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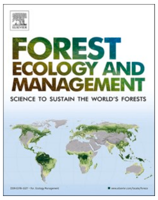

Decomposition of bark beetle-attacked trees after mortality varies across forests

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ABSTRACT

Bark beetle outbreaks result in massive amounts of deadwood which are a significant carbon reservoir that can impact forest ecosystems. Additionally, bark beetle-introduced symbiotic fungi in beetle-generated deadwood can increase termite presence and feeding. This could alter decomposition rates and saproxylic communities of bark beetle-generated deadwood. However, the fate of bark beetle-generated deadwood after tree mortality has received little attention despite the possibility bark beetles could alter decomposition processes and deadwood residence times at landscape scales following outbreaks. We tested the hypothesis that beetle-attacked trees decompose faster than unattacked trees. In Honduras, and Mississippi and Arizona, USA, we felled one recently bark beetle-attacked and one apparently healthy conspecific tree at each site that was cut into 120 experimental logs. Logs of each tree (attacked or unattacked) were assigned one of three metal mesh covering treatments: 1) fully covered to exclude all macroinvertebrates, 2) covered from above to exclude secondary bark beetle colonization, 3) no cover to allow all detrital food web organisms. Half of all logs at each site was collected after 1 and 2 years and the density loss, insect visual damage rating, and abundance of termites, ants, and beetles was measured. Bark beetle attack had the largest impacts at higher latitude and western forests: density loss between attacked and unattacked logs was consistently higher in Arizona (Flagstaff), initially slower (year 1) in Mississippi, but faster between years 1 and 2 resulting in similar density loss after 2 years, and did not differ in Honduras. Saproxylic insect wood damage rating accounted for 30% of the variation in decomposition across sites. Thus, decomposition rates of deadwood following bark beetle attack are highly variable across their geography and likely reflect important interactions among saproxylic organisms. This has implications for forest ecology and management including forest modeling with regard to carbon cycling and maintaining biodiversity of saproxylic organisms.

1. Introduction

Understanding drivers of ecosystem function is increasingly important as global change alters abiotic factors and the distribution, intensity, and direction of many ecological interactions (Parmesan, 2006; Kurz et al., 2008). Forest ecosystems constitute ~31% of Earth's terrestrial surface, ~50% of annual net carbon (C) sequestered by the terrestrial biosphere, and ~35% of terrestrial C stocks stored in vegetation and soils pools (Pan et al., 2011). The vital role of forests in global C cycles necessitates better quantification of forest C dynamics. Carbon fluxes in forests are particularly sensitive to landscape-scale disturbances such as bark beetle (Coleoptera: Curculionidae: Scolytinae) epidemics that cause large-scale tree mortality and deadwood generation and can shift entire forests from C sinks to sources (Gan, 2004; Kurz et al., 2008; Edburg et al., 2011). Bark beetles are primary herbivores of conifers worldwide, and their epidemics can generate up

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to 103 Mg ha^{-1} yr^{-1} of deadwood (Harmon et al., 1986; Kurz et al., 2008). Despite bark beetle ubiquity, how saproxylic communities interact with bark beetle-generated deadwood and impact decomposition remains poorly quantified.

Deadwood accounts for ~8% of C stored in forest ecosystems globally (Pan et al., 2011). Recent evidence suggests that saproxylic communities may better explain patterns of wood decomposition at ecosystem scales than climatic factors (Heneghan et al., 1999; Bradford et al., 2014; Ulyshen et al., 2014; Hu et al., 2018). When bark beetles attack trees, they vector a suite of symbiotic fungi to tree hosts (Klepzig and Six, 2004). One such group of fungi is the ophiostomatoid fungi (Ascomycota: Ophiostomataceae) (hereafter bluestain fungi), which do not decompose the structural components of wood, but instead metabolize resin sugars and lipids, clog water transport vessels, and cause the characteristic darkening of sapwood from which their common name "bluestain fungi" is derived (Progar et al., 2000; Wingfield et al., 1993). Some bluestain fungi in deadwood attacked by bark beetles has been linked to subterranean termite presence and often increased feeding in both laboratory and field studies (Little et al., 2012a, 2012b, 2013a; Riggins et al., 2014; Clay et al., 2017, 2021; Siegert et al., 2018).

Termites are among the most important biological drivers of woody decomposition in forest ecosystems (Cornwell et al., 2009; Jouquet et al., 2011; Bradford et al., 2014; Griffiths et al., 2021). Additionally, termites can indirectly influence the abundance and activities of other decomposers in and around deadwood via tunneling, N-fixation, and N-deposition (Jouquet et al., 2011). If bark beetle-attacked trees are transitively associated with increased termite activity, then bark beetle-generated deadwood is likely to have enhanced decomposition rates and greater biodiversity than unattacked deadwood in areas where this interaction occurs.

Surprisingly, few studies have tested how bark beetle attacks affect saproxylic organisms despite the impact of bark beetles on both the generation and initial conditions of deadwood (e.g., presence of fungi, increased wood access via holes from beetle boring, etc.; Weslien et al., 2011; Jacobsen et al., 2015) (but see Strid et al., 2014; Zuo et al., 2016). In addition to termites, ants and beetles are common ecosystem engineers that influence decomposition and succession processes in deadwood (Swift and Boddy, 1984; Ulyshen et al., 2014, 2016; King et al., 2018; Zuo et al., 2021). Ants are ubiquitous inhabitants of deadwood and impact deadwood through changes in structure from nest building, deposition of nutrients in refuse piles, movement of plant and animal tissue, and predation on saproxylic communities (Lindgren and MacIsaac, 2002; King et al., 2018). Saproxylic beetles impact deadwood decomposition through their associations with fungi (e.g., some ambrosia beetles), by increasing the surface area for microbes via tunnelling and wood fragmentation, and through their diverse species interactions including predation (Nadeau et al., 2015; Ulyshen, 2016; Kahl et al., 2017). Bark beetle-induced changes in attacked trees (e.g., physical, chemical, and biotic characteristics such as increased nutritional resources and increased access points through boring; Little et al., 2013b; Hýsek et al., 2021) could thus facilitate and support increased termites, ants, and beetles in bark beetle-generated deadwood.

We tested the hypothesis that deadwood from bark beetle-attacked trees (hereafter attacked) would differ in decomposition rate and insect communities than deadwood from trees not attacked by bark beetles (hereafter unattacked) and that patterns would be dependent on time and location. Specifically, we predicted that deadwood from 1) attacked trees would support higher insect abundances and decomposition rates than unattacked trees, 2) these effects would be greatest in later stages of decomposition after wood had been primed by saproxylic beetle and termite activity that facilitates ant and other insect colonization (e.g., prey resources), and 3) insect access to deadwood would increase decomposition rates, particularly in bark beetle-attacked trees. To test these predictions, we felled one bark beetle-attacked tree and one similar sized unattacked conspecific tree in Arizona, USA, Mississippi USA, and Siguatepeque, Honduras (hereafter Arizona, Mississippi, and Honduras). These sites represented a diversity of tree species, termite densities, and climatic conditions. At each site, trees were cut into sixty 10 cm long logs and randomly assigned to one of three covering treatments: 1) fully covered to prevent access of all large invertebrates to wood, 2) half covered to allow access from belowground but not aboveground invertebrates, and 3) no cover to allow all access to detrital food web organisms. Termites, beetles, and ants were extracted from logs and decomposition rates were quantified over two years.

2. Methods

2.1. Study sites

This study took place from June 2017 to August 2019 in Siguatepeque, Honduras (14°33'46.8" N, 87°48'54.0" W; 1118 m a.s.l.), Flagstaff, Arizona, USA (35°09'39.6" N, 111°45'36.0" W; 2105 m a.s.l.), and McNeill, Mississippi, USA (30°38'45.6" N, 89°38'27.6" W; 74 m a.s.l.). These sites were chosen to span a gradient of temperature, precipitation, elevation, dominant pine species, and termite biomass (Table 1).

2.2. Experimental design

One recently bark beetle-attacked tree and one apparently healthy, unattacked conspecific tree of similar size were selected at each site in 2017 to examine effects of bark beetle attack on deadwood decomposition. Recently attacked trees still had needles and tightly attached bark but showed obvious signs of attack including needle chlorosis and resin flowing from boring holes (Billings and Pase, 1979). Upon felling, attacked trees exhibited substantial "blue-staining" from ophiostomatoid fungal presence. Unattacked trees showed no signs or symptoms of bark beetle attack, nor signs of other insects and diseases, and were visually healthy. Trees were felled and cut into sixty 10 cm sections (hereafter referred to as logs). Logs from both attacked and unattacked trees were randomly assigned to one of three covering treatments ($n = 20$ per treatment/ tree type) to determine the relative contributions of microbes and invertebrates to decomposition rates: 1) fully covered (hereafter: FC), 2) covered from above (hereafter: HC (i.e., Half Covered), and 3) no covering (hereafter: NC). FC and HC logs were outfitted with stainless steel fine-mesh metal cloth (mesh size 0.26 ×0.47 mm). FC logs were fully wrapped in the mesh, which was secured with zip ties to exclude macroinvertebrates and limit decomposition to primarily microbes (e.g., Jacobsen et al., 2018; Seibold et al., 2021). For HC logs, fine metal mesh cloth was draped over the top of the log and secured to ground with metal garden stakes with edges of metal cloth covered in litter to exclude aboveground saproxylic invertebrates, including secondary bark beetle species while permitting access to logs by belowground decomposers (both invertebrates and microbes) (Weslien et al., 2011). Lastly, NC logs were placed directly on top of the forest floor to permit natural succession and decomposition. All logs were placed with one of the cut surfaces facing the ground, and all but FC logs were in direct contact with the forest floor (Supplementary Fig. 1).

2.3. Saproxylic Insect collection

After approximately one (12 months; 2018) and two years (23 months; 2019) (year 1 and 2, respectively), half of all logs ($n = 60$) and treatments ($n = 10$ per cage treatment per tree attacked status) were collected at each site. Logs were randomly selected and transferred from the field in individual plastic bags to the laboratory where they were placed into cloth hanging Berlese funnels with a 40 W halogen light source and insects were collected over 5 days, and preserved in 70% ethanol. Ant, beetle, and termite abundances were measured from collections and identified to the order level.

Table 1

Site climatic and termite characteristics. Average annual temperature and precipitation data were collected at each site using continuously monitoring sensors (HOBO RX3004-SyS-KIT-813 Remote Weather station, Onset, Bourne, MA) and tipping bucket style rain gauges (HOBO RG3-M, Onset, Bourne, MA). Conifer species is the tree type used in the study which also represented the dominant conifer species at each site. Termite densities are characterized from previous studies (Tuma et al., 2020).

Site	Temperature (C)		Precipitation (mm)		Elevation (m)	Conifer species	Diameter (cm)	Bark beetle species	Termite densities
	2017–2018	2018–2019	2017–2018	2018–2019					
Flagstaff, AZ, USA	10.4	16.8	402	585	2105	*Pinus ponderosa*	19.8	*Dendroctonus brevicomis/ adjunctus*	Low
Siguatepeque, HN	21.1	21.9	879	830	1118	*Pinus oocarpa*	23.4	*Dendroctonus frontalis*	Medium
McNeill, MS, USA	18.5	21.6	1085	1403*	74	*Pinus taeda*	20.1	*Dendroctonus frontalis*	High

* Due to malfunction of both rain gauges in MS during 2018–2019, data were obtained from nearby station in Slidell, Louisiana #USW00053865

2.4. Decomposition

Wood decomposition was determined by the change in density prior to deployment and after 1 and 2 years in the field. Briefly, (detailed methods are in Supplementary material), after insect extraction, two ~8 cm^3 cube subsamples of the logs (~2 cm × 2 cm x 2 cm) were cut from the log sapwood and dried at 105 °C for 48 h before weighing (Larson et al., 2001). Volume was determined from exact dimensions of subsamples, and wood density was calculated by dividing the oven dry mass by the calculated volume. Lower wood density indicates increased decomposition. Differences between the initial wood densities and year 1 and year 2 collection times were used to estimate proportion density loss as a measure of decomposition. The decomposition rate constant (k) was calculated as $k = -\ln(Mt/M0)/t$, where Mt = final wood density, M0 = initial wood density, and t = time in years (Olson, 1963). Visual insect damage rating (hereafter VIDR) was also assessed from wood cube subsamples based on an adapted AWPA E1 scale (AWPA, 2018): Briefly, 6 indicated wood was very severely attacked and easily broken and 0 indicated no damage (detailed methods are in Supplementary material).

Proportion change of wood density due to invertebrates was assessed by calculating the median proportion loss of wood density for FC logs (FC_M), both attacked and unattacked, which should only have insects that had colonized wood prior to felling and access to microbes. Then proportion mass loss due to insects (PMI) was calculated as $PMI=HC-FC_M$ or $PMI=NC-FC_M$ for HC and NC logs respectively within both attacked and unattacked treatments.

2.5. Statistical analysis–Insects

To determine how the attacked trees affect decomposition processes across a gradient of climatic and termite densities we used permutational analysis of variance (Permanova). Specifically for each site, we tested the null hypothesis that bark beetle attack (Attack: attacked, unattacked) and covering (Covering: NC, HC, FC) and their interaction had no effect on communities of ants, termites, and beetles. Abundances of ants, termites and beetles were square root transformed and Bray-Curtis dissimilarity measure was used with 9999 permutations in adonis function of the vegan package in R (Oksanen et al., 2015; R Development Core Team, 2019). Significant effects of variables with three or more levels (e.g., Covering) were followed by post-hoc analyses with adjusted p-values using pairwise.adonis wrapper function (Martinez Arbizu, 2020). To determine which insects (e.g., ants, termites, or beetles) were affected following a significant treatment (e.g., Attack or Covering) effect, we used glm with a poisson distribution on each insect's abundance. Post-hoc glms of Attack on insect abundance were restricted to NC and HC logs as FC logs were designed to exclude termites and other macroinvertebrates. We further tested the null hypothesis that there was no relationship between attack status and termite presence at each site using logistic regression in SPSS v. 23 (IBM, 2015). This analysis was also restricted to NC and HC logs. In the text, results are reported as mean ± standard deviation unless otherwise noted.

2.6. Decomposition

We tested the null hypothesis that there were no differences in initial densities between attacked and unattacked trees at each site using t-tests in SPSS. We tested the null hypothesis that change in densities (proportion density loss), absolute densities (actual densities of logs collected, not standardized by initial densities), k, VIDR, and PMI did not differ by Attack, Covering, Year, or their interactions at each site using Permanova. For all five analyses (proportion density loss, absolute densities, k, VIDR, and PMI), we used 9999 permutations and Euclidean distances in the adonis function of the vegan package in R. Significant effects of variables were followed by post hoc analyses as described above. We tested whether VIDR was a good predictor of proportion density loss and whether termite abundance was a good predictor of VIDR using linear regression in SPSS. VIDR and termite abundance were $\text{Log}_{10}(x + 1)$ transformed, and proportion density loss was arcsine transformed to meet assumptions of normality. In text results are reported as mean ± standard deviation unless otherwise noted.

3. Results

3.1. Insects

A total of 127,391 termites, ants, and beetles (hereafter 'insects') were extracted from logs with Mississippi>Honduras>Arizona for both year 1 (43,946, 3852, and 932, respectively) and year 2 (74,886, 3768, and 7, respectively) (Fig. 1). After one year, attacked logs had distinct insect communities. After two years, the effects of the covering treatment became more important in structuring insect communities, while the effects of initial bark beetle attack on insect communities disappeared (Supplementary Table 1).

After one year, attacked logs had 1.7-fold more total insects than unattacked logs in Mississippi (Supplementary Table 1) for HC and NC logs (Supplementary Table 1; Fig. 1), whereas the reverse was true in Honduras: unattacked logs had 2.9-fold more total insects than attacked logs. After two years, effects of bark beetle attack were lost and only covering treatment was significant for Mississippi and Honduras. In both years, Arizona logs had few insects and did not have enough insects to run analyses in year 2, with only 18 and 4 logs with insects in years 1 and 2, respectively. In year 1, there was no difference in the number of insects recovered among treatments (Fig. 2). No termites were collected from Arizona in either year.

3.2. Mississippi

Termite recruitment was highly variable across years and logs (Fig. 1). Termites were 4-times more likely to be found in attacked than unattacked logs (presence/absence: $\chi^2 = 4.510$, df=1, p = 0.034), and

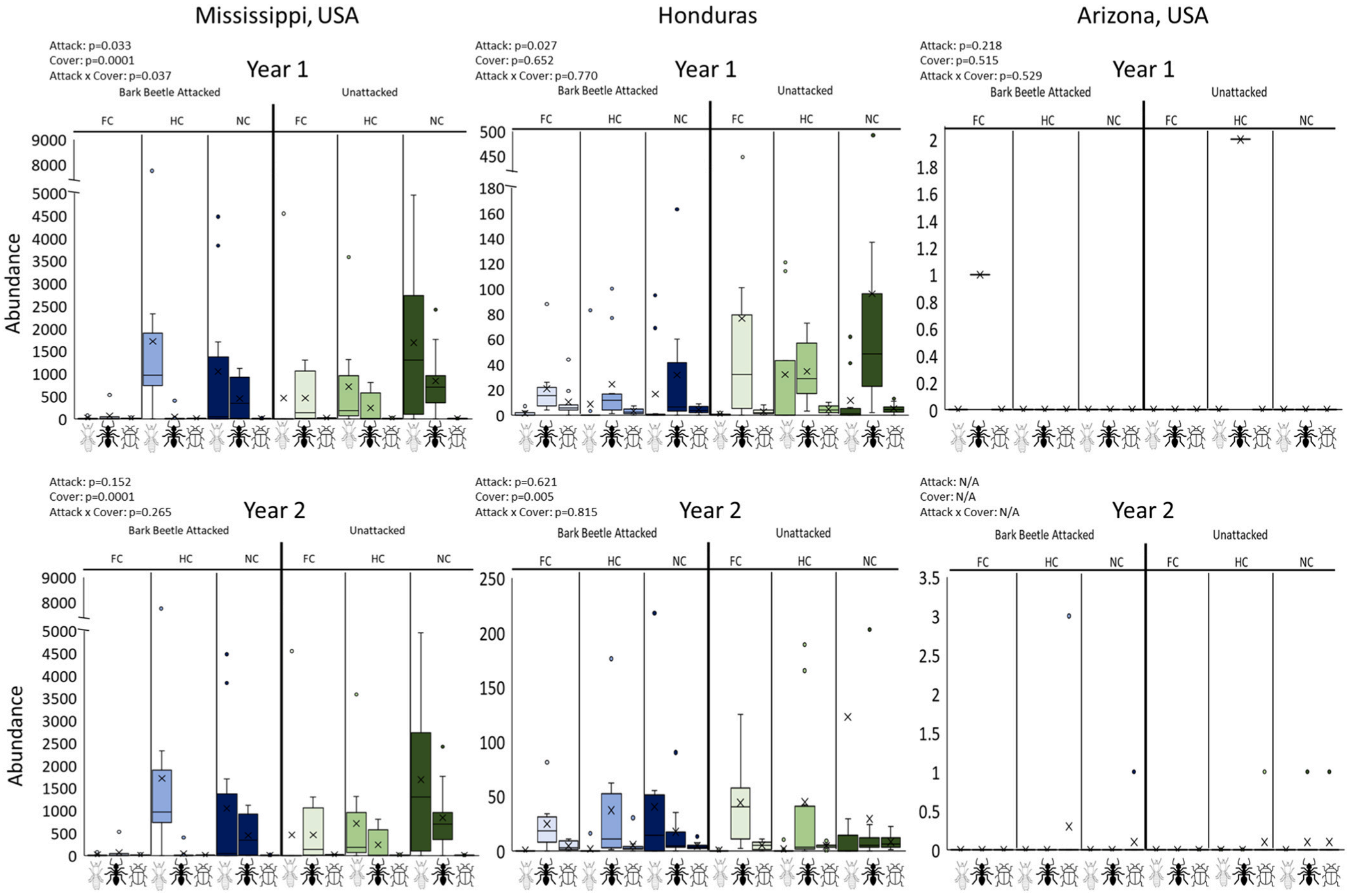

Fig. 1. Boxplots of abundance of termites, ants, and beetles (icons on x-axis represented in that order) for bark beetle-attacked (left side of middle divider: blue boxes) and unattacked (right side of middle divider: green boxes) for fully covered logs (FC: lightest color), half-covered logs (HC: medium saturation) and logs with no covering (NC: darkest color) for all three sites (Mississippi, Honduras, and Arizona) in years 1 and 2. Boxes represent the first (bottom of box) and third (top of box) quartiles, bars represent the minimum and maximum values of the data set not considered outliers. Median is represented by the horizontal line in boxes and mean by the 'x'. Circle points represent outliers (greater or less than 1.5x the interquartile range than the third and first quartiles, respectively). Note that Mississippi Years 1 and 2 and Honduras Year 1 y-axes have breaks to better visualize results.

although termites had ~1.4-fold higher mean abundance on attacked (1322 ± 2024) than unattacked logs (915 ± 1299) across years, the difference was not significant ($p = 0.70$). After one year, attacked logs (1266 ± 2112) had nearly double the mean abundance of termites than unattacked logs (670 ± 1114; $p < 0.001$; Fig. 1; Supplementary Table 1). Conversely, ants were on average 4.9-times (105 ± 153; $p < 0.001$) and beetles were 1.6-times (5 ± 5; $p < 0.001$) more abundant in unattacked logs than attacked logs (21 ± 65 and 3 ± 7 for ants and beetles, respectively). Insects differed in their individual responses: termites were ≥ 3-times more abundant in attacked HC logs than in all other attack and covering combinations ($p \leq 0.001$), whereas ants were most abundant in NC logs and unattacked logs in particular (≥4-times; $p \leq 0.001$), and beetles were most abundant in unattacked FC logs (≥1.7-times; $p \leq 0.001$). After 2 years, ants ($p \leq 0.001$) and termites ($p \leq 0.001$) were most abundant in NC logs, whereas beetles were most abundant in FC logs ($p \leq 0.001$; Supplementary Tables 1 & 2; Fig. 1).

3.3. *Honduras*

Attacked trees did not differ in their likelihood of termite recruitment (presence/absence) from unattacked logs (χ^2 =0.228, df=1, $p = 0.633$), but after one year, termites were 1.6-times more abundant in unattacked logs (20 ± 38) than attacked logs (13 ± 30; $p < 0.001$) and ants were 2.4-times more abundant (unattacked logs: 68 ± 106; attacked logs: 28 ± 42; $p < 0.001$). Mean beetle abundance was similar in unattacked logs (5 ± 4) and attacked logs (4 ± 3; $p = 0.08$). After two years, only the covering treatment resulted in differences in insect communities, with NC differing from HC and FC ($p \leq 0.04$; Supplementary Tables 1 & 2; Fig. 1). Termites were ≥ 59-times more abundant in NC logs ($p < 0.001$), and ants were ≥ 1.14-times more abundant in HC than in other covering treatments ($p \leq 0.04$), whereas beetles were similar among covering treatments ($p = 0.06$).

3.4. *Decomposition*

In general, wood decomposition was fastest in Mississippi after two years ($k = 0.34 \pm 0.24$ (year^{-1}); density loss = 47.5% ± 15.2%), then Honduras ($k = 0.29 \pm 0.12$; density loss = 42.0% ± 13.5%), and slowest in Arizona ($k = 0.10 \pm 0.04$; density loss = 18.1% ± 6.4%; Fig. 2). Attacked and unattacked wood had different initial densities: attacked wood had 10.2% lower density at time of felling in Mississippi but 13.9% greater density in Honduras (Supplementary Table 3; Supplementary Fig. 1). Overall, decomposition of attacked logs was similar (density loss = 26.4% ± 19.7%; $k = 0.22 \pm 0.19$; VIDR = 4.6 ± 2.2) to unattacked logs (density loss = 25.7% ± 16.3%; $k = 0.21 \pm 0.13$; VIDR = 4.9 ± 2.0), but patterns of decomposition differed by site and changed over time (Supplementary Table 4). Initially, attacked logs decomposed slower (Year 1: density loss = 15.7% ± 10.7%; $k = 0.18 \pm 0.14$) than unattacked logs (density loss = 17.3% ± 11.1%; $k = 0.20 \pm 0.14$), but decomposed faster than unattacked logs between years 1 and 2 resulting in a slightly higher density loss in year 2 averaged across all sites (density loss in year 2: 37.0% ± 19.0% vs. 34.4% ± 16.4%; k: 0.27

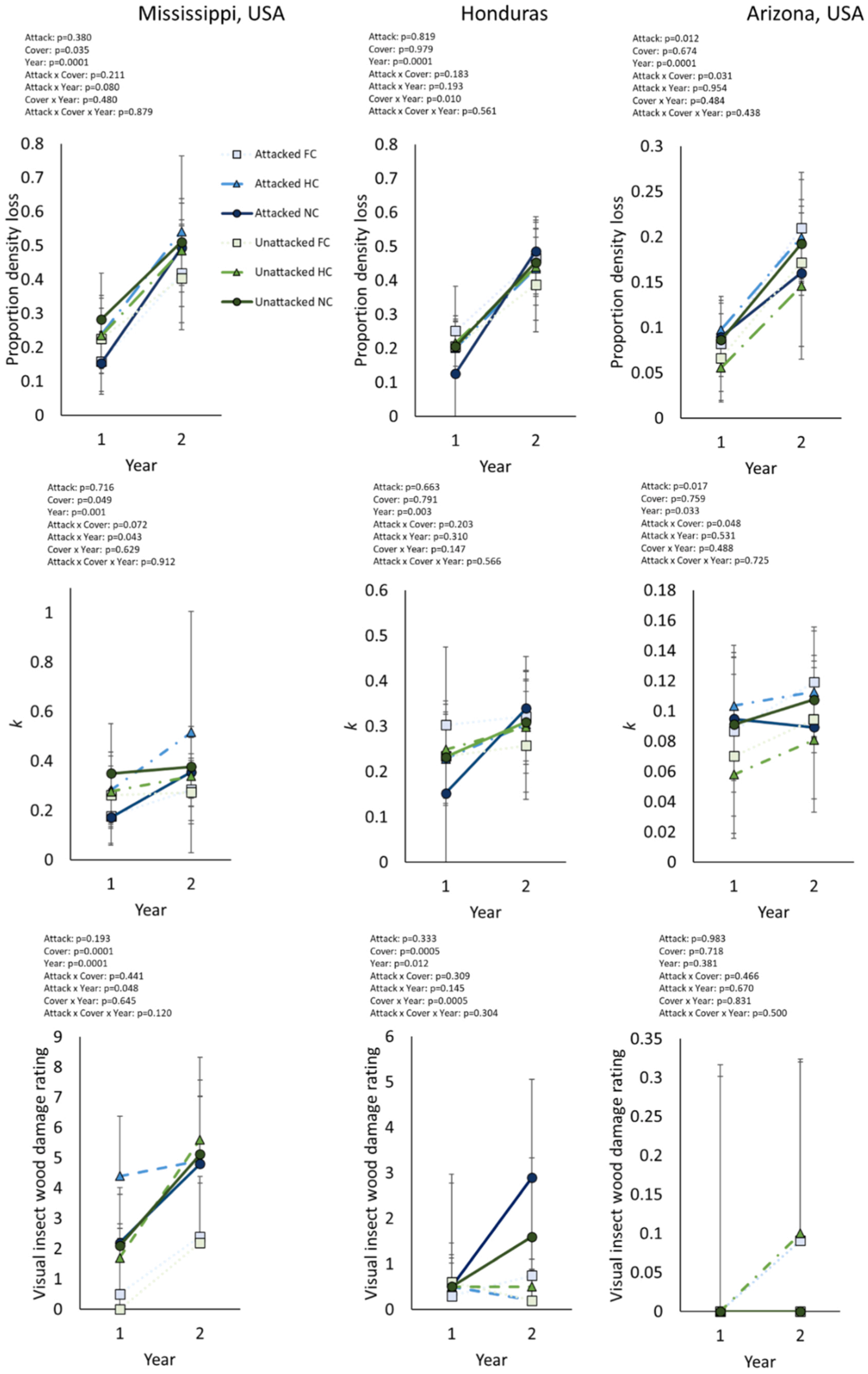

Fig. 2. Mean change in density (proportion density loss) (top panels), mean *k* (decomposition constant) (middle panels), and mean visual insect wood damage rating (bottom panels) for bark beetle-attacked trees (blue symbols and lines) and unattacked trees (green symbols and lines) for each cover treatment: full cover (FC), half cover (HC) and no cover (NC) across years and sites. Error bars represent standard deviation: only positive standard deviation bars are shown for visual insect wood damage rating for clarity.

± 0.23 vs. 0.23 ± 0.14; for attacked and unattacked respectively; Supplementary Tables 4 & 5; Fig. 2). VIDR accounted for 30% of the variation in density loss ($p < 0.001$; Fig. 3) and termite abundance accounted for 51% of the variation in VIDR ($p < 0.001$; Fig. 3).

3.5. *Mississippi*

Wood density loss, k, and VIDR increased over time and had a marginal-to-significant interaction between attack and time where attacked log decomposition rate increased by 1.8-fold between years 1 and 2, whereas unattacked log decomposition rate was similar between years (1.1-fold increase; Supplementary Tables 5 & 6; Fig. 2). After one year, the density loss of attacked wood was 6% lower than unattacked wood, regardless of covering treatment (Fig. 2; Supplementary Table 5). Similarly, when absolute densities of wood at year 1 were examined, there was no difference between attacked and unattacked wood after one year despite initial differences (Supplementary Table 7; Fig. 4). k had a marginal interaction between attack and cover treatment: k was similar over time for unattacked logs, but k increased in attacked NC and HC logs in year 2 (Supplementary Table 6; Fig. 2). After two years, decomposition of attacked logs was 1.2-fold faster ($k = 0.39 \pm 0.31$) than unattacked logs ($k = 0.33 \pm 0.13$; Supplementary Tables 5 & 6; Fig. 2), and density loss of attacked (48.4% ± 17.2%) and unattacked logs (46.5% ± 13.0%) did not differ. Absolute wood density was marginally (13.4%) lower in attacked wood than unattacked wood (Supplementary Table 7; Fig. 4). Density loss differed marginally by covering treatment and was consistent between attacked and unattacked logs (Supplementary Table 5; Fig. 2). Specifically, FC logs had 19.9% less density loss than HC logs and 18.0% less density loss than NC logs, however, there was no difference between NC and HC logs (Supplementary Table 8). Insects in both years significantly increased decomposition (Fig. 5) with the largest PMI (11.1% ± 17.2%) in attacked HC logs (Supplementary Table 9).

3.6. *Honduras*

Wood density loss, k, and VIDR increased over time and density loss and VIDR had a significant interaction between covering treatment and time. k increased 1.7- and 1.2-fold between years 1 and 2 for NC and HC logs, respectively, whereas k did not change over time for FC logs and VIDR only increased for NC logs between years 1 and 2 (Supplementary Tables 5–8; Fig. 2). After one year, attacked and unattacked wood did not differ in density loss regardless of covering treatment or time (Fig. 2; Supplementary Table 5). Similarly, when absolute densities of wood were examined, unattacked wood remained less dense than attacked wood, similar to initial differences (Supplementary Table 5; Fig. 4). After two years, there was no difference in density loss of attacked (46.3% ± 11.7%) and unattacked logs (42.7% ± 11.7%) or by covering treatment; however absolute wood density no longer differed between attacked and unattacked wood (Supplementary Tables 5 & 7; Fig. 4). Insects contributed little to density loss after one year for unattacked logs (1.5% ± 6.8%), but significantly decreased density loss in attacked logs (−9.6% ± 12.9%). Similarly, PMI increased over time across attack and covering treatments (Supplementary Table 9; Fig. 5).

3.7. *Arizona*

Wood density loss and k increased over time and was greater in attacked wood (density loss = 14.3% ± 7.6%; $k = 0.10 \pm 0.04$) than unattacked wood (density loss = 11.8% ± 7.1%; $k = 0.08 \pm 0.04$) and had a significant interaction between attack and covering treatments (Supplementary Tables 5 & 6; Fig. 2). VIDR did not change across time or treatments (Supplementary Tables 5 & 6; Fig. 2). After one year, attacked wood had 1.3-fold higher density loss and k than unattacked wood regardless of covering treatment (Fig. 2). Similarly, absolute densities of attacked logs remained lower than unattacked logs, but differences were dependent on covering treatment (Supplementary Table 7; Fig. 4). Specifically, attacked FC logs tended to have greater absolute densities than HC and NC logs, whereas unattacked NC had greater densities than other covering treatments (Fig. 4). After two years, density loss of attacked logs was still slightly greater (1.1-fold) than unattacked logs. Attacked NC logs had marginally lower density loss than attacked HC and NC logs (1.2- and 1.3-fold, respectively), and unattacked NC logs had 1.3- and 1.1-fold higher density loss than unattacked HC and NC logs, respectively (Fig. 2). Moreover, absolute wood density did not differ between attacked and unattacked wood, except for some covering treatments (Fig. 4). Specifically, attacked FC logs had lower densities than attacked NC logs and unattacked HC logs had higher densities than either FC or NC logs. Similarly, k was higher in year 2 than year 1 for all treatments (Fig. 2). Insects contributed little to density loss and had a negative effect after one year (−5.8% ± 6.7%), that increased substantially after two years (−20.2% ± 9.5%), particularly for unattacked logs (−26.6% ± 6.7% and −13.8 ± 7.4% for

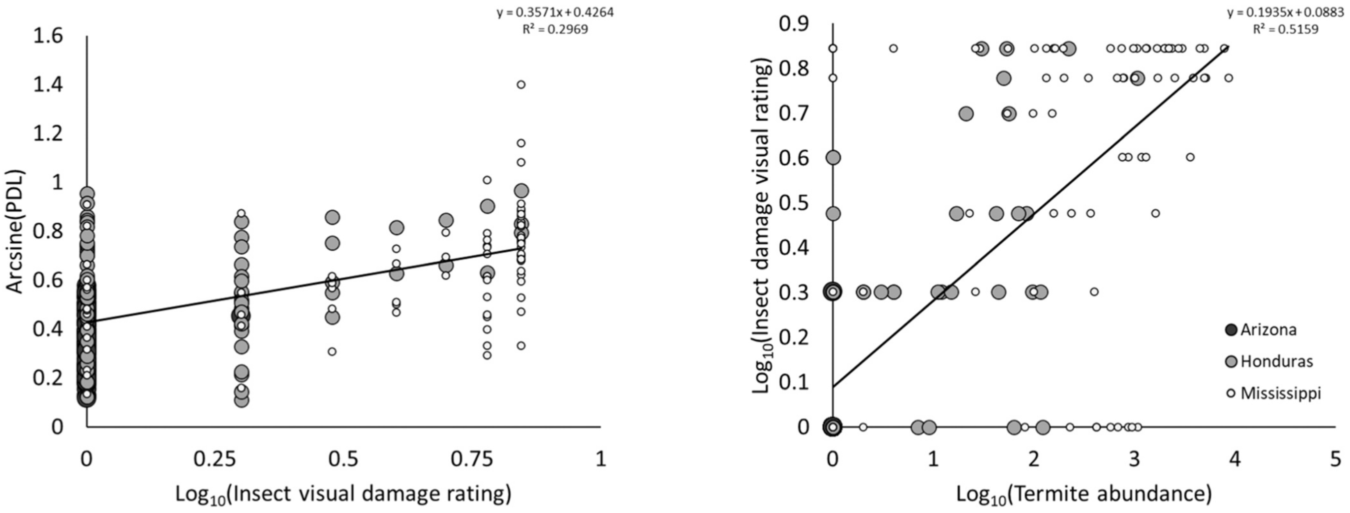

Fig. 3. Regressions of insect visual damage rating (Log$_{10}$(x + 1) transformed) as a predictor of proportion density loss (PDL: arcsine transformed) (left panel) and termite abundance (Log$_{10}$(x + 1) transformed) as a predictor of insect damage visual rating (right panel). Regression equations and R^2 values are reported on graphs. Values for Arizona are large dark grey circles, Honduras is represented by medium sized medium grey circles and Mississippi by small white circles. Values are only for HC and NC logs.

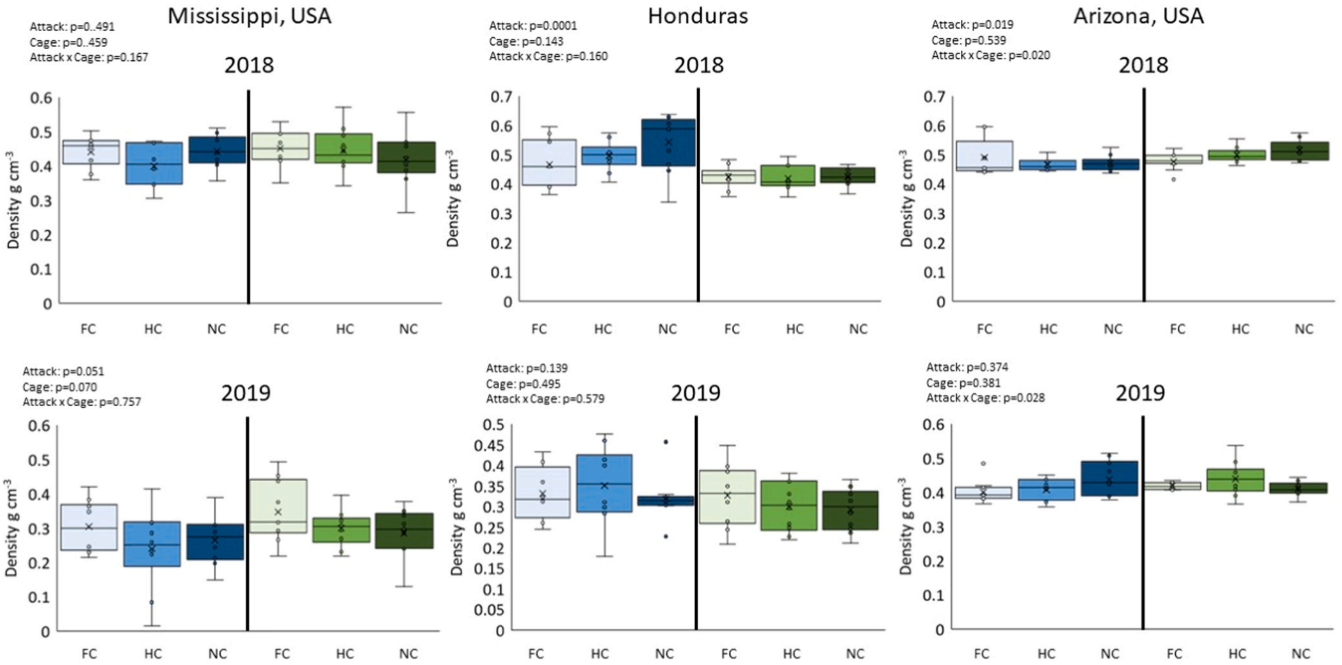

Fig. 4. Wood densities measured after one year (2018) and two years (2019) from full cover (FC), half cover (HC) and no cover (NC) treatments across all three sites. Bark beetle-attacked wood is on the left side of each panel for blue boxes, and unattacked wood is on the right side of the divide of each panel in green boxes. Here, density is not corrected from initial measurements and represents absolute density.

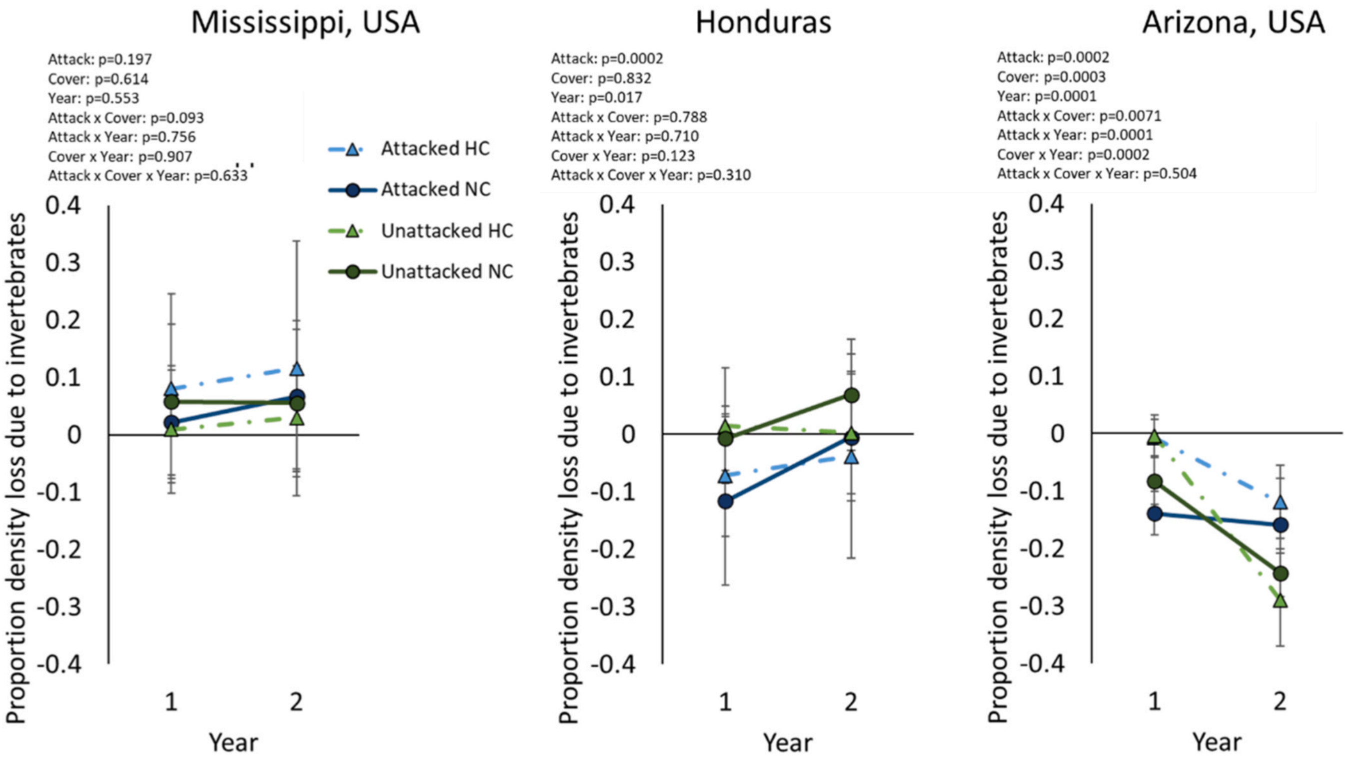

Fig. 5. Mean proportion density loss due to invertebrates of bark beetle-attacked trees (BB (Bark Beetle attack): blue symbols and lines) and unattacked trees (NB (No Bark beetle attack): green symbols and lines) for each of the cover treatments: full cover (FC), half cover (HC) and no cover (NC) across years and sites. Positive values indicated that invertebrates increased density loss (i.e., the proportion of density loss due to invertebrates increased relative to when only microbes were able to colonize). Negative values indicate that invertebrates reduced the proportion density loss relative to when only microbes were able to colonize.

unattacked and attacked respectively) and for HC logs (Supplementary Table 9; Fig. 5).

4. Discussion

Studies experimentally testing factors affecting deadwood decomposition and biodiversity are limited in quantity and geographical extent with most in temperate and boreal zones, and even fewer testing explicit ecological hypotheses (Seibold et al., 2015; but see Seibold et al., 2023). Our study spanned 20.6° latitude and 24.0° longitude and tested the effects of bark beetle tree attack on the subsequent decomposition and saproxylic communities of deadwood from temperate to tropical forests and predicted that the indirect interaction between bark beetle attack and termites mediated through bluestain fungi would drive decomposition patterns. We found evidence that biotic factors, likely driven by termites, generated site-specific spatiotemporal decomposition patterns. Our results suggest that climate alone is not sufficient to predict C flux in earth system models (Bradford et al., 2014), particularly if the cause of deadwood input is bark beetle attack. In Arizona, attacked logs consistently decomposed faster than unattacked logs. In Mississippi, attacked logs initially decomposed slower than unattacked logs followed by a faster decomposition rate of attacked logs than unatacked logs that led to similar density loss after two years. In Honduras, attacked log decomposition did not differ from unattacked logs. Effects of bark beetle-attack on saproxylic insects were site-specific: attacked logs harbored more insects in Mississippi and fewer in Honduras, and this was largely driven by termites. In Mississippi, where the greatest wood decomposition occurred, termites were 4-times more likely to be found on attacked logs than unattacked logs. Saproxylic insect-driven wood damage accounted for 30% of the variation in log density loss across sites and termite abundance accounted for 52% of the variation in VIDR. This supports growing evidence that decomposers like termites strongly impact the decomposition trajectory of deadwood, even outside of the tropics (Bradford et al., 2014, 2021; Ulyshen et al., 2014). Our results demonstrate that quantification and incorporation of biotic effects on deadwood decomposition is necessary to understand how disturbances like bark beetles impact C cycling and ecosystem productivity (Schuurman, 2005; Oleson et al., 2013).

Bark beetle attack altered deadwood successional patterns likely through their initial impacts on wood properties and mediated by associated fungal symbionts. For example, following bark beetle attack wood has reduced modulus of rupture and elasticity, increased hyphal colonization through and between wood cell lumina, and increased water uptake (Little et al., 2013b; Hýsek et al., 2021). These initial conditions such as wood density and presence of fungal symbionts may have led to strong deterministic and priority effects (Fukami et al., 2010; Weslien et al., 2011; Strid et al., 2014). Specifically, saproxylic insects can better colonize wood with tunneling (e.g, from beetle activity), bark sloughing, and lower density (Shea et al., 2002; Zuo et al., 2016). The initial attacked wood density was lower than unattacked wood in Mississippi and may partly explain its greater insect abundance after one year, and the reverse was true for Honduras, where attacked logs had higher initial wood densities (Supplementary Fig. 1). Additionally, termites were both more abundant and occurred more frequently on attacked than unattacked logs in Mississippi, which may be driven by increased wood moisture content (e.g., Bradford et al., 2021). However, termites often competitively reduce the presence and activity of decay fungi which can initially slow decomposition (Jayasimha and Henderson, 2007a; b; Bradford et al., 2021; Dossa et al., 2021). Subsequent insect and microbe interactions and colonization likely resulted in the steep increase in decomposition rates of attacked, but not unattacked logs between years 1 and 2 in Mississippi (Fukami et al., 2010; Weslien et al., 2011; Hýsek et al., 2021). The initial lag in wood density loss in Mississippi may mitigate forest C release due to tree death following bark beetle attacks and facilitate increased saproxylic biodiversity via easier wood colonization (Edburg et al., 2011; Lassauce et al., 2011). However, if decomposition rates continue to be faster for attacked wood in Mississippi and Arizona, this could further accelerate C cycling in bark beetle-attacked forests (Edburg et al., 2011).

Priority effects likely impacted insect abundances and proportion density loss. Specifically, the exclusion of initial saproxylic beetle colonizers in HC logs could have facilitated subsequent invertebrate and microbial colonizers that would have otherwise been excluded due to competition with secondary bark beetle symbiotic fungi (Weslien et al., 2011). Interestingly, insect communities became more similar over time, in alignment with recent saproxylic invertebrate succession experiments (Zuo et al., 2021; but see Seibold et al., 2023). However, our results are limited to just two years of decomposition and further changes may emerge over longer time scales. Our results demonstrate that bark beetle impact on successional patterns is site-specific and thus additional research is needed to generate a predictive framework for understanding the impact of these globally distributed biotic disturbance agents.

Our results suggest a suite of complex biotic and abiotic interactions mediate invertebrate contributions to wood decomposition. Differences in insect activity accounted for 30% of the variation in wood decomposition (VIDR; Fig. 3) but their effects varied across sites and often differed between attacked and unattacked logs (Fig. 5). Insect activity consistently increased wood decomposition in Mississippi with marginally more insect-driven density loss in attacked HC wood, likely due to lower initial wood density and the exclusion of saproxylic beetles and their fungal symbionts (Weslien et al., 2011). Of note, unattacked FC logs in Mississippi had significant numbers of beetles. Likely larvae were present in trees prior to felling or beetles may have found a way through the mesh covering or been able to oviposit through mesh as coverings were tight around wood. Regardless, beetles had little impact on decomposition (VIDR: 0 ± 2.3 and 2.2 ± 2.0 for yrs 1 and 2, respectively). In Honduras, invertebrates consistently had a greater impact on unattacked than attacked wood decomposition, which was initially less dense than attacked wood (Supplementary Fig. 1), and attacked wood exposed to invertebrates (NC) decomposed slower than FC logs in Honduras after one year (Fig. 5). In Arizona, all wood exposed to insects decomposed slower, particularly unattacked wood. This suggests negative species interactions occurred among invertebrates and fungi, which likely inhibited fungal growth and activity. Alternatively, it is possible that microclimate differences could have favored fungi in FC treatments. However, if the covering itself was driving effects, we would have expected to see similar results at all sites and for HC treatments, neither of which occurred. Our results indicate that microbial-insect interactions may significantly impact decomposition patterns and vary considerably across sites and from bark beetle attack.

This study suggests that complex interactions govern deadwood decomposition following bark beetle attack but has several potential caveats. First, we only felled a single bark beetle-attacked tree and unattacked tree at each location. This enabled us to reduce variation that may exist due to chemical, physical, and biotic changes to trees that occur following bark beetle attack and time since attack (Hýsek et al., 2021). However, future studies should systematically test the impacts of these potential sources of variation on deadwood decomposition. Second, we felled still standing trees prior to 'natural mortality' and placed logs with cut side facing soil. Both may vary in their ability to reflect natural processes but were essential to experimentally test impacts of bark beetle attack on deadwood decomposition under logistical constraints. Additionally, this process also mimics 'cut-and-leave' management strategies employed to mechanically control bark beetle populations (Billings, 2011). Lastly, longer experiments on larger deadwood across more sites are needed to determine the geography of bark beetle-mediated deadwood decomposition.

This study has implications for forest management. The frequency and intensity of natural disturbances that ultimately create deadwood through increased tree mortality are predicted to increase with global change (Gan, 2004; Kurz et al., 2008; Edburg et al., 2011). As part of the Forest Inventory and Analysis program of the Unites States Forest Service, deadwood inventories are regularly collected and data are used to inform National Greenhouse Gas Inventories and data are essential for understanding the condition and status of forest resources (Woodall et al., 2019). Our data suggest that mortality following bark beetle-attack may alter deadwood residency times and impact forest C cycling. Moreover, cut-and-leave management, where infested trees plus a buffer of green uninfested trees around the area of infestation currently under attack within a bark beetle spot (>30 beetle-infested trees) are felled toward the center of the infestation and trees are left on the ground has been increasing since the 2000 s in the USA and is the most widely used control tactic in Central Ameria (Gomez et al., 2020; Clarke et al., 2021). Our study mimicked this management strategy and suggests that deadwood residency rates vary by site and attack versus cut-and-remove, where the felled trees are removed typically for salvage logging, this deadwood resource would not be available and may change forest nutrient and regeneration patterns. Deadwood produced from bark beetle-attacked trees may also harbor distinct saproxylic communities and thus contribute to the maintenance and stability of forest biodiversity (Lassauce et al., 2011; Seibold et al., 2015).

5. Conclusions

Disturbances like bark beetle epidemics are important mediators of the terrestrial C cycle. Surprisingly, relatively few studies have examined the impact of insect disturbance on deadwood succession decomposition dynamics (Clay, 2023). Here we found site-specific impacts. Arizona (northernmost, westernmost, and highest altitude site) had consistently higher decomposition of attacked than unattacked wood. In Mississippi (mid-latitude and longitude but lowest altitude site), attacked wood had initially slower but then faster rates of decomposition. In Honduras (southernmost, easternmost, and mid-elevation site), bark beetle attack had no effect. This may suggest a geography of bark beetle-mediated impacts on deadwood decomposition where outbreaks in western and higher latitude forests result in accelerated carbon cycling. More studies that span ecological, longitudinal, and latitudinal gradients are needed to test this potential pattern.

Declaration of Competing Interest

JR is an inventor on a patent involving bluestain fungi in baiting methods for termites (US9924706B2). Author and their institutions may financially benefit from this patent.

Data availability

Data will be made available on request.

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Author Contributions

N. Clay, J. Riggins, C. Siegert, J. Tang conceived of and executed the experiment and provided funding. O. Leveron and R. Hoffstetter provided logistical support for fieldwork. J. Thomason, O. Leveron, R. Hoffstetter, N. Benedetto, and J. Dutton, helped with field and lab work. N. Clay analyzed the data and wrote the manuscript. All authors contributed to writing the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121636.

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