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ORIGINAL ARTICLE

Deadwood Supports Carnivores in Leaf Litter Communities in a Bark Beetle-Attacked Deadwood Simulation Experiment

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Abstract

Deadwood can impact forest food webs through the creation of habitat and provision of resources, but impacts may differ based on initial differences in wood characteristics and over time. Bark beetles like the southern pine beetle (*Dendroctonus frontalis* Zimmerman) attack and wound pine trees, inoculating them with Ophiostomataceae (Ascomycota; hereafter "blue stain fungi"). Blue stain fungi may increase termite presence in deadwood, and in the surrounding leaf litter, potentially leading to increased abundances of leaf litter invertebrates over time. The effects of deadwood in general, and simulated bark beetle–generated deadwood (i.e., deadwood inoculated with blue stain fungi) or non–bark beetle–generated deadwood (i.e., deadwood inoculated with just H_2O controls) were tested on leaf litter communities after one and seven years to measure both short– and long–term effects. The presence of deadwood led to distinct leaf litter communities compared to no wood across both collection years. However, there was no difference in community composition under logs between deadwood treatments. However, predatory beetles and non-ant Hymenoptera were indicators of bluestained wood. Taxa abundance differed by wood treatment, but richness and detritivore/predator ratio was greater under deadwood versus no deadwood particularly after seven years. These results contribute to the mounting evidence that deadwood has important impacts on forest biodiversity and that long–term studies are necessary to fully understand deadwood impacts on forest ecosystems.

Keywords Coarse woody debris · Community structure · Detritivores · Predators

Extended author information available on the last page of the article

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Introduction

Increased activity of native and invasive pests in response to climate change and other anthropogenic effects can increase deadwood inputs in forest ecosystems (Gan 2004; Kurz et al. 2008; Lesk et al. 2017). Specifically, some bark beetles (Coleoptera: Curculionidae: Scolytinae) attack trees, weakening or killing them, causing increased deposition of deadwood onto forest floors (Klepzig and Hofstetter 2011). In the southeastern USA, the southern pine beetle (*Dendroctonus frontalis* Zimmermann) is a common and widespread bark beetle species, and its attacks kill between 0.085 and 11.8 million m^3 worth of trees annually, generating a substantial influx of deadwood and leaf litter (Pye et al. 2011). Increased deposition of deadwood in forest ecosystems is likely to alter brown food web (BFW) community structure (Smith et al., 2001; Bardgett and Putten 2014; Orgiazzi et al. 2016; Cameron et al. 2019; Lavelle et al. 2022). Brown food web organisms (e.g., fungi, microbes, and invertebrates) decompose organic matter and recycle carbon and other nutrients back into the soil and water. However, they are significantly understudied relative to green food web organisms, which rely on living (e.g., green) plant material, despite their large ecosystem impacts (Decaëns 2010; Bardgett and Putten 2014). However, studies examining deadwood impacts on decomposer communities are scarce (Seibold et al. 2015; Ulyshen et al. 2017) as are studies examining ecological impacts of bark beetles, particularly in BFWs (Morris et al. 2016; Siegert et al. 2024).

Deadwood and leaf litter constitute ~8% and ~5% of global forest carbon stocks respectively (Pan et al. 2011) and function as sources and sinks of carbon and nutrients, and as habitat and food for BFW organisms (Laiho and Prescott 2004; Sabo et al. 2005). Deadwood serves as a long–term and environmentally regulated habitat (e.g., moisture, temperature, etc.) and its habitat complexity and nutritional resources can impact soil and litter BFWs (Marra and Edmonds 1998; Castro and Wise 2009, 2010; Ulyshen and Hanula 2009b, a; Ulyshen et al. 2017). Forest disturbance agents like insect outbreaks can impact BFWs through changes in the quantity and quality of detrital inputs. Thus, disturbances that increase deadwood are likely to impact BFW diversity and community composition, which has implications for forest ecosystem function (Bardgett and Putten 2014; Ulyshen et al. 2017; Lavelle et al. 2022).

In addition to increased deadwood input, bark beetles vector symbiotic fungi to trees during their attack, including bluestain fungi (Ascomycota: Ophiostomataceae; Six and Wingfield 2011). Bluestain fungi are non–decaying, or non–degrading fungi, that colonize and stain sapwood a dark blue or black color where they consume resins, sugars, and lipids (Wingfield et al. 1993). Bluestain fungi may act as a food source for detritivores, as it is nutritionally enriched relative to deadwood (Filipiak 2018; Clay et al. 2021) and can increase termite presence and feeding in deadwood (Little et al. 2012a, b, 2013; Riggins et al. 2014; Clay et al. 2017, 2021; Siegert et al. 2018). Termites are common BFW invertebrates and ecosystem engineers that can increase the biodiversity and productivity via construction of habitat, nutrient cycling, and increased nitrogen availability through

symbiotic gut microbe activity and fecal deposition (Jouquet et al. 2011; Lavell et al. 2016; Tuma et al. 2019). Therefore, if deadwood produced from bark beetle–attacked trees has increased termite presence mediated by bluestain fungi, this is likely to impact associated BFWs, including in the leaf litter below and adjacent to deadwood (Ulyshen et al. 2017).

Approximately 20—30% of all forest insects are saproxylic, or depend on deadwood as a form of habitat or nutrition, and many invertebrates are transient between deadwood and leaf litter depending on decomposition stage (Sabo et al. 2005; Stokland et al. 2012; Ulyshen and Šobotnik 2018; Parisi et al. 2018). For example, taxa like Blattodea, Formicidae (Hymenoptera), and Chilopoda often use and move between both leaf litter and deadwood (Hövemeyer and Schauermann 2003; Ulyshen et al. 2017). Deadwood can also impact leaf litter community structure via the creation of distinct microhabitats, increased habitat complexity, and moisture regulation from increased leaf litter depth adjacent to deadwood (Marra and Edmonds 1998; Buddle 2001; Ulyshen and Hanula 2009b, a; Castro and Wise 2009; 2010). Increased habitat structure and complexity may support increased diversity and stability of predators through mechanisms such as increased space for larger bodied predators, decreased intraguild predation, and reduced predator–prey interactions leading to greater predator–prey persistence (Castro and Wise 2009; Kovalenko et al. 2011; Borst et al. 2019). Thus, increased deadwood generated from bark beetle attacks, are likely to support greater abundance and diversity of leaf litter invertebrates, especially predators.

Deadwood impacts on leaf litter BFWs are likely to change over time as the characteristics of deadwood change through decomposition and ecological succession (Parisi et al. 2018). Initial differences in deadwood characteristics, such as those associated with angiosperms versus gymnosperms or initial colonization by fungi like bluestain fungi, can strongly impact deadwood colonization and surrounding leaf litter invertebrate communities (Zuo et al. 2020; Seibold et al. 2023). As deadwood decomposes, saproxylic beetle boring activity facilitates invertebrate and fungi access to deadwood, increasing fungal abundance and diversity which positively affect the opportunity for non–obligate saproxylic species present in leaf litter to directly use deadwood (Irmler et al. 1996; Gibb et al. 2013; Parisi et al. 2018). Beetles and termites initially create access to deadwood via tunneling and boring, with some dispersing through soil and litter to colonize deadwood (Ulyshen et al. 2017; Andringa et al. 2019; Zuo et al. 2020); as such, initial leaf litter communities are likely to be dominated by beetles and termites the first year of decomposition. As decomposition progresses, deadwood characteristics become increasingly homogenous and similar to soil characteristics (Parisi et al. 2018). Therefore, as deadwood decays and loses structure, it may increase habitat space and complexity supporting increased diversity of leaf litter invertebrates and more predators.

This study examined the effect of deadwood and simulated bark beetle–attacked deadwood (deadwood inoculated with blue stain fungus, hereafter referred to as ‘Bluestained deadwood’) on leaf litter BFW structure over time. First, we predicted that the presence of deadwood regardless of bluestain fungi would result in increased leaf litter invertebrate abundance, diversity, and distinct community compositions including increased predators. Second, we predicted that bluestained deadwood

should support the greatest leaf litter invertebrate abundances, diversity, and the highest abundance of predators. Bluestained deadwood should provide increased potential resources directly (nutrients, water content, etc.; Reid 1961; Wingfield et al. 1993) and indirectly (through the attraction of termites who increase available nutrition and space; Little et al. 2013; Jouquet et al. 2011; Clay et al. 2017). Thus, leaf litter invertebrate communities below bluestained deadwood should have the highest diversity and abundance, followed by communities below deadwood without bluestain fungus, and lastly, leaf litter communities where no wood is present. Third, we predicted that the effects of wood on leaf litter invertebrates should become stronger over time as deadwood increasingly functions as continuous habitat with soil and leaf litter. However, we predict these effects will not differ between bluestained wood and control wood as decomposed deadwood should become increasingly homogenous. To test these predictions, we manipulated the presence of an ophiostomatoid bluestain fungus (*Ophiostoma minus* (Hedgc.) Syd. & P. Syd. 1919) that is typically vectored by the southern pine beetle by either inoculating 0.5 m loblolly pine (*Pinus taeda*) deadwood bolts (hereafter referred to as 'logs') with bluestain fungi or H_2O (control logs). Leaf litter BFW communities under these two deadwood treatments or where no deadwood was present were compared after one or seven years of experimental addition of deadwood.

Materials and Methods

Study Site

This experiment was conducted in the John W. Starr Memorial Forest, which is a mixed hardwood bottomland forest in Mississippi, USA (33.2639°N, 88.8884°W). The selected stand has not been burned or logged for over 60 years resulting in a complex canopy structure. This site is predominately loblolly pine (*Pinus taeda* L.) with a midstory of sweetgum (*Liquidambar styracifua* L.), red maple (*Acer rubrum* L.), winged elm (*Ulmus alata* Michx.), and red oak (*Quercus* spp.). The soil is primarily an Urbo silt loam resulting in poor drainage and occasional flooding (Natural Resources Conservation Service 2015) with average annual rainfall at 140.3 cm and temperatures of 26.5 ºC and 6.9 ºC in the summer and winter, respectively (National Oceanic and Atmospheric Administration 2010). The collection years (2015 and 2021) for this study (see below), were similar and not characterized by drought, although drought conditions did occur during years between sampling (www.drought.gov).

Experimental Design

A large–scale decomposition experiment was established in 2014 to examine indirect impacts of bark beetles on deadwood decomposition dynamics and forest biogeochemistry. Our study specifically tests how simulated bark beetle–attacked wood impacts leaf litter invertebrate communities via the presence of bluestain

fungi using this pre–existing experimental design. Specifically, ten 30 m × 30 m plots in the same stand, each separated by ≥ 10 m, were established in 2014. Ten healthy loblolly pine trees of similar diameter at breast height (DBH: 16.0–25.4 cm) in a forest stand immediately adjacent to the focal site were felled and each was cut into 18–0.5 m long logs (180 logs total; Fig. 1). Of the 18 log sections, 16 were given one of two treatments: one) blue stain fungi (n = 80) or two) deionized water inoculation (control wood; n = 80). The other two logs per tree (n = 20) served as untreated controls where one of these logs was immediately brought to the laboratory for chemical analysis and extraction of invertebrates and the other log was left on the plots until the final collection and used to take periodic CO_2 respiration measurements. Consequently, these two logs are not further included in our study as they were not collected over time in years one and seven. As part of the larger experiment testing indirect impacts of simulated bark beetle attack on decomposition and biogeochemistry, half of each treatment (bluestained or control wood) additionally received fine metal mesh cages excluding any additional bark beetles or other aboveground insects from attacking logs but allowing access to belowground invertebrates (see Siegert et al. 2018). However, these caged log treatments were not used as part of our study because our objectives were to examine more natural impacts of deadwood on leaf litter invertebrate communities. Inoculation was performed by drilling twelve holes in each log that were three mm diameter and ten mm depth to simulate bark beetle boring activity (Progar et al. 2000) and injecting 100µl of blue stain fungi (*O. minus*), which is commonly

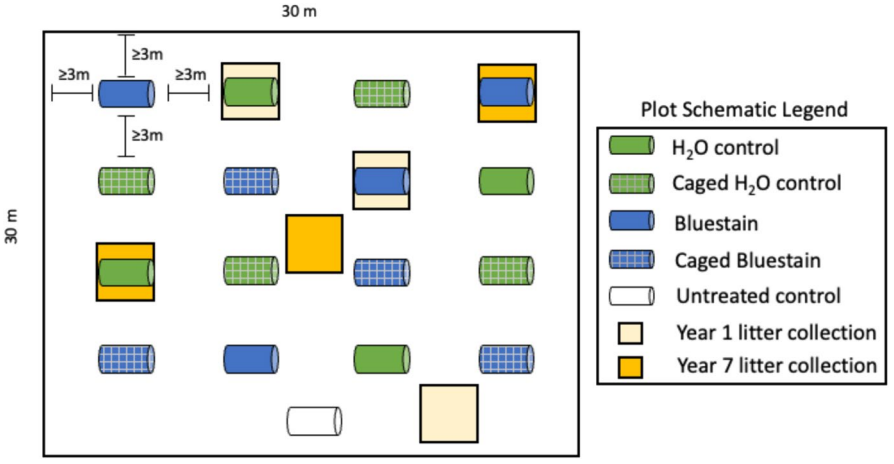


Fig. 1 Experimental design schematic. Study consisted of ten 30 m × 30 m plots, and a single plot is represented here (figure not to scale). Each plot received 17 logs: eight that were treated with bluestain fungi (blue logs), eight that were controls and treated with water (green logs), and one log that was unmanipulated (white log). Half of bluestain treated and control logs received cages (mesh pattern on logs) as part of a larger study. No data from caged logs was included as part of our study on litter invertebrates. Litter invertebrates were collected from 0.5 m × 0.5 m quadrats under one randomly selected bluestain treated log, one randomly selected control log, and one random wood-free area on plots after one year (light yellow squares), and seven years (dark yellow squares). The remaining uncaged bluestain and water control treated logs were not collected at these time intervals and were not included as part of our study

vectored by the southern pine beetle (*D. frontalis*), or deionized water (DI H_2O) with a micro–pipette. The drill bit was flame sterilized between each use. Inocula were prepared from cell stock of previously identified cultures of *O. minus* from prior studies and contained five g hyphae macerated in 100 mL of sterilized DI H_2O (for methods see Little et al. 2012a, b, 2013) and reference cell stock was stored in the Forest Entomology Laboratory at Mississippi State University. Log ends were sealed with wax to prevent moisture loss and mimic a larger log (Progar et al. 2000; Siegert et al. 2018). Logs were then placed at random in a rough grid pattern on plots separated by ≥ three m (Fig. 1).

Invertebrate Sampling

To examine impacts of deadwood presence, simulated bark beetle–generated deadwood (bluestained wood), and collection year on leaf litter invertebrate community structure, all leaf litter down to top soil was collected from 0.5 m × 0.5 m (0.25 m^2) quadrats below one) uncaged bluestained logs (n = 10; one per plot), two) uncaged control logs (n = 10; one per plot), and three) equisized quadrats of leaf litter where no logs were present (n = 10; one per plot) separated by ≥ 3 m from experimental logs on the same plot in October of years one (2015) and seven (2021) (Fig. 1). We randomly selected logs to sample leaf litter invertebrates from under each year, and quadrats sampled for litter invertebrates sampled where no logs were present were selected haphazardly to ensure random collection with no deadwood in quadrats and sufficient distance from existing experimental deadwood. Thus, in total as part of our study, leaf litter invertebrates were collected from under ten random (one per plot) uncaged bluestained logs, ten random uncaged water control logs (one per plot), and ten random plots without deadwood (n = 30 total litter invertebrate samples; three per plot) in year one and again in year seven (Fig. 1). Logs were removed during sampling as part of the larger experiment and were thus not repeatedly sampled across years.

Prior to collection of leaf litter communities, litter depth was measured in each quadrat corner by inserting a thin metal flag through the leaf litter and measuring the distance from the top of the leaf litter to the top of the mineral soil. Then, all leaf litter in quadrats was collected down to the top of the mineral soil and placed in a hand sifter (1.5 cm × 1.5 cm mesh) to remove larger debris but retain leaf litter invertebrates (Holdhaus 1910). Leaf litter, debris, and invertebrates that passed through mesh (siftate) were then placed in muslin bags and transported to the laboratory for invertebrate extraction using Berlese funnels with a 40 W halogen light bulb for 24 h. Due to logistical time constraints, in year seven collections, total volume of the siftate from each quadrat was measured, but a random 250 ml subsample of each quadrat's siftate was used in Berlese funnels, which ran for 24 h. Invertebrates were collected and preserved in a container with 70% ethanol until identification. To estimate the total number of invertebrates collected in year seven to compare with year one, the abundance of each focal taxon group was calculated using $A_T = TSV * \left(\frac{A_M}{250ml}\right)$. Here, A_T is the estimated total abundance, and A_M is the measured taxon abundance from the 250 mL subsample, and TSV is the total

siftate volume (mL) collected from the field. Logs were destructively sampled each year as part of the larger experiment; consequently, leaf litter invertebrate communities were sampled from under different logs in year one than year seven (e.g., samples are not repeated measures).

Invertebrates were identified to order level or functional groups that reflect largely lower feeding groups (detritivorous: consuming primarily plant matter including detritivores or plant feeders found in leaf litter) or higher feeding groups (predatory: consuming animal tissue including omnivores, scavengers, predators, and parasitoids) functional feeding groups. If taxa were ecologically distinct exhibiting, they were also split (e.g., ants vs. non-ant Hymenoptera). Specifically, mites (Acari) were identified to functional groups (predatory mites: e.g., Mesostigmata, Prostigmata; non–predatory mites: Oribatida), Hemiptera were identified as functional groups Heteroptera and Homoptera, Coleoptera adults were first identified to family level and then grouped into functional groups as either 'Coleoptera predators' or 'Coleoptera detritivores', and Hymenoptera were separated into ants (Hymenoptera: Formicidae, identified to genus level) or non–ants (all other Hymenoptera, which primarily included parasitic wasps: Apocrita). Coleoptera and Diptera larvae were included as separate functional groups as holometabolous insects often have distinct ecological niches as immatures versus adults. The 19 included orders and functional groups are listed in the *Statistical Analysis* section. Abundances of Acari and Collembola were estimated, because they numbered in the hundreds to thousands in these samples (Gwiazdowicz 2021). Specifically, we extracted invertebrate samples from Berlese funnels and placed them placed in 148.2 mm diameter gridded (2 cm $\times$2 cm grid squares) Petri dishes in 70% ethanol. First, all non–Acari and Collembola were removed from the Petri dish and identified, then, the remaining taxa across the Petri dish area were homogenized by gently swirling the dish and using forceps to evenly spread taxa. After which, the number of non–predatory mites, predatory mites, and Collembola in each of the ten randomly chosen grid squares were counted. Abundance of each taxon was estimated by calculating the average of each taxon among the ten squares and multiplying the average by the total area of the Petri dish (151.9 cm^2).

Statistical Analysis

For all community analyses, the following 19 orders and functional groups were included: predatory mites, non–predatory mites (i.e., Oribatida), Araneae, Blattodea (separated to Isoptera and other Blattodea), Coleoptera predators, Coleoptera detritivores, Collembola, Chilipoda, Diplopoda, Diptera, Gastropoda, Heteroptera, Homoptera, non–ant Hymenoptera, ants, Isoptera (Blattodea), Psocodea, Pseudoscorpiones, and Thysanoptera. These accounted for 81.7% of the total invertebrate abundance in year one and 99.2% of the total invertebrate abundance in year seven and are commonly used as focal taxa in other leaf litter community studies (Scheu and Falca 2000; Clay et al. 2014). All analyses included plot as a random effect variable using the "lme4" package (Bates et al. 2015; Fig. 1).

To test the null hypothesis of no difference in community composition among leaf litter communities across deadwood presence, bluestained deadwood, and collection year, we used PERMANOVA (Anderson 2001). Specifically, the Bray–Curtis distance measure on square root transformed abundances (A_T for year seven) of the 19 focal taxa groups and 9999 permutations was used with the Adonis function in the vegan package in R v4.4.3. (Oksanen et al. 2022; R Core Team 2022). Deadwood was included as a factor with three treatment levels (bluestained wood, control (H_2O inoculated deadwood), and no deadwood) and collection year as a factor with two levels: year one and seven. Plot was included as a random factor in the model, and we tested for an interaction between deadwood treatment and collection year. If we found significant effects, we used post hoc tests using pairwise Adonis (Martinez, 2017) to determine which deadwood treatments differed or subsequent PERMANOVAs on year one and year seven separately following a significant effect of collection year. Significant treatment and year effects on leaf litter communities were followed by an indicator species analysis to determine which taxa differed in either collection year or treatment using the "labdsv" package in R with taxa indication status ('d') ranging from 0 to 1 determined by the product of the relative frequency and relative average abundance in clusters (Roberts 2019). Non–metric multidimensional scaling (NMDS) was used to visualize community results using the "ggplot2," "ggpubr," and "ggvegan" packages in R (Wickham 2016; Kassambara 2023; Simpson 2019).

Similarly, we tested for effects of deadwood and collection year on taxa (orders or functional groups as described above) diversity, evenness, richness and abundance. Taxa diversity was calculated using the Shannon Diversity index ($H' = -\sum p_i * \ln(p_i)$) and evenness as Shannon's Equitability ($E_{H'} = H'/\ln(S)$), where $p_i =$ proportion of taxa, $H' =$ Shannon diversity index, $S =$ total number of taxa. The null hypothesis that there was no difference in diversity, evenness, richness, or abundance among collection year (Year) and wood treatments (Deadwood) or their interaction was tested using ANOVA. Data were tested for normality prior to analysis using a Shapiro–Wilks test. Abundance and richness were not normally distributed and were $\log_{10}$ (x) transformed and power transformed by squaring respectively.

The 19 taxa used for analysis were split into functional trophic groups (predator or detritivore) based on natural history observations and previous research using N stable isotope analysis (Supplementary Table 1; Scheu and Falca 2000; Clay et al. 2014; Ulyshen 2018). A ratio was then created using abundance of detritivores to abundance of predators per plot (detritivores/predators) and then analyzed using ANOVA to test the null hypothesis that deadwood addition and year have no effect on detritivore/predator ratios in leaf litter communities. Detritivore/predator ratio did not meet normality using a Shapiro–Wilks test and was $\log_{10}$ (x) transformed. To test the null hypothesis of no difference in leaf litter depth among deadwood treatments and collection years, we used ANOVA. Leaf litter depth violated assumptions of normality and was square–root transformed.

Results

Brown Food Webs

Overall, an estimated 54,255 invertebrate individuals were collected with 12,503 collected in year one and 41,752 in year seven when corrected with siftate volume sampled. Leaf litter communities differed in community composition across deadwood treatments (Treatment: Pseudo–$F_{(2,51)} = 2.92$, $p = < 0.001$; Fig. 2) and years (Year: Pseudo–$F_{(1,51)} = 9.96$, $p < 0.001$; Fig. 2), but the effects of deadwood treatments were similar between years (i.e., no interaction: Pseudo–$F_{(2,51)} = 1.06$, $p = 0.37$; Supplementary Table 2; Fig. 2). Specifically, leaf litter communities were different between deadwood presence and absence (bluestained wood vs no wood $p = 0.002$; control wood vs no wood $p = 0.001$), but leaf litter communities under bluestained wood did not differ from control wood ($p = 0.67$; Supplementary Tables 2 & 3; Fig. 2). Coleoptera predators and non-ant Hymenoptera were significant indicators of bluestained wood across sampling years with 7.4–fold and 3.09–fold greater abundance respectively in leaf litter under bluestained wood compared to no deadwood and 1.3–fold and 4.7–fold greater abundance respectively compared to control deadwood (Coleoptera predators: Indicator Value (IV = 0.5, $p = 0.011$; non–ant Hymenoptera: IV = 0.41, $p = 0.009$; Fig. 3a). Between collection years, leaf litter communities in year one had more Diplopoda (IV = 0.82, $p < 0.001$), Thysanoptera (IV = 0.79, $p < 0.001$), Psocodea (IV

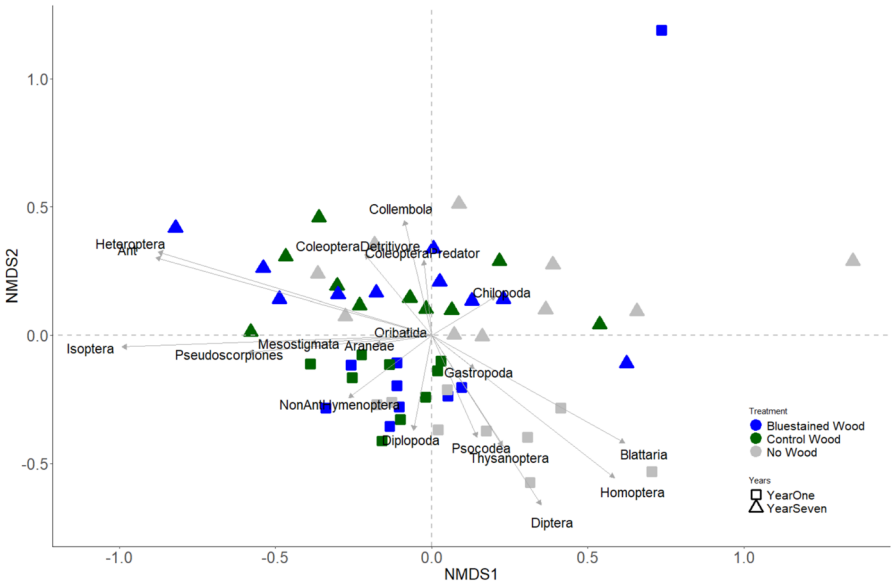


Fig. 2 Nonmetric multidimensional scaling (NMDS) of leaf litter communities related to wood treatment (shown by color of point) and collection year (shown by shape of points) where taxa are represented as vectors indicating the strength (increasing arrow length) and direction of their relationships. Stress for this NMDS was 0.163

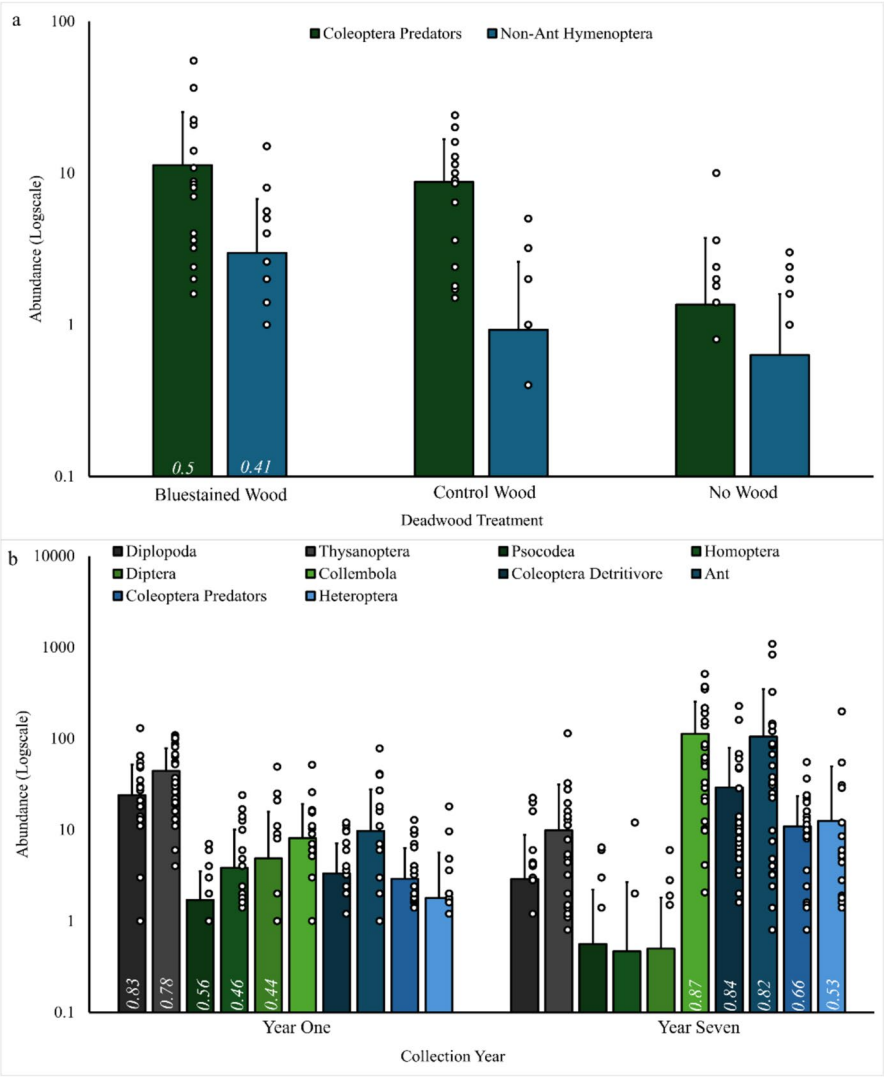


Fig. 3 Abundance of indicator taxa based on deadwood treatment (**a**) and collection year (**b**) with indicator values (IV) above taxa. Indicator values signify taxa most representative of treatments or collection years. Indicator values are between 0 and 1, and higher values indicate a stronger relationship. If no indicator value is present, then that taxon was not an indicator of that deadwood treatment or collection year and data are presented only for comparison of abundances between explanatory groups. Bars represent mean abundance and error bars are positive standard deviation. Dots represent each individual data point collected for each taxon group

= 0.55, p < 0.001), Homoptera (IV = 0.46, p = < 0.001), and Diptera (IV = 0.44, p = 0.003; Figs. 2 & 3b). Year seven leaf litter communities had more Coleoptera predators (IV = 0.65, p = 0.002), Coleoptera detritivores (IV = 0.84, p < 0.001),

Heteroptera (IV = 0.52, p = 0.03, Collembola (IV = 0.87, p < 0.001), and ants (IV = 0.82, p = 0.001; Figs. 2 & 3b).

Abundance, Diversity, Evenness, and Richness

Mean abundance (± SD) of leaf litter invertebrates collected from 0.25 m^2 plots in year one and seven was 502 ± 342 and 999 ± 1063, respectively, but did not differ between years (Year: $F_{(1,51)} = 2.68$, p = 0.11; Supplementary Table 4; Fig. 4a). Furthermore, abundance of leaf litter invertebrates by deadwood treatments did not differ depending on the year sampled (Treatment x Year: $F_{(2,51)} = 0.29$, p = 0.74). However, abundance of invertebrates under deadwood treatments (control deadwood) was ~two–fold greater than when no deadwood was present (Treatment: $F_{(2,51)} = 4.27$, p = 0.02). The taxa richness of leaf litter invertebrates was 1.4–fold higher under deadwood compared to no deadwood (Treatment: $F_{(2,51)} = 6.917$, p = 0.002; Fig. 4b) and differed by collection year (Year: $F_{(1,51)} = 13.445$, p < 0.001; Supplementary Tables 5 & 6; Fig. 4c). However, there was no interaction between deadwood treatment and collection year on taxa richness (Treatment x Year: $F_{(2,51)} = 0.028$, p = 0.97). Leaf litter invertebrate diversity and evenness did not differ among deadwood treatments or between collection years and was 1.0 ± 0.4 and 0.5 ± 0.2, respectively (Supplementary Tables 7 & 8).

Detritivore/Predator Ratio

Detritivore/predator ratios differed by deadwood treatment between years (Treatment x Year: $F_{(2,51)} = 5.46$, p = 0.007), but did not differ by treatment or year (Treatment: $F_{(2,51)} = 3.09$, p = 0.06; Year: $F_{(1,51)} = 0.828$, p = 0.37; Supplementary Tables 9 & 10; Fig. 5). Specifically, in year one collections, there were no differences in ratios of predators compared to detritivores among treatments ($F_{(2,524)} = 0.558$, p = 0.579; Supplementary Table 11). However, in year seven collections, there was significantly more predators (~ fivefold change in ratio) in leaf litter communities under deadwood compared to when no deadwood was present ($F_{(2,27)} = 7.38$, p = 0.002; Supplementary Tables 12 & 13).

Leaf Litter Depth

Mean leaf litter depth measured from 0.25 m^2 quadrats differed between deadwood treatments (6.5 cm ± 2.5 cm) and no wood (3.8 cm ± 1.5 cm) across years (Treatment x Year: $F_{(2,51)} = 4.17$, p = 0.02; Supplementary Table 14). Deadwood treatments accumulated more litter on average (6.6 cm ± 3.1 cm) compared to plots without deadwood (3.8 cm ± 1.5 cm; Treatment: $F_{(2,51)} = 9.777$, p < 0.001; Supplementary Table 14), with year seven having more accumulation (6.5 cm ± 1.4 cm) than year one (4.8 cm ± 1.4 cm; Year: $F_{(1,51)} = 4.72$, p = 0.035; Supplementary Table 14).

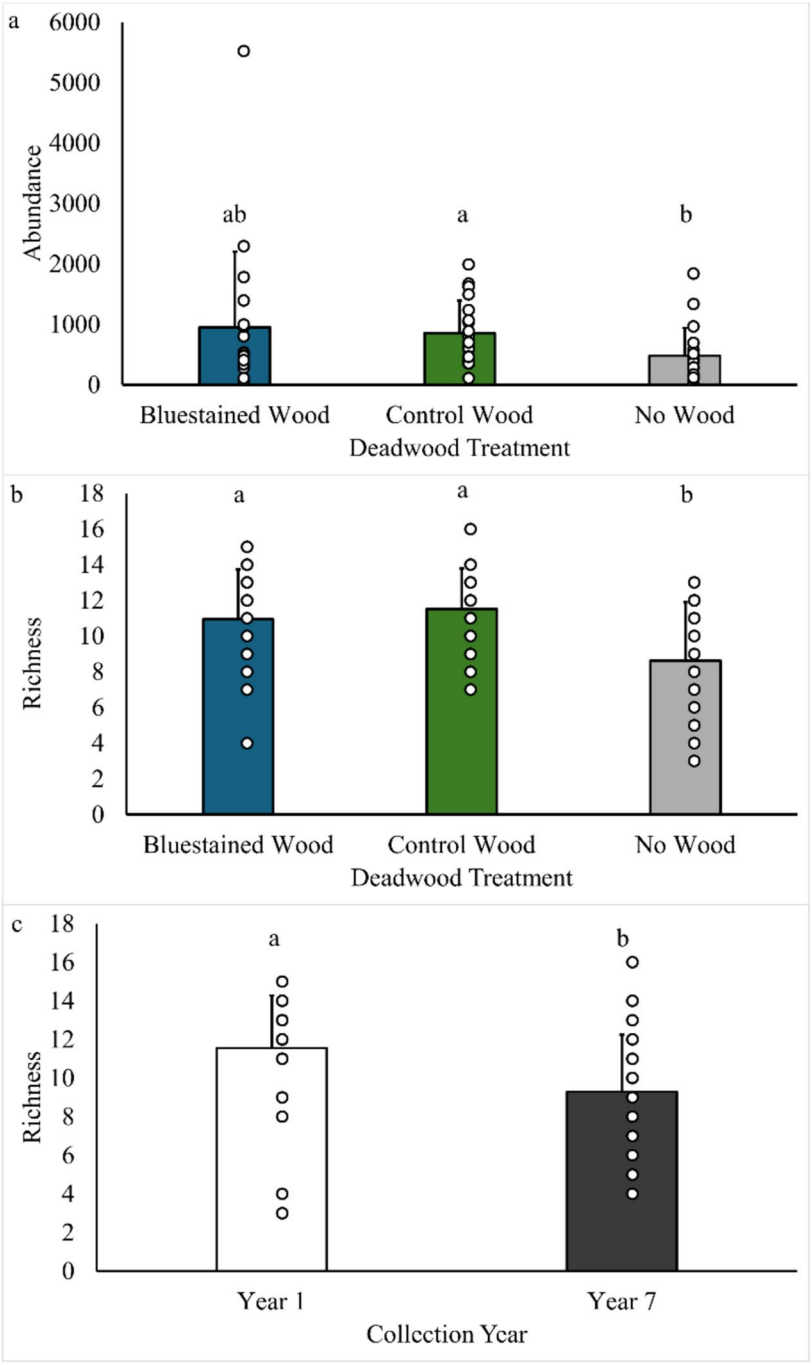
Fig. 4 Representations of the main and interaction effects on richness and abundance. (**a**) Abundance of ▶ leaf litter taxa under deadwood treatments (year one and year seven collections combined), (**b**) richness of taxa by deadwood treatments (year one and year seven collections combined), (**c**) and richness of taxa by collection year (deadwood treatments combined). Letters above bars denote significant differences between and among collection years and deadwood treatments, respectively. Bars represent mean values and error bars are positive standard deviation. Dots are the individual data points within each group

Discussion

Bark beetle activity and subsequent deposition of deadwood are predicted to increase as trees become stressed under future climate change (Gan 2004; Kurz et al. 2008; Edburg et al. 2011; Sambaraju et al. 2012; Woodall et al. 2021). The objectives of this study were to determine if deadwood impacts the abundance, distribution, and activity of leaf litter BFWs, and how patterns may differ over time as deadwood is a long–term resource and undergoes significant changes throughout decomposition (Parisi et al. 2018; Andringa et al. 2019; Zuo et al. 2020). We found that the presence of deadwood resulted in a different leaf litter invertebrate community composition compared to when no deadwood was present, with more predatory beetles and non-ant Hymenoptera under bluestained wood. However, contrary to predictions, litter communities under bluestained wood did not differ from control deadwood, but community composition and structure changed over years. Invertebrate richness increased after seven years but exhibited no differences among deadwood treatments after just one year. Moreover, after seven years the proportion of detritivores/predators was lower (more predators) when deadwood was present. Together, these results suggest that deadwood (bark beetle–generated or not) is important in creating heterogeneity in leaf litter communities (Ponsard et al. 2000), but the function of deadwood to leaf litter communities differs across decomposition likely mediated by both resource availability (bottom–up effects) and predators (top–down effects) (Power 1992).

Invertebrate abundance in litter communities below deadwood was greater than when no wood was present and may suggest that deadwood structures leaf litter BFWs through bottom–up processes as an important basal resource (e.g., food) (Power 1992; Ponsard et al. 2000; Zuo et al. 2020). Moreover, Coleoptera predators and non-ant Hymenoptera were indicators of simulated bark beetle–generated deadwood. The presence of bluestain fungi may support increased invertebrates via bottom–up mechanisms as increased nutrition by lowering the C:N ratio of deadwood (Clay et al. 2021). More basal resources support increased primary consumers, which can then support increased proportions of predators (Rosemond et al. 2001; Moore et al. 2004). Although this effect did not change across years, more predators were supported after seven years, which may suggest the function of deadwood changes over time and could lead to increased importance of top–down effects in later successional stages (Bengtsson et al. 1997). Increased leaf litter invertebrate activity can lead to increased decomposition rates and heterotrophic respiration in litter around deadwood (Schmitz and Leroux 2020).

The ecosystem size hypothesis posits that predators are space–limited and that larger ecosystems increase the presence and stability of higher trophic levels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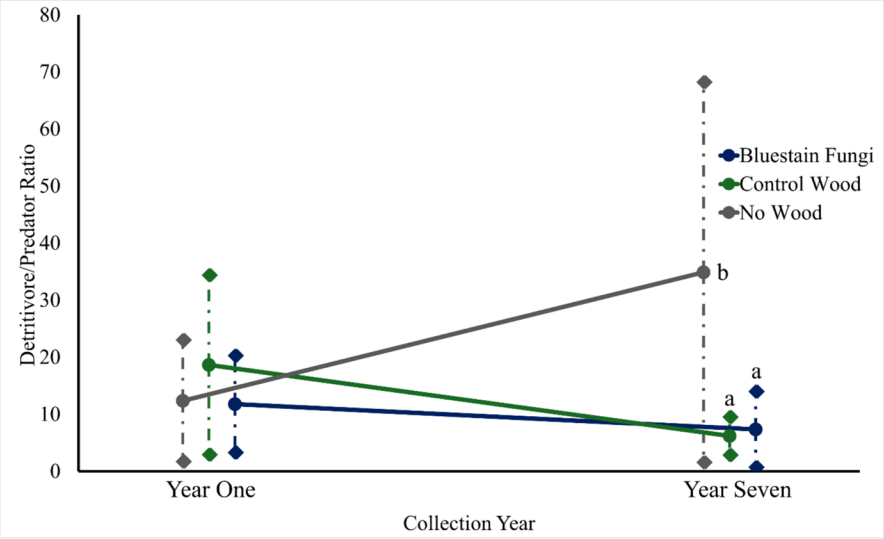

Fig. 5 Interaction plot of mean detritivore/predator ratio between years and among treatments. Increasing detritivore: predator values reflect increased proportion of detritivores and lower values reflect increased proportion of predators. Within years, different letters represent significant differences among treatments ($p < 0.05$). Error bars are positive standard deviation

including longer food chains (Cohen and Newman 1991; Post et al. 2000). After seven years, there was a lower detritivore to predator ratio in leaf litter communities under deadwood, and the primary predatory taxa Coleoptera (mostly consisting of Staphylinidae) and Hymenoptera (non–ant) were indicators of deadwood presence. The seven–year–old deadwood in this study was severely decayed, representing late–stage decay classes where deadwood has lost shape and was integrating with the soil and in many cases was significantly covered by litter (e.g., Ferro 2018; Moroni et al. 2015). Thus, late decay stage deadwood may primarily affect leaf litter invertebrates through its ability to create patches of increased habitat size and heterogeneity (Marra and Edmonds 1998; Benedetto et al. 2025). Moreover, leaf litter depth and habitat volume strongly impact the density of leaf litter invertebrates (Ettema and Wardle 2002; Kaspari and Yanoviak 2009; Shik and Kaspari 2010; Clay et al. 2014). We found that mean litter depth varied from 1.57 cm to 14.5 cm across sampled quadrats from both collection years and sampled quadrats that contained deadwood had more predators and deeper leaf litter, but no changes in leaf litter depth were found between years. This is consistent with previous work by Castro and Wise (2010), where predator richness was higher closer to coarse woody debris (CWD) than further away. Similarly, Donoso et al. (2010, 2013) found that deeper leaf litter supported increased predator to prey ratios. Thus, in addition to providing food for BFWs, deadwood also structures communities through increased habitat size and heterogeneity (Castro and Wise 2010).

Increased predator abundance under deadwood could facilitate top–down effects in late decay stages. The decrease in the proportion of detritivores to predators

after year seven was driven by a 4.2–fold increase of predators per log from year one (Mean ± SD: 43 ± 33) to year seven (179 ± 322) while detritivores only saw a 1.6–fold increase from year one (454 ± 326) to year seven (767 ± 809). Initially, detritivorous taxa increased under deadwood (e.g., gastropods; Fig. 2), but after seven years, beetles like staphylinids, which are common predators of gastropods (Symondson, 2004) increased. Increased predators can have both trophic and non–trophic interactions (Majdi et al., 2014). Risk of predation may change detritivore behavior or impact prey morphology and physiology that alter foraging efficiency, competitive interactions, and available resources (Schmitz et al. 1997; Majdi et al., 2014). Predators may also impact decomposition and nutrient cycling through nutrient retention, excretion, and carcasses (Ngai and Srivastava 2006; Hawlena et al. 2012) or by altering habitat (e.g., ecosystem engineering; Yixin et al., 2004; Sanders and van Veen 2011; Joshua et al., 2019). Thus, predators may either accelerate or slow down decomposition processes depending on the trophic levels most affected and their indirect effects on habitat and resource availability (Rosemond et al. 2001; Lawrence and Wise 2004; Lensing and Wise 2006; Hawlena et al. 2012). Future research should test for top–down impacts on leaf litter decomposition under deadwood of later decay stages.

Succession of invertebrates in deadwood is a nascent body of research (Jonsson et al. 2005; Ulyshen and Hanula 2010; Seibold et al., 2015; Zuo et al. 2020, Seibold et al. 2023); however, even less is known about succession of leaf litter communities driven by deadwood dynamics (Jabin et al. 2004; Ulyshen and Hanula 2009b, a; Ulyshen et al. 2011). Due to the unique habitat presented by deadwood and its changing physical and chemical properties throughout decomposition (Stokland et al. 2012), succession in deadwood communities is driven by both saproxylic and leaf litter invertebrates over time (Parisi et al. 2018; Zuo et al. 2020). Initial differences in deadwood can have strong effects on communities within deadwood (Zuo et al. 2020; Seibold et al. 2023). However, contrary to predictions, we found minimal–to–no impacts of blue stain inoculation on initial leaf litter invertebrate communities including changes in termite abundance. Changes in leaf litter invertebrate communities over time were likely driven in part by accessibility of deadwood to litter organisms. For example, initially, few organisms can penetrate beyond the deadwood bark selecting for increased xylophagous (wood feeding or wood boring) organisms (Irmler et al. 1996; Gibb et al. 2013; Parisi et al. 2018) and likely excluding most leaf litter invertebrates. Therefore, initially, deadwood and leaf litter likely represent distinct detrital habitats. As decomposition progresses and deadwood is physically altered, moisture content increases, which can facilitate colonization of decomposer fungi and invertebrates including mycetophagous (fungi feeding) and predatory invertebrates (Irmler et al. 1996; Gibb et al. 2013; Parisi et al. 2018; Ferro 2018). In support of this, after seven years, deadwood was significantly more decomposed and integrated with the litter than in year 1 and Coleoptera (predators and detritivores), ants, Collembola, and Heteroptera were more common under deadwood than when wood was not present. Some of the changes to leaf litter invertebrate communities reflect temporal stochasticity given there was no time by deadwood treatment interaction (Hubbell 2001). However, increased proportion of predators, richness, and changes in invertebrate abundances under deadwood versus where

no deadwood was present imply that deterministic mechanisms are also impacting leaf litter BFW succession.

Siegert et al. (2018) found that simulated bark beetle–generated deadwood from this study had increased presence of termites after 1 year, but we found no difference in termite abundance, and very few termites in general, in leaf litter communities below logs. Ulyshen et al., (2017) found increased termites in leaf litter near deadwood after 51 months of decomposition, but this was associated with chemical differences (nitrate and potential net nitrification) in the soil below and away from deadwood, which was not measured in our study. However, simulated bark beetle–generated deadwood did support increased predators such as beetles and ants, many of which are predators of termites (Vogt et al. 2002; Brunke et al. 2011). Termites may have been in the wood or soil (neither of which were measured here), and increased predator abundances in leaf litter communities below simulated bark beetle–generated deadwood may have been in at least in part a response to soil and deadwood termite presence. However, this remains untested.

Deadwood is increasingly being recognized as important for biodiversity conservation and forest health (Jonsson et al. 2005; Seibold et al. 2015; Doerfler et al. 2018; Sandström et al. 2019) and increased disturbances associated with climate change like bark beetle outbreaks are likely to alter patterns of deadwood deposition (Gan 2004; Kurz et al. 2008; Lesk et al. 2017). Our results demonstrate that deadwood supports distinct BFW communities below it and particularly over longer time scales. Additionally, we found that deadwood supports a higher proportion of predator taxa. Trophic downgrading is a common phenomenon where loss of upper trophic level consumers alters the abundance and diversity of lower trophic levels and results in a less diverse ecosystem with reduced function (Estes et al. 2011). Thus, conservation of deadwood may not only increase saproxylic and leaf litter invertebrate diversity (Doerfler et al. 2018), but may help support the stability of higher trophic levels in BFWs of forest ecosystems. Bluestained deadwood had minimal impacts on leaf litter invertebrate communities despite having distinct soil and wood chemistry from control wood and increased termite presence (Siegert et al. 2018). This further supports the likelihood that deadwood influences leaf litter invertebrate communities more strongly due to increased habitat size and heterogeneity rather than from wood chemistry (Benedetto et al. 2025). However, our study represents one of only a handful of studies to examine deadwood impacts on BFWs, and those that inhabit the leaf litter (Kappes et al. 2009; Ulyshen and Hanula 2009a, b; Castro and Wise 2009, 2010; Ulyshen et al. 2011; Klepzig et al. 2012; Seibold et al. 2017; Lythe et al. 2017). And studies have found mixed results on leaf litter organisms indicating more research is needed to predict how and why deadwood changes leaf litter community structure and function.

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Data Availability Data are available on Dryad: https://doi.org/10.5061/dryad.vq83bk456.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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