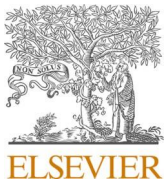
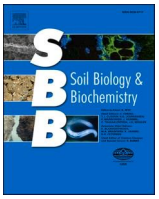
Soil Biology and Biochemistry 204 (2025) 109754



Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio



Wood decomposition in poorly-drained forested wetland soils: How important are termites?

Mary Beth Adams [a,*], Chris Miller [b], Gregory W. McCarty [c], Megan Lang [d], Steve Strano [e], Deborah S. Page-Dumroese [f], Al Rizzo [g], Bradford M. Kard [h], Martin F. Jurgensen [b]

[a] USDA Forest Service, Northern Research Station, 180 Canfield Street, Morgantown, WV, 26505, USA
[b] College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, 49931, USA
[c] USDA-Agricultural Research Service Hydrology and Remote Sensing Laboratory, BARC-West, Beltsville, MD, 20705-2350, USA
[d] US Fish and Wildlife Service, Baileys, Crossroads, VA, 22041, USA
[e] USDA Natural Resources Conservation Service, Annapolis, MD, 21409, USA
[f] USDA Forest Service, Rocky Mountain Research Station, Moscow, ID, 83843, USA
[g] US Fish and Wildlife Service, Milton, DE, 19968, USA
[h] Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, OK, 74078-3033, USA

ARTICLE INFO

Keywords:
Forested wetlands
Reticulitermes spp
termites
Water table depth
wood decay

ABSTRACT

Termites are important wood decomposers in tropical and sub-tropical forest ecosystems, but less is known about termite activity in temperate forests, especially poorly-drained wetlands. Therefore, we carried out a 5-year study to assess the effects of a seasonally-variable water table on wood decomposition by termites. The study was carried out on three forested wetland sites on the Atlantic Coastal Plain of the US where the water table was: 1) only in the mineral soil, 2) at the soil surface for 3.7 months/year, and 3) at the soil surface for 5.7 months/year, and on an adjacent drier upland forest. We used wood stakes of aspen (*Populus tremuloides* Michx.), red maple (*Acer rubrum* L.) and loblolly pine (*Pinus taeda* L.), which were placed on the surface litter, at the litter-mineral soil interface, and in mineral soil, and sampled annually. Stake mass loss was used to measure the effect of termites on wood decomposition.

Wood decomposition and termite activity on the three wetland sites was controlled by soil depth to the water table, being greatest where the water table was rarely above the mineral soil surface, and least where the litter layer was inundated the longest. At the end of 5 years the effect of termites on wood stake mass loss was highest at the litter surface (51%), and lowest in the mineral soil (30%) where microbial decay dominated. However, small differences in surface elevation can affect termite activity and wood mass loss in the mineral soil. Termites likely fed on stakes during drier summer months, often only on the stake surface, and favored aspen, less for red maple, and least for pine. Termites dominated decomposition in the upland. Stake mass loss was lowest on the litter surface but exceeded 85% at all three soil locations. In contrast to the wetlands, termites showed little difference in wood stake feeding preference. This effect of soil water content on termite feeding preference has not been observed elsewhere.

Our study suggests that altered precipitation amounts projected in future climate scenarios could have a greater effect than temperature on wood decomposition by termites in poorly-drained wetland ecosystems. Much more information is needed on termite activities in mineral soil across different climate regimes, and what factors control termite preference for wood species in soils with different water regimes.

1. Introduction

Forested wetlands are important landscape features in many areas of the world, where they provide critical ecosystem services (*e.g.,* nutrient and sediment retention, wildlife habitat, streamflow generation and regulation), and help mitigate climate change by carbon (C) storage (Mitsch and Gosselink, 2000; Trettin et al., 2020; Poulter et al., 2021). However, C stocks in wetland soils are difficult to document accurately

* Corresponding author.
E-mail address: mary.b.adams@usda.gov (M.B. Adams).

https://doi.org/10.1016/j.soilbio.2025.109754
Received 12 August 2024; Received in revised form 13 December 2024; Accepted 16 February 2025
Available online 18 February 2025
0038-0717/Published by Elsevier Ltd.

(Trettin et al., 1996; Nahlik and Fennessey, 2016), and relative to upland ecosystems, organic matter (OM) decomposition in forested wetlands is not well understood, especially woody material (Wissinger et al., 2021).

The majority of decomposition studies in forested wetlands have used tree leaves or needles as the OM substrate (*e.g.,* Ozalp et al., 2007; Gingerich and Anderson, 2011; Liu et al., 2017; Mueller et al., 2018; Xie et al., 2019), with much less attention given to wood (Gentry and Whitford, 1982; Braccia and Batzer, 2008; Ulyshen, 2014). Wood is a common component of wetland soil (surface residue, stumps, coarse roots), is important for C sequestration (Heath et al., 2002), and its slow decomposition integrates soil abiotic and biotic conditions over prolonged periods (Harmon et al., 1986; Chen et al., 2005).

Fungi are the main biological drivers of wood decomposition in both upland and wetland soils (*e.g.,* Rayner and Boddy, 1988; van der Wal et al., 2015), but recent studies have shown that termites have an important role in many tropical and subtropical forests (Cheeseman et al., 2018); Seibold et al., 2021; Zanne et al., 2022). However, periodic flooding and poor soil drainage in many forested wetlands limit OM decomposition, as lower soil oxygen content reduces the activity of soil microorganisms and invertebrates, including termites (Forschler and Henderson, 1995; Ozalp et al., 2007; Boon et al., 2014; Ulyshen, 2014, 2016; Nahlik and Fennessey, 2016; Wissinger et al., 2021).

Subterranean termites in North America are found in a wide variety of soils and forest types, but their distribution is generally controlled by temperature (*e.g.,* Wang and Powell, 2001; King et al., 2013; Bradford et al., 2014). Termites impact wood decomposition by direct consumption, but also indirectly when they change the microbial community by bringing in fungal spores and hyphae during colonization (Ulyshen et al., 2016). Wood species-specific wood-decay fungi have been shown to increase or to reduce wood colonization by termites (Getty and Haverty, 1998; Cornelius et al., 2004; Kamaluddin et al., 2016). Numerous laboratory studies have examined wood decomposition by subterranean termites, but high spatial heterogeneity of termite populations and variable distribution of wood on and in the soil make it difficult to extrapolate laboratory results to stand or forest levels (Maynard et al., 2015; Jurgensen et al., 2019).

In nearly all studies on wood decomposition by termites in forest ecosystems, wood was placed on the soil surface as a food source, usually a single wood genus or species (mostly *Pinus*) to reduce the variability of wood properties in the decomposition process (Ulyshen, 2014; Seibold et al., 2021; Zanne et al., 2022). Less often several wood species were used to assess the preference of termites for different wood properties (*e.g.,* Roh et al., 2018; Kim et al., 2021; Page-Dumroese et al., 2023). The few studies in forested wetlands have shown that termites are a factor in wood decomposition on the surface of flooded and poorly-drained soils (Forschler and Henderson, 1995; Ulyshen, 2014; Wissinger et al., 2021). However, little information is available about termite activity in the underlying, wet mineral soil, or whether termites on the soil surface are affected by mineral soil properties and high-water table. Recent studies in upland soils have shown that wood decomposition by termites at the soil surface may not reflect termite activity in deeper soil horizons (Wang et al., 2019; Jurgensen et al., 2020).

Therefore, we carried out a study to assess the effects of soil water conditions, as controlled by seasonally-variable water table fluctuations, on wood decomposition by termites at different locations in the soil profile: on the surface of the litter layer, at the litter layer-mineral soil interface, and in the mineral soil (hereafter referred as "soil locations"). This entailed establishing study plots in three wetland sites, which varied from where the water table was at the litter layer surface for many months of the year, to where the water table was only in the mineral soil. An adjacent upland forest site, where the water table would rarely be a factor in wood decomposition, was also included in the study. We used wood stakes as an index of wood decomposition and to monitor termite activity. Our hypotheses were that wood decomposition and termite activity were: 1) highest in the wetland soil where the water table was only in the mineral soil, and lowest in the soil where the water table was longest at or above the soil surface, 2) highest on the litter layer surface on all wetland sites, and decreased with increasing soil depth, and 3) highest in the upland site and similar at all soil depths.

2. Methods and materials

2.1. Study site description

The study was in the Atlantic Coastal Plain Physiographic Province within the Chesapeake Bay Watershed near Princess Anne (38° 12′ N, 75° 37' W) in Somerset County, Maryland (NRCS, 2015). There are an estimated 13.5 million ha of freshwater wetlands in the Eastern U.S Atlantic coastal plain, about half of which are forested (Dahl and Stedman, 2013). Historically, the area was a deciduous and mixed-forest wetland, and for many years had a network of drainage ditches to facilitate loblolly pine (*Pinus taeda* L.) silviculture. Our study took place within a ~800 ha forested wetland that had been drained decades ago and is being restored to original soil hydrology by removing or plugging drainage ditches and culverts and adding rock weirs to raise the soil water profile (NRCS, 2015).

Based on a map of projected changes in water levels, we selected three wetland sites with differing depths to the water table: 1) water table only in the surface mineral soil (SAT), 2) water table at or above the surface litter layer for several months of the year (INUND), and (3) a natural wetland with a normally fluctuating water table not affected by the restoration activities, where the water table was at the surface many months of the year (NAT). In addition, an adjacent drier, mixed hardwood-pine upland site (UPLND) 1.3 m higher in elevation was also included in the study. Thus we have 4 sites representing treatment levels.

Dominant soils within the three wetland sites were the Pone and Corisca series, both classified as mesic Typic Umbraquults with less than 5% slope (Supplemental Table 1A; Soil Survey Staff, 2009). The upland soil is a Klej series and classified as a mesic, coated Aquic Quartzipsamments (Soil Survey Staff, 2009). The average growing season is from April 10 - October 28 (201 days), with a maximum yearly air temperature of 19.7° C and a low of −2.2°C. Average annual rainfall is 1124 mm.

2.2. Wood stakes

We used stakes of three wood species as our standard substrates, loblolly pine (Pinus taeda L.), trembling aspen (*Populus tremuloides Michx.*), and red maple (Acer rubrum L.), which have different wood properties (*e.g.* density, lignin to cellulose ratio, nutrient content) that favor different microbial and invertebrate communities (Blanchette, 1984; Botch et al., 2010; Ulyshen, 2016). Aspen stakes had the lowest density, red maple the highest, and pine had the widest range of density (Supplemental Table 1B). Wood stakes can be inserted into mineral soil with minimal disturbance, allowing decomposition to be measured at different soil depths (Jurgensen et al., 2006), and have been used in upland (González et al., 2008; Risch et al., 2013; Wang et al., 2019; Kard et al., 2022) and wetland soils (Ulyshen, 2014; Jurgensen et al., 2019, 2020).

Boards of loblolly pine from Mississippi, aspen from the Upper Peninsula of Michigan, and red maple from Maryland were used to make stakes. Two surface (2.5 cm × 2.5 cm x 15 cm) and two field mineral soil (2.5 x 2.5 × 30 cm) stakes were cut from a longer, kiln-dried, knot-free, sapwood board of each species. A center section (10-cm long) was used as a laboratory control (time = 0) to determine stake mass loss during the study. The top of each mineral soil stake was treated with a wood sealer to prevent water moving upwards through the stake. For additional details on wood stake fabrication, see Jurgensen et al. (2006).

2.3. Experimental design

In September 2012 three replicate plots (3 m × 3 m in size) were established in each of the three wetland sites, and in the adjacent upland site (4 sites x 3 replicates = 12 total plots). We used open (not caged or meshed) stakes (Ulyshen, 2016), and 25 stakes of each species were placed horizontally 30 cm apart and alternated by wood species on top of the litter layer (Surface), and another 25 stakes at the litter layer-mineral soil interface (Interface) in each wetland and upland site replicate (Supplemental Fig. 1A). After removing the surface leaf litter, a 2.5 cm square coring tool was used to make holes to a mineral soil depth of 30 cm, 25 stakes/species (Mineral) were installed vertically 50 cm apart, and the litter layer was replaced. Collectively, the stake placement on the litter surface, at litter mineral interface, and the mineral soil will be referred to as "soil locations" to differentiate them from quantitative soil depth measures. A total of 2650 wood stakes were used in the study: 4 sites x 3 replicates x 3 wood species x 3 soil locations x 5 sampling dates x 5 stakes. Red maple Surface and Interface stakes were not placed on one NAT replicate plot (n = 50) due to an error in stake production.

Beginning in September 2013 and annually for the next 4 years, five stakes of each wood species were randomly sampled from each soil location in all site replicates. However, in 2016 (year 4) stakes could not be retrieved from many wetland plots, due to flooding during Hurricane Hermine (Supplemental Fig. 1B). Therefore, the 2016 data were excluded from our wetland site analyses, but were included in the upland analyses. All stakes were weighed in the field on a portable electronic balance to determine field water content at extraction. Stakes were air-dried and shipped to the College of Forest Resources and Environmental Science at Michigan Technological University, Houghton, MI for processing and analysis.

2.4. Laboratory analyses

In the laboratory, all stakes were cleaned of adhering soil, dried at 105 °C for 48 h and weighed. Stakes were then separated into two groups: (1) microbial decayed – stakes with no evidence of termite damage, thus representing bacterial and fungal agents, and (2) termites – stakes with evidence of termite damage, such as visible etching and feeding marks, galleries within the stake, or exit holes (Supplemental Fig. 1C), which could include mass loss from microbial decay that occurred before, during, or after termite feeding. Any soil moved into the stakes by termites was physically removed with small scrapers and the cleaned stake reweighed. The volume of wood removed by termites from each stake was visually estimated and agreed to by three evaluators, who placed each termite-damaged stake into one of four damage classes: <1–5% stake mass loss (only on stake surface), 5–25%, 26–50%, and >50%.

The effect of mineral soil depth on termite activity and microbial decay was evaluated by cutting 2.5 cm blocks from stakes at the 5, 15, and 25 cm soil depth. However, this was not possible for upland mineral soil stakes due to rapid termite deomposition at all three depths. Also, it was difficult to obtain an adequate number of suitable termite-damaged stakes from each wetland mineral soil depth, so we only cut wood blocks from microbial-decayed wetland mineral soil stakes sampled in 2013, 2014, and 2015. Mass loss from termite and microbial-decayed stakes was determined by subtracting the oven-dry weight of individual field stakes from the oven-dry weight of its corresponding laboratory control (t = 0). Average mass loss of stakes extracted yearly at the three soil locations (n = 5) was used as site observations in statistical analyses.

2.5. Soil and water table measurement

Our wood stake decomposition study sites were placed near to a nest of sensors, which was located in one replicate of each wetland and upland site. Soil depth to the water table was measured using Hobo U20 water level recorders (Onset Corp., Bourne, MA), and averaged monthly and yearly through the study (2013–2017). We calculated wetland hydroperiod by summing the number of days during each stake sample year (October 1-September 30) when the water table was at or above the surface litter layer soil, between 0 and 30 cm, between 30 and 60 cm, and below 60 cm depth in the mineral soil.

Soil moisture content at 30 cm depth was monitored using the SMC-M005 soil moisture sensor (Meter Group, Pullman, WA), and logged with a Hobo H21 Microstation (Onset Corp, Bourne, MA. Daily average soil moisture was calculated and averaged monthly, but due to sensor failure large amounts of data are missing from the SAT, INUND, and UPLND sites in the first 2.5 years of the study. However, a more complete record was available for the NAT site, which provided evidence for seasonal patterns.

Soil temperature was monitored every 3 h at the 10 cm mineral soil depth using a Hobo Tidbit temperature sensor and logger (Onset, Corp., Bourne, MA), and averaged monthly from 2013 to 2017. Soil degree days were calculated monthly from the number of days average daily temperature exceeded 10 °C, which is often used in soil OM decomposition studies (Carey et al., 2016).

2.6. Statistical analyses

Statistical analyses were carried out using SAS version 9.4 (SAS Institute, Cary, NC, United States) and assessed at $\alpha \leq 0.05$ significance. PROC GLM analysis of variance (ANOVA) was utilized for this factorial design. Factors in this analysis were wood species (aspen, maple, and pine), extraction year (2013, 2014, 2015, 2016, and 2017, although only the UPLND site included 2016), site (NAT, INUND, SAT, UPLND), soil location (Surface, Interface, Mineral soil). There were three replicates within each wetland site and the upland forest site. The response variable was stake mass loss as a proportion of original mass; each factor and all possible interactions were considered in the model (Supplemental Table 2).

Arcsine square root transformation was used to homogenize the mass loss error term (Steel and Torrie, 1980). While this transformation provided better adherence to the assumptions of the ANOVA than the untransformed data, the Levene's Test still indicated heterogeneity of variance. The Kruskal–Wallis nonparametric procedure was performed, and the results were consistent with those reported in the initial ANOVA analysis, so we report the results from the ANOVA approach. Further analyses were carried out by introducing wood density and ring-count as covariates to the stake mass loss model. Significant correlations between covariates were investigated utilizing SAS PROC CORR. Post-hoc assessments of significant effects and interactions were conducted with SAS PROC MEANS utilizing Tukey's range test. Assessment of wetland and upland replication (plot) effects were carried out for each species. The frequency of stake termite damage among among wood species, sites, and among soil replicates were compared with Fisher's exact test using SAS PROC FREQ. We used SAS PROC TTEST to determine if termite feeding on the stake surface (<5% volume loss) had a measurable effect on mass loss compared to microbial-decayed stakes.

Termites significantly increased stake decomposition at each soil location when ALL stake mass loss was 281 greater than Microbial stake mass loss ($p \leq 0.05$). Since our open stake decomposition method usually resulted in reduced numbers of Microbial stakes as the study progressed, we only determined net termite effect when both Microbial and Termite stakes comprised at least 20% of the total stakes removed from each soil location/sample date, usually n = 3.

To evaluate the effect of depth within the mineral soil on the decay process, we cut 2.5 cm wood blocks from Mineral stakes at the 5, 15, and 25 cm soil depth. However, it was difficult to obtain an adequate number of blocks at the three soil depths from Termite stakes at each wetland site, so we used wood blocks from Microbial stakes sampled in 2013, 2014, and 2015.

3. Results

3.1. Soil water content and temperature

Large amount of soil water data was missing from the wetland sites early in the study, but when averaged over the last 3-years, there was no significant difference ($p = 0.438$) in water content at the 30 cm mineral soil depth in the wettest winter month (February – 47.5%), and in the driest summer month (August – 33.9%). The upland soil was significantly drier in the winter (25.4%) and in the summer (19.4%) than the wetlands ($p = <.0001$). Soil temperatures in the wetlands at the 10 cm soil depth were generally lower than in the upland site throughout the year (Supplemental Fig. 2A). There was little difference in soil degree days between the NAT and INUND soils, but the SAT soil was significantly cooler (Supplemental Figure B).

3.2. Water table depth

Soil depth to the water table varied widely among the three wetland sites during each year, ranging from at-or-above the litter surface during the winter/spring months to more than 1 m deep in the mineral soil in the summer (Supplemental Fig. 3). In contrast, the water table in the surface mineral soil in the upland was rarely present. When averaged over 5-years, the water table was longer at-or-above the surface of the NAT soil than in the INUND soil, and almost never at the surface of the SAT soil (Supplemental Table 3A). The number of days the water table was below the mineral soil stake depth of 30 cm was greater on the SAT and INUND sites than on the NAT site (Supplemental Table 3B). Since soil depth to the water table was highly correlated with mean monthly 30 cm soil water content across all sites ($r^2 = .808$ to .950), we used water table depth as a qualitative approximation of water content at different depths in the mineral soil.

3.3. Termite damage

Of the 2120 stakes removed from the wetland and upland sites over the 5-year study, 1270 had evidence of termite damage (60%), and 572 (45%) had volume loss from termite feeding on the stake surface of less than 5% (Supplemental Tables 4 and 5). However, there was no significant difference in stake mass loss between these surface-damaged stakes and stakes with no termite damage (aspen: $p = 0.325$, red maple: $p = 0.388$, pine: $p = 0.496$). Therefore, we assumed that mass loss of stakes with no termite damage and termite stakes with <5% volume loss was due to microbial decay (Microbial stakes), and mass loss in termite stakes with volume loss >5% was a from a combination of termite feeding and microbial decay (Termite stakes). Microbial and Termite stake mass loss were combined to give an average (ALL stakes) mass loss of each wood species at each soil location. The "net effect" of termites on wood decomposition was the difference in mass loss between Termite and Microbial stakes (see Siebold et al., 2021). Net termite effect was determined if both Microbial and Termite stakes comprised at least 20% of the stakes removed from each soil location, usually $n = 3$.

3.4. Wood decomposition

As expected, the explanatory power of extraction date on stake mass loss (time on/in the soil) in the full ANOVA model was large. However, wood species had a greater effect on decomposition than water table depth and location in the soil profile (Table 1), which was likely due to large differences in stake density (Supplemental Table 1B). Therefore, individual wood species ANOVA models were used in our analyses, and the impact of water table depth and soil water content on wood decomposition across wetland and upland sites is separated by species. Wood stake decomposition among site replicates was also highly significant ($p= <.0001$), which is addressed in section 3.7.

Table 1
Main effects of ANOVA model, where wood stake mass loss is the dependent factor, and site, extraction date (time in/on the soil), soil location, and wood species are the independent factors.

Factor	DF	F	p
Extraction Date	4	606.49	<.0001
Wood Species	2	252.57	<.0001
Site (Soil Hydrology)	3	108.4	<.0001
Location in soil	2	26.2	<.0001
Replicate (plots)	13	12.8	<.0001

3.4.1. Wetlands

3.4.1.1. Aspen. While microbial decay dominated aspen decomposition on the litter surface and at the litter-mineral soil interface on the NAT site, termites significantly increased mass loss on the SAT and INUND sites with each sampling (Supplemental Table 6A). The net termite effect on mass loss varied between these two sites, which increased and decreased at both soil locations as the study progressed, but at the end of 5 years there was no significant difference in mass loss among soil locations (Fig. 1A). However, the effect of microbial decay could not be separated from termite activity, since nearly all stakes sampled had termite damage, which shows the problem of using an open-stake method to determine net termite effects in a long-term wood decomposition study.

Termites had no effect on aspen decomposition in the NAT mineral soil, and mass loss slowly increased in the INUND and SAT mineral soil throughout the study (Supplemental Table 6A). By the conclusion of the study, termite activity in the INUND mineral soil increased aspen stake mass loss by 33%, but the effect of termites was significantly higher (46%) in the SAT mineral soil (Fig. 1A). This greater termite activity in the SAT mineral soil will be addressed in section 3.7.

There was no significant difference between aspen stake decomposition on the litter surface and at the litter-mineral interface on the three wetland sites, but mass loss was significantly higher in the SAT mineral soil (Fig. 1A). Termites increased aspen mass loss with each successive sampling at the litter surface and at litter-mineral interface on all three wetland sites, but it was not until 3 and 5 years that ALL stake mass loss was significantly greater than Microbial stake mass loss. A statistically significant effect of termites on stake mass in the mineral soil only occurred on the SAT site after 5 years (Supplemental Table 6A).

3.4.1.2. Red maple. Microbial decay dominated red maple stake decomposition on the NAT site during the study, and mass loss was significantly lower than on the other two wetland sites (Supplemental Table 6B). In contrast, termites slowly increased red maple mass loss on the INUND and SAT litter surface and at the litter-mineral interface with each sampling, but at the end of the study there was no significant difference between the sites at both soil locations (Fig. 1B). Similar to aspen, termites had widely variable effects on red maple decomposition on these two sites, where net termite effect increased on the SAT litter surface and at the litter-mineral interface, as the study progressed, and decreased on the INUND site due to significantly higher mass loss from microbial decay.

Termites had little effect on red maple decomposition in the mineral soil of the three wetland sites during the first 3 years, as only one of 135 stakes sampled had termite damage (Supplemental Table 6B). However, at the end of 5-years termites were active in both the INUND and SAT mineral soil, and similar to aspen, red maple mass loss was significantly higher in the SAT mineral soil (Fig. 1B).

Red maple stake mass loss was highest on the litter layer surface of each wetland site, less at the litter-mineral interface, and least in the mineral soil, which generally reflects termite activity at each soil location (Supplemental Table 6B). Termites steadily increased red maple mass loss over time, but ALL stake mass loss was significantly greater

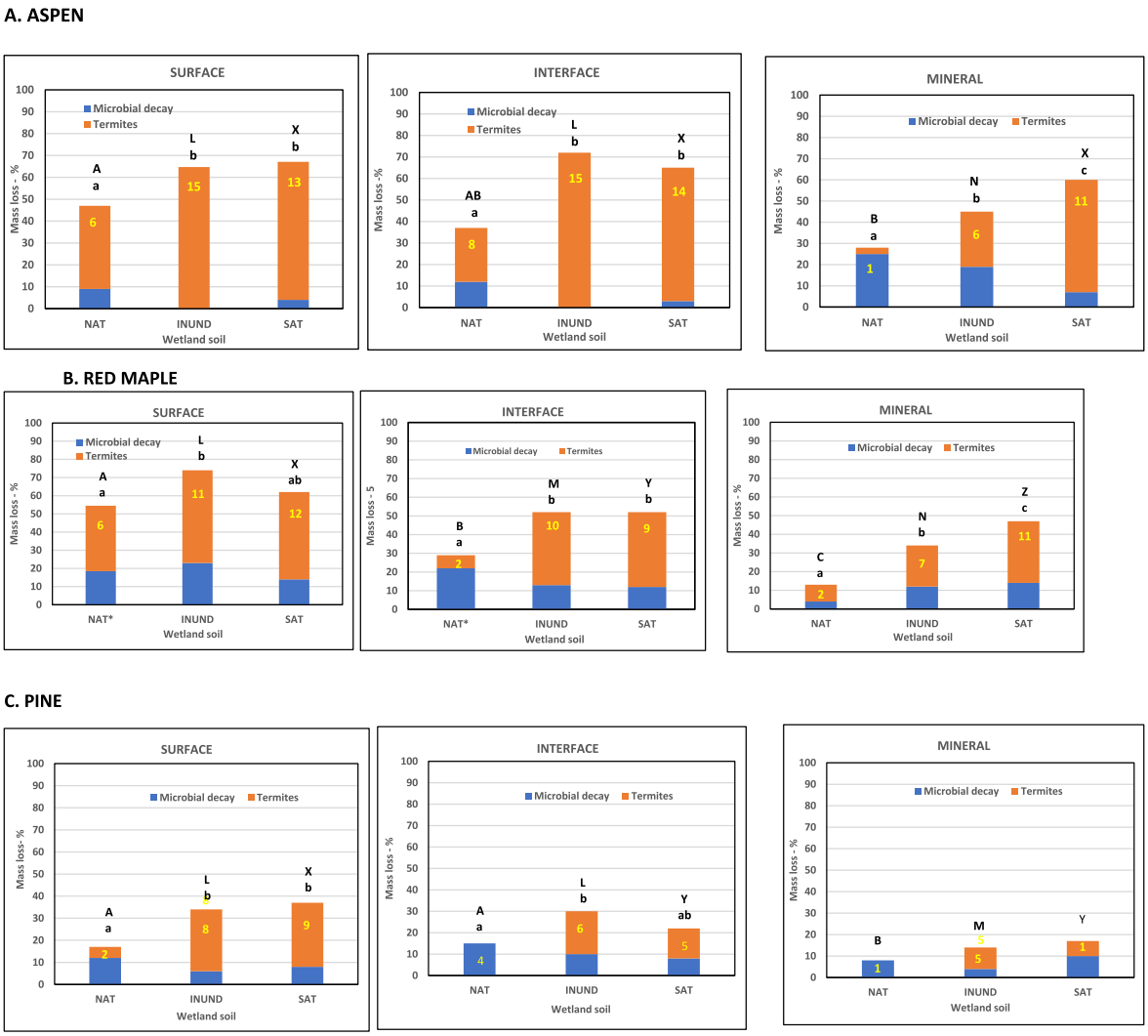


Fig. 1. Mass loss of aspen, red maple, and pine stakes from microbial decay and termites at three soil locations after 5-years on three forest wetland sites on the Atlantic Coastal Plain, USA. [See text for site descriptions; n = 15 stakes for all soil locations, except n = 10 for red maple with *; yellow numbers: number of stakes with termite damage; small letters: significant difference in combined microbial decay and termites stake mass loss among wetland sites at each soil location; Capital letters: significant differences in combined stake mass loss among soil locations at each site, p = <.05.]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

than Microbial stake mass loss only at the three soil locations on the SAT site after 5-years.

3.4.1.3. Pine. Termites had no effect on pine decomposition on the NAT site, where they fed on only 4 of 180 stakes over the 5 years (Supplemental Table 6C). In contrast, pine mass loss was significantly higher on the INUND and SAT litter surface and at the litter-mineral interface, as termite activity slowly increased until over 50% of pine stakes at the 5-year sampling had termite damage. While termites increased ALL stake mass loss as the study progressed, there was no significant difference between ALL stake and Microbial stake mass loss at both soil locations. Termites were rarely found in the mineral soil, and there was little difference in pine decomposition among the three wetlands. At the end of the study mass loss in the mineral soil was less than 17%, which was significantly less than on the surface litter and at the litter-mineral interface (Fig. 1C).

3.4.2. Upland

Wood decomposition on the upland site was dominated by termites, as 87% of all stakes sampled over the 5-years had termite damage. Termites rapidly increased mass loss at all three soil locations (Supplemental Table 7), but their net effect on the litter surface and at the litter-mineral interface varied greatly, ranging from an increase of 31% to a negative 7%. While the effect of termites on wood decomposition in the mineral soil could only be determined for the first 2 or 3-years after stake placement, they increased mass loss from 35% to 43%. In contrast to the wetlands, mass loss of each wood species was lower on the litter surface than in the mineral soil (p = 0.0003 to < .0001).

3.5. Mineral soil depth

In the previous wetland and upland sections, mass loss in the mineral soil was from the entire 30 cm stake. Therefore, to determine the effect of mineral soil depth on termite activity and microbial decay, we proposed to cut 2.5 cm blocks from stakes at the 5, 15, and 25 cm soil depth. However, due to rapid stake decomposition at all soil depths on the upland, this was not possible. It was also difficult to obtain an adequate number of suitable termite-damaged stakes from each wetland site, so we could only measure the effect of mineral soil depth on microbial decay. There was no significant soil depth interaction between wetland sites and sampling date for each wood species (aspen: p = 0.743, maple:

p = 0.961, pine: p = 0.999), so mass loss was averaged by species across sites and sample dates (Fig. 2). Decomposition was highest near the mineral soil surface and decreased with depth for all wood species (Fig. 2), with 45% of stake mass loss from 0 to 10 cm, 32% from 10 to 20 cm, and 23% from 20 to 30 cm.

3.6. Wood species

Stake density differed significantly among the three wood species and varied widely within each species (Supplemental Table 1B). However, individual stake density was not significantly correlated to mass loss across the wetland sites (aspen: p = 0.335; red maple: p = 0.316; pine: p = 0.976) or in the upland (aspen: p = 0.899; red maple: p = 0.381; pine: p = 0.593).

Termites showed definite wood species feeding preferences in the wetland sites. When averaged across the three sites, termites found significantly more aspen, less red maple and fewer pine stakes at each soil location (Fig. 3A). However, by the end of 5 years red maple mass loss was similar to aspen on the surface litter and at the litter-mineral interface but was significantly less in the mineral soil (Fig. 4**A**). In contrast, the termite discovery and decomposition of pine stakes was significantly less at the three soil locations**.** Surprisingly, many stakes showed termite damage only on the stake surface over the 5 years, but there was no difference among wood species, which averaged 55% on the surface litter, 61% at the litter-mineral soil interface, and 72% in the mineral soils (Supplemental Table 4).

On the upland site termites were much less selective in their feeding, as 91% of aspen, 84% of pine, and 82% of red maple stakes had evidence of termite damage (Supplemental Table 7). While the difference among wood species was small, termites found more aspen stakes at the three soil locations (Fig. 3B). By the end of 5 years mass loss of each species was greater than 85%, which was significantly higher (p = <.0001) than on the wetland sites at each soil location (Fig. 4B). Similar to the wetlands, stakes with termite damage only on the surface were also found in the upland, but the number was much less, averaging 19% on the surface litter, 22% at the litter - mineral soil interface, and 9% in the mineral soil. Except for red maple, no surface-damaged termite stakes were found after 3 years (Supplemental Table 4).

3.7. Site replicate variability

Mass loss difference among replicate plots in the overall model was highly significant (p < 0.0001; Table 1), so we evaluated whether this could have affected the comparisons of decomposition among sites. Stake mass loss showed no consistent pattern among mass loss, except on the SAT site, where it was higher in replicate 1 for each species (Table 2A). When the ANOVA was rerun using a dataset without SAT replicate 1, nearly all significant mass loss differences between the SAT and INUND sites were removed (Supplemental Table 8).

Higher mass loss in SAT replicate 1 was from increased termite activity (Table 2B), which would be favored by drier soil conditions in this replicate, as indicated by lower stake water contents throughout the study (results not shown). Lower soil water content in SAT replicate 1 was likely the result of a greater soil depth to the water table, as it was 17 higher in elevation than replicate 2, and 21 cm higher than in replicate 3 (Supplemental Table 1A). In contrast, the difference in surface elevation among the three replicates of the NAT and INUND wetland sites was less than 9 cm.

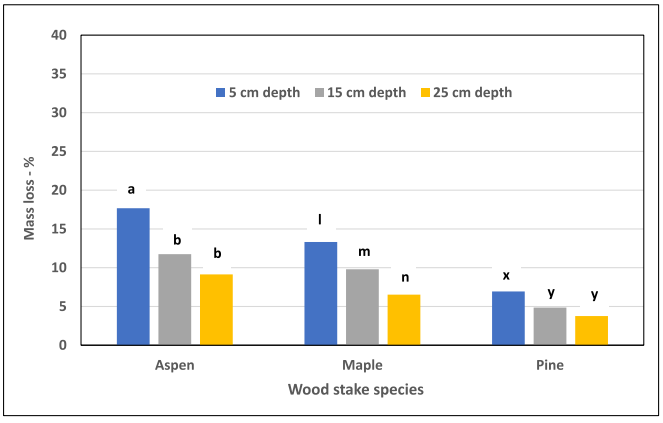


Fig. 2. Effect of depth in the mineral soil on microbial decay of aspen, red maple, and pine stakes in forest wetlands on the Atlantic **Coastal Plain, USA.** [Mass loss is an average of three sites across the 2013, 2014, and 2015 sample dates. Small letters: significant difference among mineral soil depths within each species, p = <.05.]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

Recent wood decomposition studies have sought to separate the effect of termites and other insects from microbial decay in the wood decomposition process by comparing the mass loss of wood open to insect colonization to that of caged or mesh-covered wood to exclude insects (*e.g.* Seibold et al., 2021; Zanne et al., 2022). In contrast, our primary study objective was not to separate microbial decay mass loss from termite activity, but to determine the effects of termites on wood decomposition in soils with different hydrology and water contents. We used open stakes, which eliminated possible microclimate differences with caged stakes on the litter surface (Stoklosa et al., 2016) and avoided the problem of inserting mesh-covered stakes into mineral soil with minimal disturbance. However, as pointed out by Ulyshen (2016) and shown in our study, using open stakes reduces the number of microbial-decayed stakes, but we were able to determine the net effect of termites on wood decomposition at nearly all soil locations on wetland sites, and up to three years on the upland.

Instead of wood with bark attached, we used kiln-dried stakes, which could change wood properties that affect termite behavior and wood decomposition (Ulyshen and Wagner, 2013). However, in a meta-analysis by Njoroge et al. (2024), the overall impact of invertebrates on decomposition did not differ between natural and processed wood. The size of wood used also affects decomposition, as termite activity was higher in large wood pieces with bark (logs) that stay wet longer, and higher in small wood samples without bark (stakes) that lose water more rapidly. However, we found no study comparing bark-free wood with coarse root in mineral soil.

4.1. Decomposition in wetlands

The results of our study showed that water table fluctuations and frequency of flooding strongly affected wood decomposition and termite activity at different soil locations on each wetland. As we hypothesized, mass loss from termites was highest where the water table was rarely at the soil surface (SAT), and lowest where the water table was at or above the litter layer for almost 6 months (NAT). Termites would be favored by greater aeration at or near the soil surface, while microbial decay dominated decomposition in the mineral soil (Ulyshen 2016). However, the small difference in mass loss between SAT and INUND surface litter and litter-mineral interface stakes was a surprise. In contrast to the SAT site, the water table was at or near the INUND soil surface for many months during winter and spring, which suggests that termite decomposition of litter layer stakes on both these sites likely occurred during the summer, when the water table was deeper in the soil.

High water content in the mineral soil restricted termite movement, as they were not found in the NAT soil. Termites slowly increased wood decomposition in the INUND and SAT soils throughout the study, but after 5 years both termite activity and stake mass loss were much greater in the SAT soil than in the INUND soil, even though there was relatively

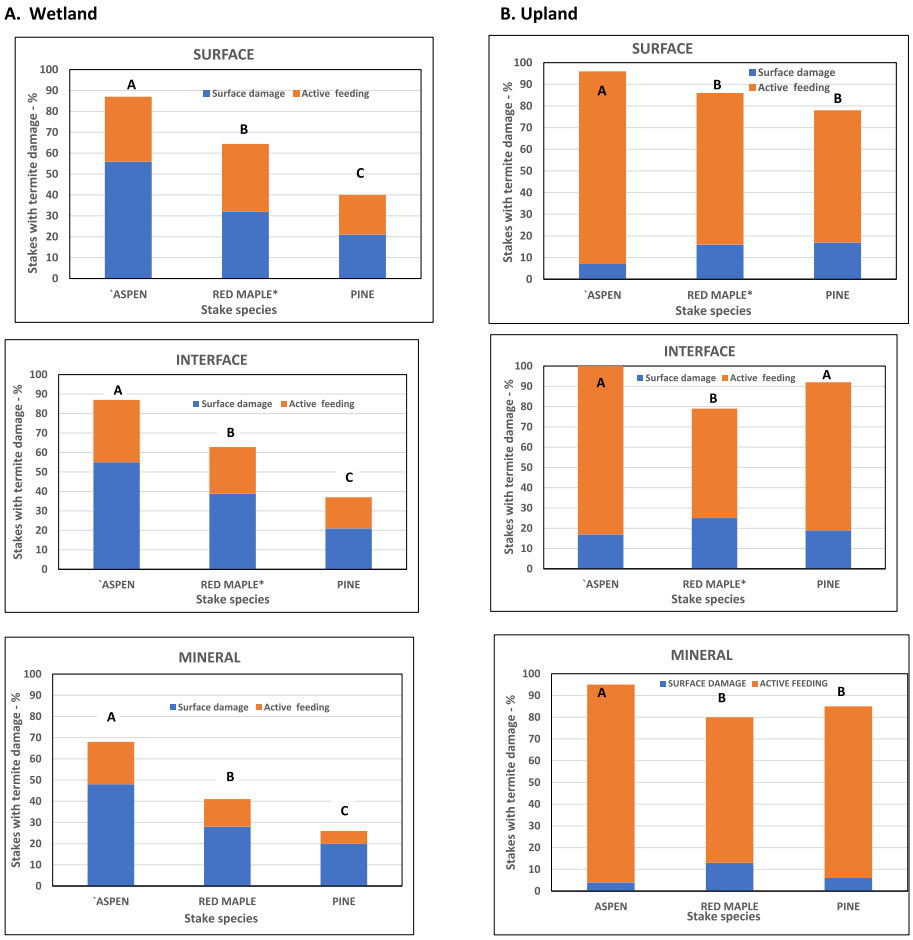


Fig. 3. Numbers of aspen, red maple, and pine stakes with active termite-feeding (greater than 5% stake volume loss) and with termite damage only (less than 5% volume loss on stake surface) over 5 years at three soil locations on three forest wetland sites and an upland site on the Atlantic Coastal Plain, USA. [Wetlands averaged across 3 sites, Upland: n = 75 stakes/species at each soil location; Wetland: n = 180 stakes/species at each soil location, except n = 160 stakes at red maple locations with *. Stake surface damage from termites: less than 5% stake volume loss, active termite-feeding: greater than 5% stake volume loss. Large letters: significant differences in number of all termite-damaged stakes among species; p = <.05.]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

little time difference when the water table was below the mineral soil stakes on both sites (>30 cm).

The number of wetland stakes with termite damage increased with time, especially between the 3-year (2015) and the 5-year (2017) sampling, which seems to show termites were more active during the last two years of the study. Unfortunately, due to a hurricane in September 2016 we could not collect 4-year stakes, but water table measurements over the study indicate that both the 2016 and 2017 sample years were not favorable for termites. Therefore, the increased termite damage found in the September 2017 stakes likely occurred during the very dry three months after the 3 year sampling (September 2015), and show how yearly differences in water table fluctuations can affect wood decomposition by termites.

The few termite studies we found on wood decomposition in temperate forest wetlands were conducted on floodplain soils in the southern U.S (*e.g.*, Gentry and Whitford, 1982; Braccia and Batzer, 2008; Ulyshen, 2014), that are usually flooded for several months in late winter-early spring (Burke and Chambers, 2003). Such seasonal inundation reduced decomposition of pine logs placed on the soil surface of Mississippi hardwood/pine forests for 31 months (Ulyshen, 2014), but the decreased log mass loss was attributed to lower microbial decay, not termites. However, termites were 5–6 times more active on wood stakes inserted into the unflooded mineral soil.

As noted above, compared to the INUND mineral soil, the high termite activity in the SAT soil was not reflected by the length of time the water table was below the mineral soil stakes (>30 cm). However, our results showed that termites only increased SAT mineral soil stake mass loss in one replicate with a 20 cm higher surface elevation, which is not reflected in the SAT site water table depths. Mounding a fine-textured, poorly-drained South Carolina soil increased soil surface elevation by 16 cm, which allowed termite access to aspen stakes in the mineral soil and increased mass loss by 30% (Jurgensen et al., 2019). Therefore, slight elevation differences among soil replicates need to be recognized when conducting decomposition studies in wetland soils when termites are present.

The effects of small-scale differences in soil water content on wood decomposition by both termites and microorganisms have also been reported by (Bradford et al., 2014)and Page-Dumroese et al. (2019). However, the location of termites on replicated plots can affect wood decomposition, as stakes placed closer to termite nests in one of three replicates significantly increased aspen and pine mass loss after a wildfire in an upland California forest (Jurgensen et al., 2020).

4.2. *Decomposition in the upland*

In contrast to the wetlands, termites dominated wood stake decomposition at all three soil locations in the upland, but contrary to our hypothesis, stake mass loss and termite activity were less on the litter surface than in the mineral soil, which was likely due to drier conditions at the litter surface relative to the mineral soil. Similar results were

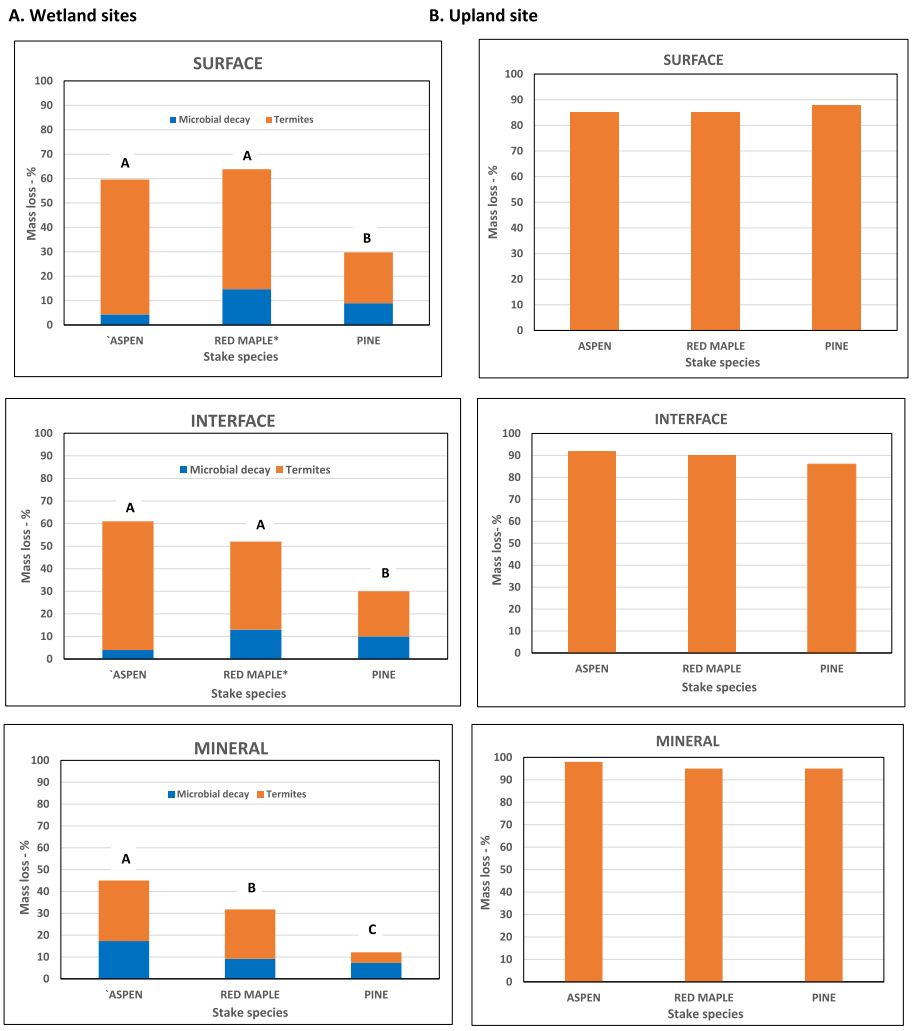


Fig. 4. Mass loss of aspen, red maple, and pine stakes at three soil locations after 5 years on three forest wetlands and an adjacent forest upland on the Atlantic Coastal Plain, USA. [See text site descriptions. Upland site: n = 15 stakes/species, wetland sites: n = 60 stakes/species except as noted with *. Capital letters: significant differences in average Termite and Microbial-decayed (ALL) stake mass loss among species, p = <.05.]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

found by Jurgensen et al. (2020) in a California Mediterranean-type soil, where termites fed on only 2% of aspen stakes on the dry soil surface, compared to 53% in the wetter mineral soil (Jurgensen et al., 2020). Low water content at the surface of upland forest soils without termites also reduced microbial decay of aspen and pine stakes after wildfire and timber harvesting (Page-Dumroese et al., 2019; Wang et al., 2019). However, temperature controlled microbial decomposition of aspen and pine stakes on an uncut, upland Finnish boreal forest, where temperature and mass loss was highest on the litter surface and decreased in the mineral soil (Finér et al., 2016).

4.3. Termite behavior

As discussed by Zanne et al. (2022), wood decomposition by termites is a two-step process: 1) discovery – termites locate wood, and 2) actively feed on the wood. On our drier upland site termites quickly found stakes and continued to feed, until at the end of the study over 85% of stake mass was removed. In contrast, when termites found stakes in the wetlands, they often fed only on the stake surface and did not continue to feed into the stake (Cheeseman et al., 2018; Wijas et al., 2024). Wijas et al. (2024) also reported that termites discovered more pine blocks on the soil surface of dry Australian Savannah sites than on wet rainforest edges. A likely explanation is that termites found stakes during the drier summer months but could not actively feed before the water table rose later in the year. However, the question then becomes why termites did not feed on surface-damaged stakes in subsequent summers?

One possibility is that the microbial community in the wetland soils negatively affected termites activity, as studies have shown that different wood-decay fungi can decrease termite feeding (Becker, 1976; Kamaluddin et al., 2016). Another is that fungal decay reduced stake mass to such a level that it was no longer a suitable food source when termites returned the following summer. Studies have shown that wood decomposition by termites increased after fungi reduced wood mass by 10%–30%, depending on wood, fungi, and termite species (Amburgey and Smythe, 1977; Jones, 1993). However, Becker (1976) and Lenz et al. (1991) reported that when pine mass loss from fungal decay was greater than 5%–20%, the decomposition by *R. flavipes* was decreased. The effect of fungal communities on wood decomposition in wetlands is an important area for further research, as we could not find any information on wood-decay fungi and termite activity in poorly-drained soils.

We did not identify the termites in our study, as only one species (*Reticulitermes flavipes)* was reported to be in Maryland (Maryland Dept of Agriculture, 2024). However,it is possible that different termite species were active on the wetland and upland sites, as *R. mallettei* has been collected from Delaware to Georgia (Johnson and Forschler, 2022), and

Table 2
Mass loss (A) and termite-feeding patterns (B) in aspen, red maple, and pine stakes averaged over 5-years in the three replicates on the Restored to Saturation (SAT) wetland site. [Small letters: significant difference in mass loss among replicates within soil locations for each species, p = <.05. + Stakes on the litter surface and at the litter-mineral soil interface combined.].

A. Stake mass loss

SOIL LOCATION	Wood stake mass loss		
	Aspen %	Red maple %	Pine %
SURFACE			
Replicate 1	57.3[a]	43.1	23.4[x]
Replicate 2	34.4[b]	33.2	13.5[y]
Replicate 3	38.6[b]	40.6	14.7[y]
INTERFACE			
Replicate 1	47.7[a]	36.6[r]	17.9[x]
Replicate 2	24.6[b]	19.1[s]	5.4[y]
Replicate 3	34.4[b]	19.1[s]	6.6[y]
MINERAL			
Replicate 1	36.1[a]	23.3	12.1
Replicate 2	26.3[ab]	18.9	7.6
Replicate 3	14.2[b]	17.8	4.3

B. Termite-feeding pattern

SOIL LOCATION	ASPEN			RED MAPLE			PINE		
	Termite-damaged Stakes			Termite-damaged Stakes			Termite-damaged stakes		
	Surface only	All stake	Mass loss	Surface only	All stake	Mass loss	Surface only	All stake	Mass loss
	n	n	%	n	n	%	n	n	%
SURFACE[+]									
Replicate 1	9	26	53.0[a]	15	14	41.5[a]	7	18	33.3[a]
Replicate 2	19	12	34.8[c]	17	8	33.0[b]	9	6	18.7[b]
Replicate 3	11	21	40.8[b]	15	12	40.4[a]	8	5	28.1[a]
MINERAL SOIL									
Replicate 1	6	13	45.2[x]	6	5	32.5	7	3	20.4
Replicate 2	8	7	34.8[y]	6	2	24.0	4	–	15.0
Replicate 3	7	2	24.5[z]	3	4	28.9	5	–	10.2

R. virginicus and *R. hageni* have been found in Washington D.C. (B. T. Forschler, Personal communication).

4.4. Decomposition differences between the wetland and upland

The effect of termites on wood mass loss on the wetland and upland sites varied widely, ranging from 0% to 47% across soil locations, wood species, and time since stake placement. This was especially pronounced on the upland, where high microbial-decayed stake mass loss on litter surface and at the litter-mineral interface occasionally resulted in a negative termite effect. Wood decomposition in the wetlands was controlled by soil aeration, as stake mass loss and termite activity were generally highest on the litter surface, slightly less at the litter-mineral soil interface, and much lower in the mineral soil. In contrast to the wetlands, decomposition on the upland site was dominated by termites, mass loss was higher at all soil locations, and lower on the litter surface than in the mineral soil. We could not find any study in the literature that compared termite activity on wood decomposition at different depths in wet and dry soils.

In the wetlands termites showed a definite feeding preference for aspen over red maple and pine. Since all stakes were close in each replicate plot, it is likely that foraging termites found stakes of each species (Su et al., 1984) but preferred to feed on lower density aspen wood (Behr et al., 1972; Bultman and Southwell, 1976; Ohkuma, 2003; Judd and Corbin, 2009; Shanbhag et al., 2013). Aspen was also preferred over pine by termites in a poorly-drained South Carolina forest soil (Jurgensen et al., 2019). Termite activity was greater on red maple stakes than on pine stakes, even though red maple has a higher wood density. However, pine could be a poorer choice for termites due to its higher lignin to cellulose ratio (Waller and LaFage, 1987; Oi et al., 1996). Ulyshen and Wagner (2013) suggested that wood density variability within species could affect decomposition by termites. However, the wide range of wood densities in our aspen, red maple, and pine stakes had no significant impact on wetland mass loss results.

In contrast, we found relatively little difference in termite decomposition among the three wood species on the upland site. Many field and laboratory studies have shown that pine is rapidly consumed by termites (*e.g.*, Arango et al., 2006; Lee and Forschler, 2016), where it is often used as a standard food source (*e.g.*, Griffiths et al., 2019; Seibold et al., 2021; Zanne et al., 2022; Wijas et al., 2024). The greater incidence of termite feeding on pine stakes in the upland may have been a function of a higher population, which could feed on more food sources even if some were less desirable. Kim et al. (2021) reported that higher temperature increased the preference of termites for oak over pine in South Korean upland forests. However, higher temperatures in our upland soil had little effect on termite preference for pine.

Wood decay fungi more favorable to termite colonization of the pine stakes may have been present in the upland soil (Ulyshen, 2016), or pine stakes in the wetland soils may have been decayed by fungi less favorable to termites (Becker, 1975; Kamaluddin et al., 2016; Ulyshen et al., 2016). The effects of soil water content on wood decomposition by termites in wetland and upland soils need further investigation.

The main objective of our study was to determine how wood decomposition by termites in the mineral soil is affected by fluctuations in the water table. Similar to our results, many other studies reported that the number of wood samples found by termites increased with time, as did mass loss in each sample (Seibold et al., 2021; Zanne et al., 2022). However, average ALL stake mass loss from increased termite activity at each soil location was not significantly higher than Microbial stake mass loss until after 3 or 5 years on our wetland sites, and only 2 or 3 years in the upland soil locations.

4.5. Climate change implications

Using results from six continents, Zanne et al. (2022) showed that termite decomposition of pine blocks on the soil surface was sensitive to temperature and concluded that higher temperatures in future climate scenarios would increase the role of termites in wood decay. Mean annual precipitation was not a significant predictor of termite activity, but they projected that increased rainfall in dry ecosystems would increase wood decomposition by termites. Cheeseman et al. (2018) also reported that termite activity was water-dependent in an Australian savannah and in a seasonally dry tropical forest. In contrast, Seibold et al. (2021) suggested that wood-decaying insects could be negatively affected by low soil aeration in some ecosystems when precipitation is high. However, the effect of both temperature and precipitation on termite activities in the mineral soil was not addressed in these studies.

Based on our results and predictions that the frequency and amount of precipitation will become more variable and extreme in the future (*e.g.,* Maity and Maity, 2022), we propose that precipitation could have a greater effect than temperature on wood decomposition by termites in wetland ecosystems. Our study showed that increased soil water content from decreased depth to a water table can have a large impact on termite activities, and higher rainfall, increased frequency of inundation, and hydrologic restoration of previously drained wetlands could reduce termite populations and their effect on wood decomposition (Forschler and Henderson, 1995; Ulyshen, 2014). Conversely, decreased rainfall, increased evaporation from higher temperatures, and water management activities in wetland soils (mounding, drainage) could lower water content and increase termite activity.

At present, little is known about wood decomposition by termites below the soil surface across different climate regimes and soil drainage classes. This information is needed, as current carbon models don't adequately address termite effects on wood decomposition. Also, the interaction of wood-decay fungi on termite activity in wet soils may have important impacts on wood decomposition and C cycling and warrants further study. Given the importance of wetlands for providing a plethora of ecosystem services, it is imperative to better understand termite behavior and carbon cycling in both wetland and upland soils.

5. Conclusions

Relatively small changes in soil moisture regimes can alter termite activity and decomposition in temperate forest wetlands. Wood decomposition by termites in the wetlands was controlled by seasonal fluctuations in soil depth to the water table and time of inundation. Stake mass loss was highest on the litter surface and decreased with increasing soil depth, and small differences in wetland surface elevation can greatly affect termite activity. In contrast, termites dominated stake decomposition in the upland and was lowest on the drier litter surface. Termite feeding behavior and wood stake species preference differed between the wetlands and upland. Finally, our study suggests that increased precipitation amounts as projected in future climate scenarios could have a greater effect than temperature on wood decomposition by termites in wet ecosystems. Much more information is needed on termite activities and wood decomposition in the mineral soil in different climate regimes and across soil drainage classes.

CRediT authorship contribution statement

Mary Beth Adams: Writing – review & editing, Writing – original draft, Resources, Project administration, Investigation, Formal analysis, Conceptualization. **Chris Miller:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Gregory W. McCarty:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Megan Lang:** Writing – review & editing, Resources, Conceptualization. **Steve Strano:** Writing – review & editing, Resources, Investigation, Data curation. **Deborah S. Page-Dumroese:** Writing – review & editing, Writing – original draft, Resources, Methodology, Conceptualization. **Al Rizzo:** Writing – review & editing, Resources, Investigation. **Bradford M. Kard:** Writing – review & editing. **Martin F. Jurgensen:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We greatly acknowledge the careful work of the NRCS, ARS, and the US Fish and Wildlife Service and collaborators in creating the opportunity for this study, and the landowners who permitted us to use this site. This work was funded in part by the NRCS Conservation Effects Assessment Project (CEAP) and the USDA Long Term Agroecosystem Research (LTAR) Network. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA, US Fish and Wildlife Service, or US government determination or policy.

We were fortunate to have incredible field crews to help with this very labor-intensive study, not always under the best conditions: Brian Jennings, Vance Monroe, Shelley Devereau, Alex White, Laura Jurgensen, Brian Simpson, John Juracko, and JoAnne Tirocke. Special thanks to Brian Forschler for many helpful termite discussions, Carl Trettin for reviewing the paper, and Kas Dumroese for help on graphics. The efforts of the 2 anonymous reviewers and Elsevier Editors are also very appreciated.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2025.109754.

References

Amburgey, T.L., Smythe, R.V., 1977. Factors influencing termite feeding on brown-rotted wood. Sociobiology 3, 3–12.

Arango, R.A., Green III, F., Hintz, K., Lebow, P.K., Miller, R.B., 2006. Natural durability of tropical and native woods against termite damage by *Reticulitermes flavipes* (Kollar). International Biodeterioration & Biodegradation 57 (3), 146–150.

Becker, G., 1975. Laboratory tests on the natural resistance of wood species against different termite species. In: IUFRO Division, vol. 5. Centre technique forestier tropical, pp. 95–108.

Becker, G., 1976. Termites and fungi. Mat. u. Org., Beih. 3, 465–478.

Behr, E.A., Behr, C.T., Wilson, L.F., 1972. Influence of Wood Hardness on Feeding by the Eastern Subterranean Termite, *Reticulitermes flavipes* (Isoptera: Rhinotermitadae), vol. 65. Annals Entomological Society America, pp. 458–460.

Blanchette, R.A., 1984. Screening wood decayed by white rot fungi for preferential lignin degradation. Applied and Environmental Microbiology 48 (3), 647–653.

Boon, P.I., Pollard, P.C., Ryder, D., 2014. Wetland microbial ecology and biogeochemistry. In: Batzer, D.P., Sharitz, R.R. (Eds.), Ecology of Freshwater and Estuarine Wetlands. University of California Press, Berkeley, CA, pp. 87–131.

Botch, P.S., Brennan, C.L., Judd, T.M., 2010. Seasonal effects of calcium and phosphates on the feeding preference of the termite *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Sociobiology 55 (2), 489–498.

Braccia, A., Batzer, D.P., 2008. Breakdown and invertebrate colonization of dead wood in wetland, upland, and river habitats. Canadian Journal of Forest Research 38 (10), 2697–2704.

Bradford, M.A., Warren, Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E., Wieder, R.W., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. Nature Climate Change 4, 625–630.

Bradford, M.A., Warren II, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E., Wieder, R.W., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. Nature Climate Change 4, 625–630. https://doi.org/10.1038/nclimate2251.

Bultman, J.D., Southwell, C.R., 1976. Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica 1, 71–95.

Burke, M.K., Chambers, J.L., 2003. Root dynamics in bottomland hardwood forests of the Southeastern United States Coastal Plain. Plant and Soil 250, 141–153.

Carey, J.C., et al., 2016. Temperature response of soil respiration largely unaltered with experimental warming. Proceedings of the National Academy of Sciences 113 (48), 13797–13802. https://doi.org/10.1073/pnas.160536113.
Chen, X., Wei, X., Scherer, R., 2005. Influence of wildfire and harvest on biomass, carbon pool, and decomposition of large woody debris in forested streams of southern interior British Columbia. Forest Ecology and Management 208, 101–114.
Cheeseman, A.W., Cernusak, L.A., Zanne, A.E., 2018. Relative roles of termites and saprotrophic microbes as drivers of wood decay: a wood block test. Austral Ecology 43 (3), 257–267.
Cornelius, M.L., Bland, J.M., Daigle, D.J., Williams, K.S., Lovisa, M.P., Connick Jr, W.J., Lax, A.R., 2004. Effect of a lignin-degrading fungus on feeding preferences of Formosan subterranean termite (Isoptera: Rhinotermitidae) for different commercial lumber. Journal of Economic Entomology 97 (3), 1025–1035.
Dahl, T.E., Stedman, S.-M., 2013. Status and trends of wetlands in the coastal watersheds of the conterminous United States 2004 to 2009. US Department of the Interior Fish and Wildlife Service and the National Oceanic and Atmospheric Administration's National Marine Fisheries Service. https://api.semanticscholar.org/CorpusID:135347681.
Finér, L., Jurgensen, M., Palviainen, M., Piirainen, S., Page-Dumroese, D., 2016. Does clear-cut harvesting accelerate initial wood decomposition? A five-year study with standard wood material. Forest Ecology and Management 372, 10–18. https://doi.org/10.1016/j.foreco.2016.03.060.
Forschler, B.T., Henderson, G., 1995. Subterranean termite behavioral reaction to water and survival of inundation: implications for field populations. Environmental Entomology 24 (6), 1592–1597.
Gentry, J.B., Whitford, W.G., 1982. The relationship between wood litter infall and relative abundance and feeding activity of subterranean termites *Reticulitermes* spp. in three southeastern coastal plain habitats. Oecologia 54 (1), 63–67. https://doi.org/10.1007/BF00541109.
Getty, G.M., Haverty, M.I., 1998. Consumption of sound and decayed Ponderosa pine and douglas-fir by *Reticulitermes* spp. (Isoptera: Rhinotermitidae) from northern California. Journal of Economic Entomology 91 (3), 650–654.
Gingerich, R.T., Anderson, G.T., 2011. Litter decomposition in created and reference wetlands in West Virginia, USA. Wetlands Ecology and Management 19, 449–458.
González, G., Gould, W.A., Hudak, A.T., Hollingsworth, T.N., 2008. Decay of aspen (*Populus tremuloides* Michx.) wood in moist and dry boreal, temperate, and tropical forest fragments. AMBIO: A Journal of the Human Environment 37 (7), 588–597.
Griffiths, H.M., Ashton, L.A., Evans, T.A., Parr, C.L., Eggleton, P., 2019. Termites can decompose more than half of deadwood in tropical rainforest. Current Biology 29 (4), R118–R119.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133–302.
Heath, L.S., Kimble, J.M., Birdsey, R.A., Lal, R., 2002. The potential of US forest soils to sequester carbon. The Potential of US Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press, pp. 385–394.
Johnson, A., Forschler, B.T., 2022. Biodiversity and distribution of *Reticulitermes* in the southeastern USA. Insects 13, 565. https://doi.org/10.3390/insects13070565.
Jones, S., 1993. Effect of a decay fungus on subterranean termite (Isoptera: Rhinotermitidae) response to bait toxicant treated wood. In: Wildey, K.B., Robinson, Wm H. (Eds.), Proceedings of the First International Conference on Urban Pests.
Judd, T.M., Corbin, C.C., 2009. Effect of cellulose concentration on the feeding preferences of the termite *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Sociobiology 53 (3), 775–784.
Jurgensen, M.F., Miller, C.A., Page-Dumroese, D.S., 2020. Wood decomposition after an aerial application of hydromulch following wildfire in a southern California chaparral shrubland. Frontiers in Forests and Global Change 3 (93), 11.
Jurgensen, M.F., Miller, C.A., Trettin, C.T., Page-Dumroese, D.S., 2019. Bedding of wetland soil: effects of bed height and termite activity on wood decomposition. Soil Science Society of America Journal 83, S218–S227.
Jurgensen, M.F., Reed, D.D., Page-Dumroese, D.S., Laks, P., Collins, A., Mroz, G.D., Degorkski, M., 2006. Wood strength loss as a measure of decomposition in the northern forest mineral soil. European Journal of Soil Science 42, 23–31.
Kamaluddin, N.N., Nakagawa-Izumi, A., Nishizawa, S., Fukunaga, A., Doi, S., Yoshimura, T., Horisawa, S., 2016. Evidence of subterranean termite feeding deterrent produced by brown rot fungus *Fibroporia radiculosa* (Peck) Parmasto 1968 (Polyporales, Fomitopsidaceae). Insects 7 (3), 41.
Kard, B.M., Page-Dumroese, D.S., Cook, S.P., Jurgensen, M.F., Tirocke, J.M., 2022. Termite feeding on aspen and pine stakes on a high elevation sagebrush-steppe rangeland in southeastern Idaho. Southwestern Entomologist 47, 565–573.
Kim, S., Han, S.H., Li, G., et al., 2021. The initial effects of microclimate and invertebrate exclusion on multi-site variation in the mass loss of temperate pine and oak deadwoods. Scientific Reports 11, 14840. https://doi.org/10.1038/s41598-021-94424-w.
King, J.R., Warren, R.J., Bradford, M.A., 2013. Social insects dominate eastern US temperate hardwood forest macroinvertebrate communities in warmer regions. PLoS One 8 (10), e75843, 2013.
Lee, T.-Y., Forschler, B.T., 2016. Wood preference of *Reticulitermes virginicus* (Blattodea: Rhinotermitidae) using no-, two-, and four-choice designs and seven different measures of 811 wood consumption. Journal of Economic Entomology 109 (2), 785–791. https://doi.org/10.1093/jee/tov391.
Lenz, M., Amburgey, T.L., Zi-Rong, D., Mauldin, J.K., Preston, A.F., Rudolph, D., Williams, E.R., 1991. Interlaboratory studies on termite-wood decay fungi associations. II. Response of termites to Gloeophyllum trabeum grown on different species of wood (Isoptera, Mastotermitidae, Termopisidae, Rhinotermitidae, Termitidae). Sociobiology 18, 203–254.
Liu, G., Sun, J., Tian, K., Xiao, D., Yuan, X., 2017. Long-term responses of leaf litter decomposition to temperature, litter quality and litter mixing in plateau wetlands. Freshwater Biology 62 (1), 178–190.
Maity, S.S., Maity, R., 2022. Changing pattern of intensity-duration-frequency relationship of precipitation due to climate change. Water Resource Management 36, 5371–5399. https://doi.org/10.1007/s11269-022-03313y.
Maryland Dept of Agriculture, 2024 accessed April 2024. https://mda.maryland.gov/plants-pests/pages/termites_ants.aspx.
Maynard, D.S., Crowther, T.W., King, J.R., Warren, R.J., Bradford, M.A., 2015. Temperate forest termites: ecology, biogeography, and ecosystem impacts. Ecological Entomology 40 (3), 199–210.
Mitsch, W.J., Gosselink, J.G., 2000. The value of wetlands: importance of scale and landscape setting. Ecological Economics 35 (1), 25–33.
Mueller, P., Schile-Beers, L.M., Mozdzer, T.J., Chmura, G.L., Dinter, T., Kuzyakov, Y., de Groot, A.V., Esselink, P., Smit, C., D'Alpaos, A., Ibáñez, C., Lazarus, M., Neumeier, U., Johnson, B.J., Baldwin, A.H., Yarwood, S.A., Montemayor, D.I., Yang, Z., Wu, J., Jensen, K., Nolte, S., 2018. Global-change effects on early-stage decomposition processes in tidal wetlands–implications from a global survey using standardized litter. Biogeosciences 15, 3189–3202.
Nahlik, A.M., Fennessey, M.S., 2016. Carbon storage in US wetlands. Nature Communications 7, 13835. https://doi.org/10.1038/ncomms13835.
Njoroge, D.M., Dossa, G.G., Schaefer, D., Zuo, J., Ulyshen, M.D., Seibold, S., Zanne, A.E., Oberle, B., Harrison, R.D., Liu, S., Li, X., 2024. The effects of invertebrates on wood decomposition across the world. Biological Reviews, 2024.
NRCS, 2015. Draft Final Report for Remote Sensing of Wetland Restoration Hydrology. USDA NRCS Agreement 67-3B190-019 (not published).
Ohkuma, M., 2003. Termite symbiotic systems: efficient bio-recycling of lignocellulose. Applied Microbiology and Biotechnology 61 (1), 1–9.
Oi, F.M., Su, N.-Y., Koehler, P.G., Slansky, F., 1996. Laboratory evaluation of food placement and food types on the feeding preference of *Reticulitermes virginicus* (Isoptera: Rhinotermitidae). Journal of Economic Entomology 89 (4), 915–921.
Ozalp, M., Conner, W.H., Lockaby, B.G., 2007. Above-ground productivity and litter decomposition in a tidal freshwater forested wetland on Bull Island, SC, USA. Forest Ecology and Management 245 (1–3), 31–43.
Page-Dumroese, D.S., Cook, S.P., Kard, B.M., Jurgensen, M.F., Miller, C.A., Tirocke, J.M., 2023. Prescribed burning alters insects and wood decay in a sagebrush-steppe rangeland in southwestern Idaho, United States. Rangeland Ecology & Management 90, 134–145.
Page-Dumroese, D.S., Jurgensen, M.F., Miller, C.A., Pickens, J.B., Tirocke, J.M., 2019. Wildfire alters belowground and surface wood decomposition on two national forests in Montana, USA. International Journal of Wildland Fire 28, 456–469. https://doi.org/10.1071/WF18218.
Poulter, B., Fluet-Chouinard, E., Hugelius, G., Koven, C., Fatoyinbo, L., Page, S.E., Rosentreter, J.A., Smart, L.S., Taillie, P.J., Thomas, N., Zhang, Z., Wijedasa, L.S., 2021. A review of global wetland carbon stocks and management challenges. In: Krauss, K.W., Zhu, Z., Stagg, C.L. (Eds.), Wetland Carbon and Environmental Management. American Geophysical Union Monograph Series, pp. 1–20. https://doi.org/10.1002/9781119639305.ch1.
Rayner, A.D.M., Boddy, L., 1988. Fungal communities in the decay of wood. In: Marshall, K.C. (Ed.), Advances in Microbial Ecology, Advances in Microbial Ecology, vol. 10. Springer, Boston, MA. https://doi.org/10.1007/978-1-4684-5409-3_4.
Risch, A., Jurgensen, M.F., Page-Dumroese, D.S., Schutz, M., 2013. Initial turnover rates of two standard wood substrates following land use change in subalpine ecosystems in the Swiss Alps. Canadian Journal of Forest Research 43, 901–910.
Roh, Y., Lee, S., Li, G., Kim, S., Lee, J., Han, S.H., Chang, H., Salim, K.A., Son, Y., 2018. Changes in the contribution of termites to mass loss of dead wood among three tree species during 23 months in a lowland tropical rainforest. Sociobiology 65 (1), 59–66.
Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., et al., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8.
Shanbhag, R.R., Sundararaj, R., Erbilgin, N., 2013. Physical and chemical properties of some imported woods and their degradation by termites. Journal of Insect Science 13 (1), 1–8. https://doi.org/10.1673/0331.013.6301.
Soil Survey Staff, 2009. Keys to soil Taxonomy. USDA-natural Resources 896 Conservation Service, tenth ed. Washington, DC.
Steel, R.G.D., Torrie, J.H., 1980. Principles and Procedures of Statistics, a Biometrical Approach, second ed. McGraw-Hill, New York, p. 633. https://doi.org/10.2307/2287561.
Stoklosa, A.M., Ulyshen, M.D., Fan, Z., Varner, M., Seibold, S., Müller, J., 2016. Effects of mesh bag enclosure and termites on fine woody debris decomposition in a subtropical forest. Basic and Applied Ecology 17 (5), 463–470.
Su, N.-Y., Tamashiro, M., Yates, J.R., Haverty, M.I., 1984. Foraging behavior of the Formosan subterranean termite (Isoptera: Rhinotermitidae). Environmental Entomology 13 (6), 1466–1470.
Trettin, C.C., Davidian, M., Jurgensen, M.F., Lea, R., 1996. Organic matter decomposition following harvesting and site preparation of a forested wetland. Soil Science Society of America Journal 60 (6), 1994–2003. https://doi.org/10.2136/sssaj1996.03615995006000060053x.
Trettin, C.C., Kolka, R.K., Marsh, A.S., Bansal, S., Lilleskov, E.A., Megonigal, P., Stelk, M. J., Lockaby, G., D'Amore, D.V., MacKenzie, R.A., Tangen, B., Chimner, R., Gries, J., 2020. Wetland and hydric soils. In: Pouyat, R.V., Page-Dumroese, D.S., Patel-Weynand, T., Geiser, L.H. (Eds.), Forest and Rangeland Soils of the United States

under Changing Conditions. Springer, Cham, pp. 99–126. https://doi.org/10.1007/978-3-030-45216-2_6.
Ulyshen, M.D., 2014. Interacting effects of insects and flooding on wood decomposition. PLoS One 9, e101867.
Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates. Biological Reviews 91, 70–85.
Ulyshen, M.D., Diehl, S.V., Jeremic, D., 2016. Termites and flooding affect microbial communities in decomposing wood. International Biodeterioration & Biodegradation 115, 83–89.
Ulyshen, M.D., Wagner, T.L., 2013. Quantifying arthropod contributions to wood decay. Methods in Ecology and Evolution 4 (4), 345–352.
van der Wal, A., Ottosson, E., De Boer, W., 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. Ecology 96 (1), 124–133.
Waller, D.A., LaFage, J.P., 1987. Nutritional ecology of termites. In: Slansky, F.J., Rodriguez, J.G. (Eds.), The Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York, pp. 487–532.
Wang, C., Powell, J., 2001. Survey of termites in the Delta experimental forest of Mississippi. Florida Entomologist 84 (2), 222–226.
Wang, W., Page-Dumroese, D., Jurgensen, M., Miller, C., Walitalo, J., Chen, X., Liu, Y., 2019. Restoration thinning impacts surface and belowground wood decomposition. Forest Ecology and Management 449, 117451.
Wijas, B.J., Flores-Moreno, H., Allison, S.D., Rodrigues, H.C., Cheeseman, A.W., et al., 2024. Drivers of wood decay in tropical ecosystems: Termites versus microbes along spatial, temporal and experimental precipitation gradients. Functional Ecology 38, 546–559.
Wissinger, S.A., Klemmer, A.J., Braccia, A., Bush, B.M., Batzer, D.P., 2021. Relationships between macroinvertebrates and detritus in freshwater wetlands. Freshwater Science 40 (4), 681–698.
Xie, Y., Xie, Y., Xiao, H., 2019. Differential responses of litter decomposition to climate between wetland and upland ecosystems in China. Plant and Soil 440 (1/2), 1–9. https://doi.org/10.1007/s11104-019-04022-z.
Zanne, A.E., Flores-Moreno, H., Powell, J.R., Cornwell, W.K., Dalling, J.W., Austin, A.T., Classen, A.T., Eggleton, P., Okada, K.I., Parr, C.L., Adair, E.C., et al., 2022. Termite sensitivity to temperature affects global wood decay rates. Science 377 (6613), 1440–1444. https://doi.org/10.1126/science.abo3856.