated decomposition (Ulyshen and Wagner 2013).

Prior to field placement a 45°-angle cut was made for the base of each post, creating a wedge that facilitated easier insertion into the soil. Then the fresh mass of each post was recorded to the nearest 0.5 g, along with the post dimensions (length and width measures), at which point each post received a uniquely numbered AI tag. Thirteen additional posts were similarly handled and then cut to yield four 2-cm-tall cross-sectional slices, the heights and widths of which were recorded, weighed fresh, and then dried at 70°C to constant mass. Nine of these subsamples were drilled with an 8-mm-diameter bit to generate sawdust, which was oven dried at 70°C, weighed, and then combusted at 550°C for 16 h to estimate organic matter content via loss on ignition (LOI). Metrics from the 13 additional posts were used to estimate the range of initial wood moisture, density, and organic-matter content values for the 180 field-incubated posts.

Posts were scored after ~ 4 mo and then 1, 3, 4, and 5 yr following field placement as standing or downed. One year following field placement, we measured litter depth and downed dead wood local to each post given that their abundance and composition can influence fungal activities. Litter depth was measured where the post was inserted, and fine woody material (FWM) within a 1-m radius of the post was measured in the following size classes: <1 , 1–5, and 5–10-cm-diameter and <1 m long for the largest size class. Coarse woody material (CWM)

was defined as longer than 1 m with a diameter >5 cm. Its volume was estimated within a 1-m radius of the post. Distance to the nearest piece of CWM was also recorded, along with its dimensions and decay class using the 1–5 rating (Waddell 2002). At post placement and when measuring the FWM and CWM, soil temperature and moisture was measured at 5-cm depth at the base of every post using a food thermometer and a volumetric soil moisture probe (Campbell Hydrosense™). Relative spatial differences in these soil microclimate variables are considered robust across time (Vachaud et al. 1985, Vanderlinden et al. 2012). However, to evaluate this expectation we also measured these variables at each site on multiple occasions each year between 2006 and 2015, from which we calculated the mean conditions to characterize site-level microclimate.

In June 2018, we harvested the posts. When downed, the bottom of the post was recovered from where it met the soil (i.e., the interface). Posts were scored for presence or absence of termite and borer activity in the buried, interface, and aerial sections of the post. Although multiple termite species are found in the region (Hyseni and Garrick 2019), all termites in the posts we observed belonged to the species *R. flavipes*, an observation consistent with an earlier survey of termites at both locations (King et al. 2013). Soil adhering to the posts was lightly brushed away and posts were subsampled with a circular saw into aerial, interface, and buried cross-sectional pieces that were ~ 2 cm tall. The aerial section was taken at ~ 105 cm along the post, which was ~ 15 cm below the top of the aerial part of the post. The interface section was taken at the soil–air interface, with the bottom of the section flush with the soil surface. The buried section was taken at 14–16 cm below the soil surface, so ~ 8 cm above the 45°-angle cut and within the surface mineral A horizon. Two posts were lost to a fire at Whitehall, meaning that 178 posts total were recovered in 2018, which yielded 534 total sections. These were placed into sealed plastic bags and returned to the lab for processing.

Wood analyses

Post sections were carefully brushed clean of soil and other foreign material, and animal presence scored (e.g. termites or ants) prior to their removal. Mineral soil within the section, used to line the galleries created by *R. flavipes*, was not removed but was accounted for in a subset of posts, as described later in this subsection. Length and width were measured and the fresh mass of the section recorded, along with volume estimated by water displacement (with the section wrapped in water-repellent plastic sheet). Surface decomposition was visually estimated as percentage of the cross-sectional area of the post section with “damage.” The section was then dried to constant mass at 70°C before being weighed again. These metrics were used to determine moisture content of the wood (i.e., difference between fresh and

oven dried mass, divided by fresh mass) and extent of decomposition as surface damage (cross-sectional) area of wood remaining and wood density.

To quantify microbial and termite activity to provide additional insight into the decomposition process, the above protocol was modified for 60 of the posts and hence 180 sections. Five standing posts per transect were selected (30 per location), starting with the second post at the base of a transect and then every third post. When the intended post was downed, the next standing post along the transect was selected. Sawdust was collected from each section when fresh by drilling holes in a gridded pattern using an 8-mm-diameter drill bit. The sawdust was separated into two samples, with one set of samples used to estimate moisture content and organic matter content via LOI as described for the harvested and initial posts, respectively. The second sample was used to estimate total microbial activity following Maynard et al. (2018). Briefly, we used a modified substrate-induced respiration approach (Beare et al. 1990, Fierer et al. 2003) that incubates at 20°C a fresh sawdust subsample with autolyzed yeast extract in deionized water as a labile carbon substrate and measures respiration over a 4-h period with an infrared gas analyzer (IRGA; Model LI-7000, Li-Cor Biosciences, Lincoln, Nebraska, USA). Carbon dioxide concentrations were converted to rate of C-CO₂ production, as mass C produced per hour per dry mass—equivalent wood. The short timescale of the assay has been shown to be a good proxy for total microbial biomass in soils and litters (Fierer et al. 2003, Frey et al. 2004) and is highly correlated with direct measures of fungal biomass (Beare et al. 1990). However, bacteria do contribute to wood decomposition, including indirectly through processes such as nitrogen fixation. Hence, although fungi dominate wood decomposition (Tláskal et al. 2021), we refer to the assay as a measure of total microbial activity, because it does not separate fungal and bacterial activity in dead wood.

We used the LOI values to estimate mineral soil contamination of the wood as a proxy for termite activity. Both observations and experiments have shown that *Reticulitermes* species actively transport a substantial mass of soil into the galleries they create in dead wood; lining those galleries with a mix of soil, wood particles, and fecal material (Ulyshen et al. 2014 and references therein). In experiments, over a period of 5 yr, *Reticulitermes* species transported enough soil into dead wood pieces to account for ~20% of dry mass (Ulyshen et al. 2014). Thus, over the time span of our experiment, soil mass is indicative of termite activity. The LOI data further allowed us to examine decomposition processes in relation to changes in organic-matter wood density and mass loss, thereby enabling us to correct for mineral soil contamination of the section (Ulyshen and Wagner 2013). For mass loss, we used the dimension data along with changes in organic matter density for each 2-cm-thick post section to estimate a standardized mass remaining.

Statistical analyses

The primary goal of our analysis was to investigate decomposition of standing dead wood to make inferences about how and why snag fall is so strongly dependent on temperature. We therefore examined decomposition of buried, interface and aerial post sections, and how termites and microbial activity, in the context of other factors such as microclimate, influenced the process. The focus of this causative statistical inferential approach is on identifying the conditional effect size of a causal variable relative to other known controls (sensu Holland 1986). Our decision regarding which variables to include as fixed effects in our statistical models was therefore based on known biological mechanisms that relate each predictor to the response variable rather than model selection (Hobbs et al. 2012, Bradford et al. 2021). We focused on identifying robust parameter estimates and so examined how model structure influenced regression coefficients for the controls under investigation (e.g., microbial and termite activity).

Given the spatial structure of our experimental set-up, with sections clustered per post, posts clustered per transect, and transects clustered per location—and our focus on estimating effect sizes of putative controls—we used hierarchical mixed models. We evaluated linear mixed models (LMMs), using the lmer function for Gaussian-distributed data and the glmer function for binomially distributed data, in the lme4 package for the “R” statistical program (version 4.0.3). For the three random effects, post identity was nested within transect, which was nested within location (to access data and code see Bradford [2021]). Fixed effects included years standing, post section as a binary variable (i.e., aerial 1 or 0 and interface 1 or 0, where buried is the 0, 0 possibility of these two model terms), litter depth, woody material volume within 1 m of the post (FWM + CWM), distance to nearest piece of CWM and its volume, soil temperature, soil moisture, and termite and borer presence or absence. Additionally, for the subset of 180 sections, we ran an additional analysis and included estimates of termite activity (i.e., 100-LOI% values) and microbial activity as continuous variables. We tested the distribution of the decomposition response variables and fit the appropriate error structure, which are reported in the supplemental data tables.

Given the potential for strong correlations among our predictors, such as microbial activities and post section (e.g., sections in ground contact, versus aerial sections, would be expected to be moister and more accessible to colonization by fungi that facilitate rapid decomposition), we evaluated the square root of the variance inflation factors (vif) for the main effects models. If values were <2.0 we retained the main effects in the same model, given the expectation that collinearity was low enough to limit its influence on the coefficient estimates of the predictors. We then evaluated ecologically relevant two-way interactions, such as microbial by termite

activity, to assess their influence on the interpretation of the main effects of the predictors. We calculated the r^2 values for our models following Nakagawa and Schielzeth (2013) to retain the random effects structure.

To examine the effect sizes of the focal predictors (e.g., termites) on decomposition, we took two approaches. First, we compared the size of the standardized coefficients, where standardizing involved subtracting the mean of the factor from each observed value and dividing it by two standard deviations (Gelman 2008). The approach puts binary and continuous variables, including those with different units, on the same scale and further permits unambiguous determination of the size and sign of interaction effects (Gelman 2008). Second, we plotted the influence of changing termite and microbial activities on decomposition. To do this, we used the unstandardized regression relationship derived from our statistical models, held all other factors at their mean for the data set, and varied termite and microbial activities across the range of values observed across the posts. To verify the robustness of our coefficient estimates, we conducted a sensitivity analysis following Bradford et al. (2019) to evaluate how inclusion/exclusion of predictor variables, and different forms of the same predictor (e.g., soil moisture estimated local to the post or from a multi-year mean across the site), influenced our conclusions. Models presented are those where coefficient estimates are relatively insensitive to model structure.

RESULTS

All posts

Time to first post fall—due to decomposition of buried and interface wood—was more rapid at the southern location, with 10 posts downed 3 yr after placement, whereas the first post fall was not recorded at the northern location until Year 4 (Table 1). At the southern sites, a further 17 posts fell by Year 4 and 11 by Year 5, giving 38 posts down total in 5 yr, whereas at the northern location only 13 posts total fell in the 5 yr (Table 1).

Overall, ~ 3 times more posts fell at the southern than northern sites.

The buried sections for 14 of the 38 downed posts at the southern location were fully decomposed, meaning we could not collect remaining wood for those post sections. Termites were present in all 24 of the buried sections we could recover, and were also present in the buried sections of 43 of the 50 posts still standing at this location (Table 2). By contrast, only 3 of those 50 standing posts had termites in the interface sections and none were found in the aerial sections. Conversely, termite colonization of downed posts in what had been the aerial and interface sections was common at the southern location, with more than half of each of those sections colonized (Table 2). In stark contrast, none of the downed posts at the northern location had termites, and only seven standing posts were colonized, with this colonization restricted to buried sections (Table 2).

Wood moisture, which both acts as a control on wood decomposition rates and increases as wood decomposes (Dix 1985, Sollins et al. 1987), was higher in buried and interface sections of standing posts than in the aerial section, yet varied markedly (from around 10% to 80% moisture) among posts for those former two sections (Fig. 1a). Moisture values of the aerial sections increased when posts were downed, presumably driving strong main effects of years standing and post section (Appendix S1: Table S1). Specifically, moisture values in aerial sections of standing posts were generally <20%, and approached or exceeded this value when downed (Fig. 1a), which is considered to be an approximate threshold for fungal-mediated wood decomposition (Dix 1985). Consequently, when examining potential predictors of the wood decomposition variables, wood moisture could not be run in the same models as years standing and section because it was strongly correlated with these factors. In addition to the fact that moisture content increases with the extent of wood decomposition (Sollins et al. 1987), it is then perhaps unsurprising that percent damage of the wood cross-sectional area by decomposers was positively associated with wood

TABLE 1. Number of posts that fell across the 5 yr of field observations at the six forest sites at the northern and southern locations.

Years post placement in the field	Northern location			Southern location		
	Posts down (no.)	Cumulative posts down (no.)	Cumulative posts down (%)	Posts down (no.)	Cumulative posts down (no.)	Cumulative posts down (%)
0	0	0	0	0	0	0
1	0	0	0	0	0	0
3	0	0	0	10	10	11.4
4	5	5	5.6	17	27	30.7
5	8	13	14.4	11	38	43.2

Note: The cumulative percentage of posts downed is based on $n = 90$ recovered posts at the northern location and $n = 88$ at the southern location.

TABLE 2. Number of post sections that were colonized by termites for posts that were standing or downed after 5 yr in the field at the six forest sites at the northern and southern locations.

Post position	Post section	Northern location		Southern location	
		Sections with termites (no.)	Sections with termites (%)	Sections with termites (no.)	Sections with termites (%)
Standing	Aerial	0	0	0	0
	Interface	0	0	3	6.0
	Buried	7	9.1	43	86.0
Downed	Aerial	0	0	24	63.2
	Interface	0	0	22	57.9
	Buried	0	0	24†	100†

Note: The total number of posts recovered at each location was 90 at the northern location and 88 at the southern location, with 13 and 38 posts downed, respectively (Table 1).

†Although 38 posts were downed at the southern sites (Table 1), 14 of the buried sections of the downed posts were entirely decomposed, meaning that there were only 24 buried sections that could be observed to score termite presence or absence. As such, the percentage of colonized sections is based on $n = 24$ for this section, whereas it is based on 38 for the other downed post sections at the southern location.

moisture, and that wood moisture was negatively associated with the area of the wood remaining and wood density. Yet the explanatory power of these associations markedly differed, with wood moisture alone explaining 75%, 53%, and 38% of the observed variation in damage, mass remaining, and wood density, respectively.

The lower explanatory power for density is likely the result of termites bringing mineral soil into the decomposing wood, which then obscured changes in wood density values associated with decomposition. Indeed, introduction of mineral soil at the southern location meant that some density values were twice as high as the initial median wood density (Fig. 1b) and there was a positive effect of termite presence on wood density in the regression model (Appendix S1: Table S2). We accounted for this introduction of mineral soil by determining organic matter percentages of the remaining wood for the subset of posts (*Standing post subset*). The other two decomposition variables revealed that, unless posts were downed, there was little decomposition of the aerial sections and, regardless of location, decomposition of the buried sections ranged from little to extensive decomposition (Fig. 1b–d). Overall, the main and interaction effects of years standing and post section had the strongest effects on decomposition rates, highlighting that the vertical position of the post wood was often an order of magnitude more influential (compare standardized coefficients in Appendix S1: Tables S3–S4) than termite or borer presence, and also microenvironmental conditions such as soil moisture, temperature, and woody material stocks.

Standing post subset

The subset of 60 standing posts (180 sections) allowed us to investigate decomposition in the absence of the influence of post fall, to correct for mineral soil contamination of the remaining wood, and to evaluate the proximate effects of the decomposer organisms. Mineral soil ingress was particularly pronounced at the southern

location, reducing percentage organic matter (OM) from 99.86% (initial wood) to values as low as $\sim 50\%$ in some buried sections (Fig. 2d). Reductions in wood density, expressed as g OM cm^{-3} wood, and in the wood OM mass remaining, were most strongly dependent on the vertical placement of the wood, with the differences among wood sections lessened when soil moisture was higher (Appendix S1: Tables S5–S6). Most notably, however, there was little decomposition of aerial sections and, for interface and buried sections, decomposition ranged from little to extensive loss of density and mass (Figs. 2b, c).

The pronounced variation in wood density and mass loss was matched by variation in our estimates of microbial and termite activities (Figs. 2c, d and 3b, c). As with the all-post data set, post section was strongly associated with wood moisture content, which in turn was strongly and positively associated with wood OM mass loss (Fig. 3a) and also organism activities (Appendix S1: Tables S7–S8). As such, there was strong collinearity among post section, wood moisture, and organism activities, so that coefficients for these predictors were not meaningful when run in the same model. Notably, however, the same amount of microbial or termite activity could translate to very different amounts of remaining OM mass (Fig. 3c, d). Termite–microbial interactions appeared associated with much of this variability in decomposition outcomes, with the interaction effect of microbial and termite activities as large as their main effects (Appendix S1: Table S8). The interaction appeared driven by multiple dynamics, with increasing termite activity at lower microbial activities causing a more than 10-fold reduction in remaining OM mass (Fig. 3d), whereas at high microbial activities, termite activities had no influence on decomposition rates and even a negative effect at the highest microbial activities (Fig. 3d). The positive signs of the main effects and negative sign of the interaction effect (Appendix S1: Table S8) suggested that termites and microbes might limit the other's activities at high densities. Notably, we

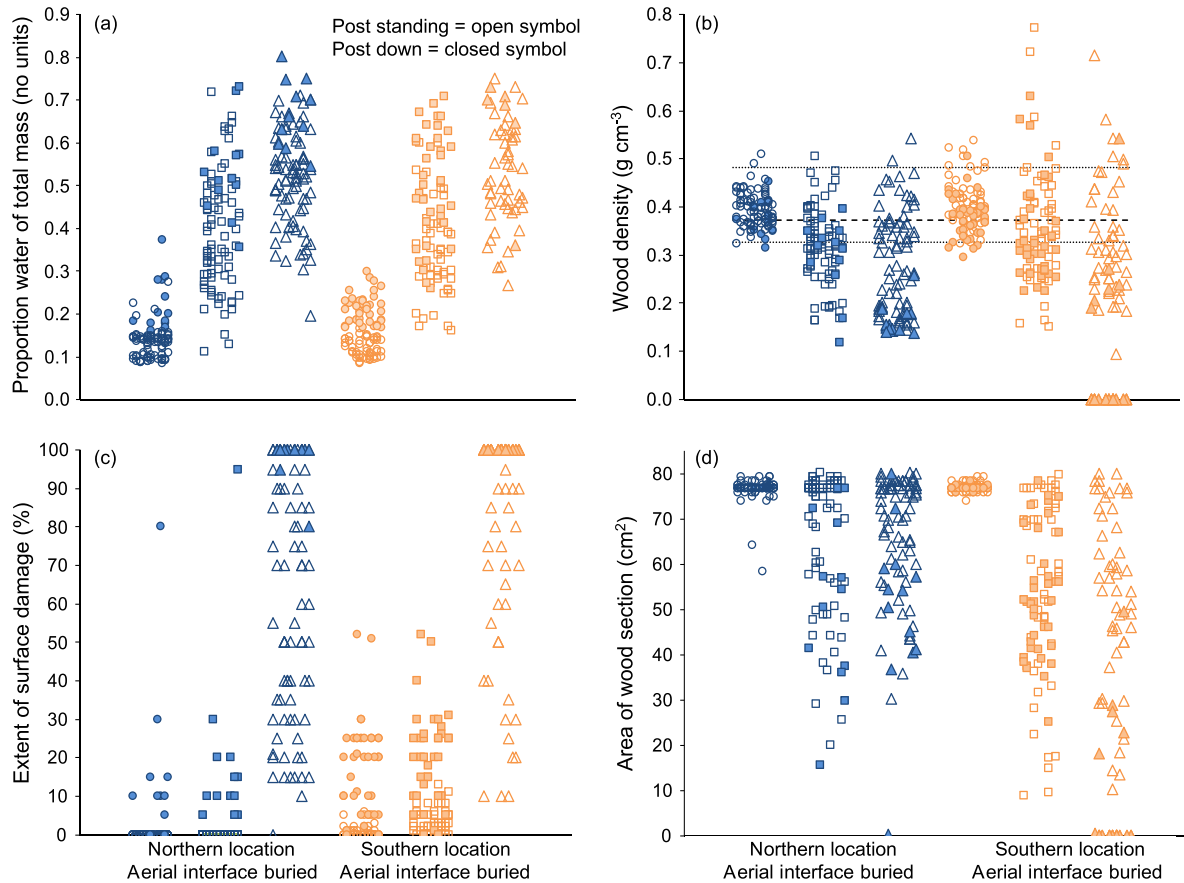


FIG. 1. Decomposition of standing and downed wooden posts by location and post section. Shown are individual observations for $n = 90$ posts at the northern location and $n = 88$ at the southern location, for each of three post sections (aerial, soil–air interface and buried) giving 534 observations total. Wood moisture content (a) is much lower in aerial sections and increases when posts are downed. Three different ways of scoring wood decomposition—(b) density loss, (c) surface damage, and (d) remaining wood area—were strongly affected by post section and also whether posts were standing or downed. In (b) the horizontal dashed line and the dotted lines show the median and range of initial wood densities, respectively.

observed a strongly unimodal relationship between termite and microbial activities (Appendix S1: Fig. S1). As such, very high termite activities were only associated with the lower range of observed microbial activities, and decomposition rates under these conditions exceeded those observed for microbes alone (Fig. 3d).

DISCUSSION

We designed our experiment to test whether the high termite abundances at our southern location (King et al. 2013) might, in part, explain the strong correlation between mean annual temperature and snag abundances and fall rates in eastern U.S. temperate forests (Maynard et al. 2015, Oberle et al. 2018b). Interpretation of termite influence was complicated, however, by termite presence in >90% of the buried-post sections we recovered at our southern location, meaning we had few observations of uncolonized posts. We had expected termite colonization to be clumped based both on territoriality among colonies and empirical assessments of

downed wood (King et al. 2013). Notably those empirical assessments were conducted with surface downed wood and, indeed, we did find much lower colonization of interface sections (28% of standing and downed posts colonized at the southern location). Termite colonization of dead wood may therefore be much more common in temperate forest than inferred from surface downed wood assessments. By eating away buried wood, it seems reasonable to assume that termites accelerate snag fall rates, thereby reducing the abundance and longevity of snags.

Given the near ubiquitous colonization of buried wood by termites at our southern location, we further probed the question as to whether termite activities result in faster decomposition rates than those observed with microbes only, by using mineral soil contamination of the subset of standing posts as an estimate of extent of termite colonization. Subterranean termites in our study region are the only decomposers known to incorporate large volumes of mineral soil into decomposing wood (Ulyshen and Wagner 2013). In standing posts, at

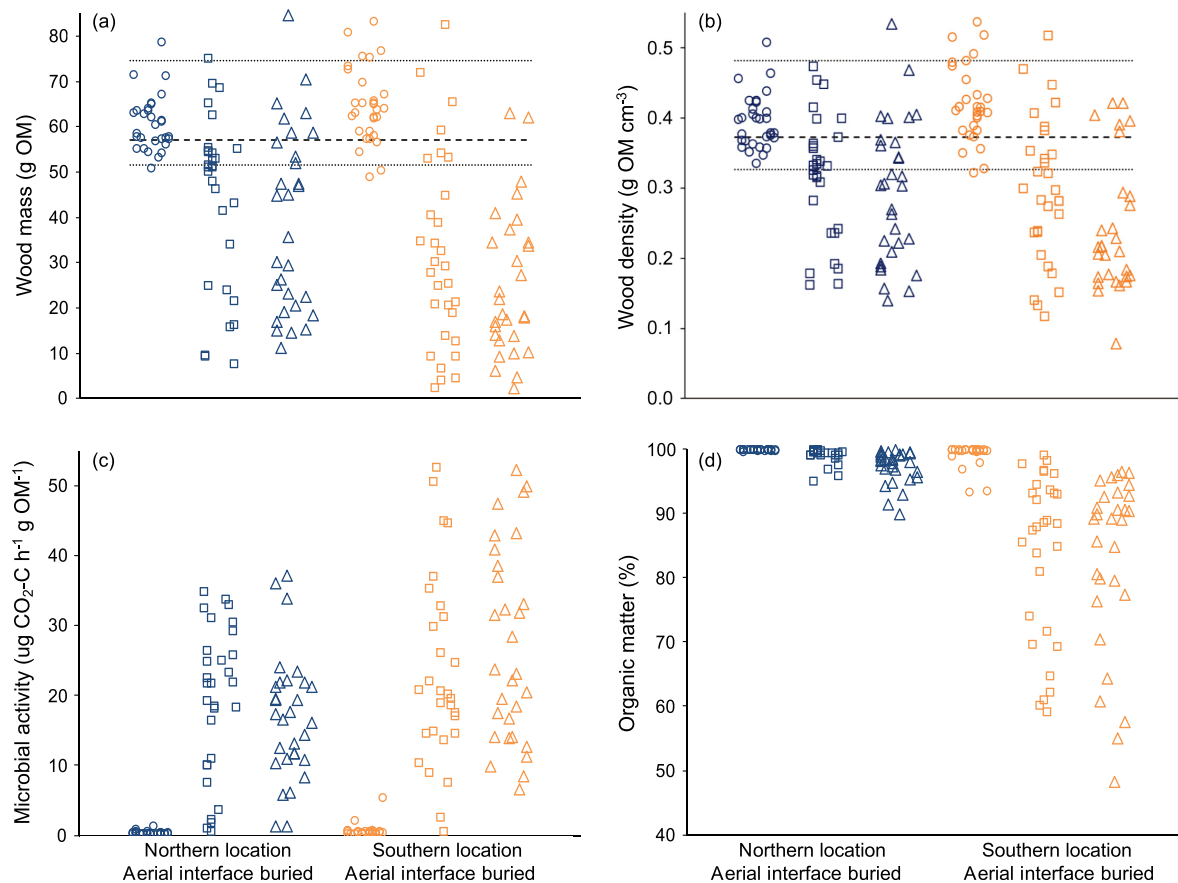


FIG. 2. Decomposition of the subset of standing wooden posts by location and post section. Shown are individual observations for $n = 30$ posts each at the northern and southern locations, for each of three post sections (aerial, soil-air interface, and buried) giving 180 observations total. After correcting for mineral soil contamination, post section remains a strong determinant of decomposition extent, with lower (a) mass remaining and (b) wood density for interface and buried post sections. The greater decomposition in these sections is associated with (c) higher microbial activities and (d) lower organic matter concentration, where the latter is primarily influenced by termites transporting mineral soil into the decomposing wood. Y-axis units in (a)–(c) are expressed after correcting for this mineral contamination, and hence wood mass is represented as grams of organic matter (OM). In (a) and (b) the horizontal dashed line and the dotted lines show the median and range of values, respectively, in posts harvested to quantify initial conditions.

low termite and high microbial activities, as much as 80% of the wood was consumed, whereas the highest termite activities consumed as much as 97.5% of the wood. Notably, we did not observe both high termite and microbial activities in the same piece of wood (Appendix S1: Fig. S1), at intermediate activities termites and microbes appeared to compensate for one another in terms of decomposition, and at the highest activities at which they co-occurred, decomposition was impeded (Fig. 3d). Such a set of dynamics likely arises through interference competition, but a series of harvest points that track wood decomposition, fungal biomass, and termite activity across time would be required to evaluate this inference robustly. What is known is that wood-rot fungi and temperate termites exhibit a range of behavioral, chemical, and enzymatic immune responses to one another (Martin and Bulmer 2018). Yet the consequences of these interactions for wood

decomposition dynamics require detailed study because interactions between termites and wood-rot fungi range from negative to positive, with it being suggested, for example, that termites expedite decomposition by facilitating fungal colonization (Maynard et al. 2015). Knowledge of how termites influence bacteria involved in wood decomposition appears unexplored, potentially because fungi dominate microbial-mediated wood decomposition in temperate ecosystems (Tláškal et al. 2021). Regardless, our data do suggest that high termite activity results in higher decomposition rates than high microbial activities alone, an observation supported by termite-exclusion experiments in tropical forests (Griffiths et al. 2019).

Our results suggest that positive effects of temperature on snag fall rates across the eastern United States (Oberle et al. 2018b) involve both direct effects of temperature on microbial activity and indirect effects driven

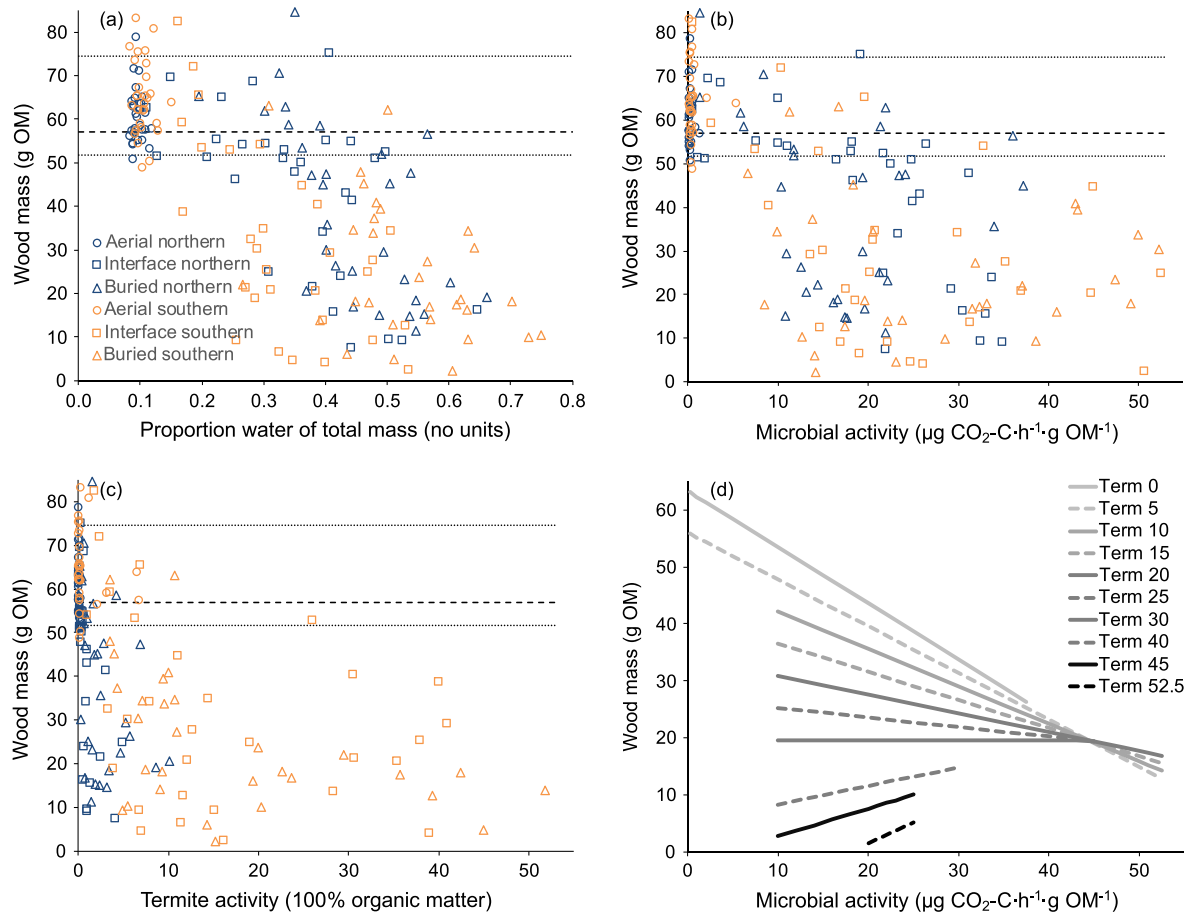


FIG. 3. Decomposition extent of the subset of standing wooden posts in relation to moisture and organism predictors. Shown are individual observations for $n = 30$ posts each at the northern and southern locations, for each of three post sections (aerial, soil-air interface and buried) giving 180 observations total. Wood organic matter (OM) mass remaining is corrected for mineral soil contamination and shown in relation to (a) wood moisture, (b) microbial activity, (c) termite activity (estimated based on 100 - % organic matter shown in Fig. 2d), and (d) termite-microbial interactions. In (a)–(c) the horizontal dashed line and the dotted lines show the median and range of values, respectively, in posts harvested to quantify initial conditions. In (d) the termite by microbial interaction is plotted using the unstandardized regression coefficients from the analysis presented in Appendix S1: Table S8, where all other predictors are held at their mean values and microbial and termite activities are systematically varied across the observed range in their values (shown in [b] and [c]). The relationship between termite and microbial activities is shown in Appendix S1: Fig. S1.

by decomposer community turnover from more fungal-dominated in northern parts of the forest, to fungal and termite co-dominated wood decomposition in southern regions. Although wood-boring animals such as beetles did increase surface damage of the wood, they had little effect on wood density and mass loss, suggesting that termites and fungi may be the most important wood decomposers to focus on for understanding snag fall rates in our region. Our observations contribute to mounting evidence (King et al. 2013, Ulyshen et al. 2014, Maynard et al. 2015) that subtropical termites are abundant in southern, warm temperate forests and exert an important influence on decomposition rates of wood in contact with the ground, including snags. The impact of termites as the key animal group affecting dead wood decomposition rates thus appears to span

from tropical forests, where they are recognized for their substantial contributions to wood decomposition (Abe et al. 2000, Cornwell et al. 2009, Giardina 2019), into temperate forests. To conclusively verify, however, the extent to which termites expedite snag fall in warm temperate forests will require observations of belowground wood of natural and experimentally created (e.g., by girdling) snags. Such experimental work should manipulate termite access to snags and consider factors such as bark presence and stem diameter, which can influence the decomposition rates of standing deadwood (Ulyshen et al. 2016, Oberle et al. 2018a), and fungal endophytes that can alter wood-rot fungal colonization and decomposition (Cline et al. 2018).

Although recognizing the limitations of space-for-time substitutions (Lauenroth and Sala 1992), our data

suggest that if termite abundances increase with projected warming in more northern parts of eastern U.S. temperate forest, that snag fall rates may be expedited through consumption of buried wood. The consequent effects on dead wood stocks, snag-associated biodiversity, and also potentially energy flows through decomposer food webs (i.e., termite vs. microbial-channels for dead wood) may not be restricted to eastern U.S. temperate forests. *Reticulitermes flavipes* is invasive in Europe and South America, and its range is projected to expand appreciably by 2050 as a result of changing climate (Buczowski and Bertelsmeier 2017). In its native range, the potential for its abundance to increase with warming will be facilitated by the fact that the range of *R. flavipes* extends across all eastern U.S. temperate forests and beyond 45° N (Maynard et al. 2015), meaning that abundance can increase through filling in of the northern parts of its range rather than the slower process of range expansion. Nevertheless, termite activities were strongly associated with wood moisture and soil moisture, as opposed to temperature, generally had a stronger influence on decomposition rates. Thus, the extent to which *R. flavipes* biogeographic range responds to climate change may depend on complex interactions among temperature, moisture, and other environmental characteristics, such as wood traits, that influence termite fitness (Maynard et al. 2015).

Notably, wood moisture was strongly associated with all of our decomposition metrics, vertical position of the wood section, and also termite and microbial activities. Wood-rot fungal activities are strongly sensitive to moisture (Maynard et al. 2019, Rinne-Garmston et al. 2019) and our data suggest that termite activities in our region are equally moisture sensitive, matching recent findings in tropical ecosystems (Cheesman et al. 2018). Supporting this inference, *R. flavipes* feeding is known to be sensitive to the moisture of its food and surrounding environment (Ulyshen et al. 2016), which may help explain why wood moisture and decomposer organism activities were so strongly correlated in our study that they could not be run in the same statistical models (Fig. 3, Appendix S1: Tables S7–S8). The challenge with causally interpreting our wood moisture content data, however, arises from the fact that wood moisture increases as a product of decomposition (Sollins et al. 1987). Moisture content therefore becomes an increasingly poor metric for estimating moisture availability to wood-rot fungi (Dix 1985). Nevertheless, low moisture availability is commonly invoked to explain why aerial versus ground-contact wood decomposes more slowly (Renvall 1995, Yatskov et al. 2003, Petrillo et al. 2016, Hararuk et al. 2020). Notably, a value of ~20% moisture content is commonly considered to inhibit basidiomycete fungal-mediated decomposition (Dix 1985), and the aerial sections of the standing posts generally had moisture values that fell below this threshold (Fig. 1a). Yet optimum moisture content values for growth of wood-rotting basidiomycetes is much higher,

in the range of 50% or more for undecayed wood (Dix 1985), and many of the buried and interface post sections had moisture values below this. As such, projecting snag abundance and longevity under climate change may revolve around understanding change in microclimate moisture availability, as opposed to macroclimate or temperature (see Lembrechts and Lenoir [2020], Zellweger et al. [2020]).

Given that moisture is a key determinant of snag dynamics, projections of changing snag-fall rates are further complicated by the fact that soil moisture variation can be orders of magnitude greater than temperature variation at fine scales (meters to kilometers) in forest understories (Bradford et al. 2014, Loescher et al. 2014). Our observations reveal that this variation in moisture is further magnified when considering the vertical dimension relevant to snag decomposition, with aerial parts of standing posts <1 m from the forest floor much drier on average than those at the interface, buried or for downed wood. Variation in moisture among posts was further exacerbated when posts fell which, as expected, increased wood moisture content. For the aerial sections at the southern location the increase in moisture was particularly pronounced (Fig. 1), giving rise to strong interactive effects of post section by years standing whereby the very minimal decomposition of standing aerial sections was accelerated once the wood was downed. Nevertheless, even in the buried sections of standing posts, wood moisture ranged from <30% to >70% (Fig. 1a). We deliberately omitted wood moisture content as a predictor in our main statistical models (Appendix S1: Tables S1–S8) given that moisture content generally increases as an outcome of decomposition (Sollins et al. 1987). Yet wood moisture availability remains a key regulator of decomposer activity (Dix 1985, Smyth et al. 2011, Oberle et al. 2018a, Hararuk et al. 2020). As such, given insights from mathematical proofs such as Jensen's inequality (Ruel and Ayres 1999), the high variation in moisture that we observed poses particularly difficult challenges for scaling causative relationships between microclimate moisture and wood decomposition, to stand and regional scales relevant to forest carbon budget and biodiversity projections (see Heffernan et al. [2014]). These challenges will be magnified by the fact that decomposition rates of downed wood at the same location and with variables such as wood species and log size controlled for, is itself highly variable (Bradford et al. 2014, Griffiths et al. 2021, Smith and Peay 2021) as also observed in our current study for both interface and buried wood (Figs. 1 and 2). Nevertheless, our results suggest that turnover in the wood-saprotroph community, from fungal to termite co-dominated, exerts important control on decomposition rates, capturing both within and among-site variation in wood decomposition rates.

Our two locations have a mean annual temperature difference of ~4°C (13° vs. 17°C MAT) which, based on a U.S.-scale assessment of the mean probability a snag

will fall after 5 yr (Oberle et al. 2018b), suggests that snags should fall at a mean rate ~ 1.24 times faster at our southern versus northern location. We observed about three times more posts fall at our southern vs. northern location in 5 yr, and the discrepancy from the mean continental rate may be within the error of that estimate, and is likely also influenced by our design which controlled for other factors that influence fall rate, such as bole diameter and wood durability (Hu et al. 2018, Oberle et al. 2018b). Nevertheless, snag fall rates were greater with higher MAT, as expected based on the Oberle et al. (2018b) observations with real snags across the continental United States. Our study builds on such broader-scale assessments by querying how turnover in wood decomposer communities may help to explain broader-scale relationships between climate and decomposition causatively. Certainly, it is appreciated that the functional traits, interactions and abundances of the dominant saprotrophs decomposing wood vary predictably with spatial climate gradients and can strongly affect wood decomposition rates (Dickie et al. 2012, King et al. 2013, Maynard et al. 2018, Lustenhouwer et al. 2020). Our data add to this literature by suggesting that higher fall rates of snags at our southern location may in part be explained by the transition from primarily fungal-mediated to increasingly termite-mediated decomposition as MAT increases. The extent to which such regional patterns in saprotroph communities and decomposition rates will track changing climate is strongly uncertain. Resolving these questions will be critical for projecting with increased certainty how climate change will influence snag abundances in temperate forests, and consequently forest carbon stocks and biodiversity.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3484/supinfo>

OPEN RESEARCH

Data, metadata, and code (Bradford 2021) are archived in the Dryad data repository: <https://doi.org/10.5061/dryad.rxdbrv7m>