Bark coverage and insects influence wood decomposition: Direct and indirect effects

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ABSTRACT

Rates of terrestrial wood decomposition are known to vary widely depending on regional and local climatic conditions, substrate characteristics and the organisms involved but the influence of many factors remain poorly quantified. We sought to determine how bark and insects contribute to decomposition in a southeastern U.S. forest. Open-topped stainless steel pans with screened bottoms were used to prevent subterranean termite (Rhinotermitidae: *Reticulitermes* spp.) colonization from "protected" logs. After a 20-month study period, we compared mass loss and lignin content between these and logs assigned to "unprotected" treatments that permitted termite colonization. The experiment was repeated for 1) logs from which bark had or had not been initially removed and 2) logs with sealed or unsealed ends. Logs with bark lost significantly (∼2.4-fold) more mass than those without bark, likely due to the moisture-conserving properties of bark. Logs with unsealed ends lost significantly more mass than those with sealed ends. There was no significant difference in mass loss between protected and unprotected logs but logs with visible termite activity lost significantly more mass than those without termite damage. Few differences in lignin content were detected in this study but when logs with bark were analyzed separately, those with visible damage from long-horned beetles (Coleoptera: Cerambycidae) had lower lignin content than those without cerambycid activity. This suggests that cerambycids may promote decomposition indirectly through interactions with fungi or other organisms capable of degrading lignin. Our results suggest that insects can have significant direct and indirect effects on wood decomposition and clearly demonstrate the importance of bark in determining wood decay rates and insect activity.

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1. Introduction

Although woody debris represents a major terrestrial carbon store (Cornwell et al., 2009) and supports at least one fifth of forest insect biodiversity (Elton, 1966; Stokland et al., 2012), the importance of insects to its decomposition remains poorly understood. Insects associated with dead wood can be assigned to various functional groups including phloem and wood feeders, fungus and detritus feeders and predators. Different species are active at different stages of decomposition and all taxa have the potential to influence decomposition either directly or indirectly through interactions with other species (Ulyshen, 2016). Many of the first insects to colonize recently dead wood are known to

vector spores or mycelia of rot fungi or facilitate the movement of fungi into logs, for example, with the potential to thereby indirectly affect decomposition and alter the composition of future fungal communities (Jacobsen et al., 2015; Leach et al., 1937; Persson et al., 2009; Strid et al., 2014). Social insects (ants and termites) commonly dominate saproxylic insect communities and may exert considerable influence on wood decomposition and related processes. In warmer climates, for example, termites are often among the most numerous insects found within dead wood (King et al., 2013) and have been shown to consume larger volumes of wood than all other insects combined (Ulyshen et al., 2014). While termites continue to receive a great deal of attention from researchers as important structural pests in urban areas, little is known about their ecology in forested systems (Maynard et al., 2015) and only a handful of studies have attempted to quantify their contributions to the decomposition of naturally-occurring woody substrates (Ulyshen, 2016).

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Methodological issues continue to impede efforts to quantify the role of insects in terrestrial decomposition. The most critical of these is the persistent challenge of excluding invertebrates without otherwise affecting microclimatic conditions known to influence microbial decomposers. According to Kampichler and Bruckner (2009), for example, this methodological issue renders more than 50 years of litterbag research inconclusive. Studies aimed at quantifying the contributions of insects to wood decomposition suffer from the same problem, with mesh bags, insecticides and other insect-exclusion methods known to alter microbial activity compared to unprotected substrates (Stoklosa et al., 2016; Ulyshen and Wagner, 2013). Differences in microclimate between treatments in such studies may be minimized by focusing on select taxa instead of attempting to exclude all invertebrates. In Finland, for example, Müller et al. (2002) showed that bark beetles promoted decomposition in spruce logs by only briefly exposing one set of logs to colonization by these insects. For the rest of the experiment, these logs were enclosed within cages identical to those used in the control treatment. In Malaysia, Takamura and Kirton (1999) and Takamura (2001) excluded termites by placing sections of wood in small trays with screened bottoms. The open-topped design allowed other insects to colonize the logs, thereby underestimating the total insect effect, but minimized differences in microclimate between treatments.

Wooden stakes or blocks of standardized dimensions have long-been used in applied termite research as a way to compare feeding preferences among tree species or chemical treatments (Bultman and Southwell, 1976). Wooden blocks have also been used to study the role of termites in decomposition but are not representative of naturally-occurring substrates (Ulyshen and Wagner, 2013; and references therein). Most importantly, wooden blocks lack the cambium and bark layers which are required by a diverse assemblage of phloem- and wood-feeding insects as a food resource and oviposition substrate (Stokland et al., 2012). In addition to their tunneling activities, these species are known to play an important role in facilitating fungal colonization (Leach et al., 1937) and can have lasting priority effects (Weslien et al., 2011). Whether or not bark is present may also influence microbially-driven decomposition, either positively or negatively. As suggested by Cornwell et al. (2009), bark may limit microbial access to wood during the initial stages of decomposition but may ultimately have a positive effect by enhancing moisture retention. To our knowledge, the role of bark in determining wood decay rates remains untested. Cut surfaces are a typical trait of dead wood in managed forests resulting from harvesting. These open areas may allow colonization of certain wood-decaying fungal species and reduce the importance of insects for vectoring and giving access to fungi. At the same time, such logs may dry out more quickly which may negatively influence microbial activity. The overall effect of cut ends on wood decomposition remains unclear.

Here we present the results from the fourth study in a series of experiments aimed at estimating the contributions of insects to wood decomposition in the southeastern United States. In the first study, termites were found to consume 15–20% of wood volume from pine logs over a several year period but unexpectedly had no effect on mass loss (Ulyshen et al., 2014). These results may either reflect an inhibition of microbial decomposers by insects or a stimulatory effect of the insecticide used to exclude termites. The second study, using stainless steel mesh bags to exclude insects, found insects to be responsible for ~14–20% wood loss in unflooded and seasonally flooded forests (Ulyshen, 2014). Due to uncertainties about how the mesh bags may have affected these results, a third study sought to specifically test for the mesh effect while measuring the contributions of insects to fine woody debris loss. Because the mesh bags were found to increase moisture levels and speed up wood decomposition, it was concluded that insects

contribute more to the process than the observed value of 9–10% (Stoklosa et al. 2016). These findings support the notion that insects contribute importantly to decomposition but also underscore the need for alternative exclusion methods less likely to alter microclimatic conditions.

In the current study, we tested a modification of the open-topped tray first used by Takamura and Kirton (1999) for excluding termites from experimental logs. Because logs placed in such trays are completely exposed from above to flying insects, this approach can only speak to the effects of termites and other excluded soil invertebrates on decomposition. By largely eliminating any microclimatic differences between treatments, however, this approach has the potential to produce reliable estimates on how termites affect decomposition. In a subtropical southeastern U.S. forest, we tested the hypotheses that (i) termites significantly accelerate wood decomposition; (ii) wood with bark decomposes significantly faster than wood without bark; (iii) bark coverage and termites interact to affect decay rates, with bark coverage stimulating termite activity; and (iv) termites more strongly affect the decomposition of logs with sealed ends relative to those with unsealed ends. Two metrics were used to measure decomposition in this study. The first was mass loss which is commonly used in developing decay models. The second was lignin content. Lignin is largely responsible for the strength of the lignocellulose complex comprising wood and constrains decay rates. The degradation of lignin is thought to be largely driven by fungi and other microbes but the activities of these organisms can potentially be impacted by interactions with wood-dwelling insects (Ulyshen, 2016).

2. Materials and methods

2.1. Study location and design

The experiment took place in a mixed pine/hardwood forest on the Noxubee Wildlife Refuge, Noxubee Co., Mississippi, U.S.A. (33°14′56.1″N 88°46′07.3″W). The climate of the region is classified as humid subtropical with annual precipitation and temperature averaging 140 cm and 16.9 °C, respectively (usclimatedata.com, accessed 3-Nov-2015). The 72 logs used in this study came from 14 sweetgum (*Liquidambar styraciflua* L.) trees felled for this purpose at a single Mississippi location on 28 May 2013. The logs were 35 cm in length and were, on average, 8.5 ± 0.2 cm in wood diameter (not including bark). Immediately preceding and following each log, 10-cm-thick disks were cut. Measurements made on these subsamples were used to estimate the initial dry weight (without bark), initial cross sectional area and initial specific gravity of each log (see Section 2.2). In order to test the role of bark in decomposition, bark was removed from half the logs at the beginning of the experiment. In addition, the ends of half the logs with bark and half of those without bark were sealed with three layers of black plastic and secured in place with wire to test how this would affect the observed effect of termites on decomposition.

A row of six locations (replicate blocks) was established approximately 100 m from and parallel to the forest edge, with locations separated from one another by ~10 m. Six plots were established at each location, arranged in two rows and three columns and separated from one another by about 1 m. The six plots at each location were randomly assigned to one of six treatments consisting of a pan/termite factor with three levels and a bark factor with two levels (i.e., with or without bark). Regarding the pan factor, two plots received a stainless steel pan (Vollrath Super Pan V item number 30022, $52.7 \times 32.4 \times 6.5$ cm) with closed mesh bottoms ("closed pans") to prevent colonization by termites. Two other plots received identical pans with open mesh bottoms ("open pans") to permit termite access. The remaining two plots

were assigned to the "no pans" treatment where logs were placed in direct contact with the forest floor (Fig. 1A). A rectangular opening measuring 40.6 cm × 20.3 cm was cut in the bottom of each pan using a plasma cutter. The stainless steel mesh used in closed and open pans had 0.3 mm openings, a mesh size shown in previous work to be effective at excluding termites (Ulyshen, 2014). Galvanized bolts were used to securely pinch the mesh between the pans and strips of aluminum in the closed pans to prevent any termite entry. The open pans were lined with the same mesh but with the addition of three rectangular openings (2.5 × 19 cm and separated by 7.5 cm) designed to permit termite entry (Fig. 1A).

Two logs were added to each pan × bark combination, one with sealed ends and one with unsealed ends as described above. In total there were 12 logs at each of the six locations and 72 logs overall (Fig. 1A). At the beginning of the experiment, leaf litter was cleared away at the center of each plot in order to place the treatments in contact with the mineral soil. Care was taken to ensure that no leaves, stems of other structures would allow termites to climb into the closed pans. As the experiment got covered in leaves each autumn, it was necessary to clear around the outside edges of the pans to prevent termite access each winter. Leaves that fell into the pans were left in place to better match natural conditions, however.

2.2. Wood measurements

The 10-cm-thick disks cut on both sides of each log were initially weighed with and without bark and before and after drying to a constant weight at 65 °C. These data were used to calculate the proportion of initial disk weight consisting of dry wood (i.e., (dried disk weight without bark)/(initial disk weight with bark)). After removing bark from the disks but before drying them, disk tracings were made on sheets of paper for use in quantifying the cross-sectional surface area of each disk (using image analysis software). Also before drying, the disks were submerged in a water bath placed on top of a tared scale to determine the volume of each. Dried disk weight without bark and these volume measurements were used to calculate specific gravity for each disk. By averaging these data for the two disks adjacent to each log, we were able to estimate the initial dry wood weight (without bark), initial cross sectional area and initial specific gravity for the experimental logs. Initial dry wood weight without bark (drywoodwt) was estimated for each log from measured initial wet weight with bark (logwetwt) using the following equation: drywoodwt = logwetwt × x, with x representing the proportion of intial disk weight consisting of dry wood as averaged across the two disks.

At the end of the experiment (27 January 2015, after 20 months in the field), the logs were returned to the laboratory, cleaned of bark and soil, when necessary, and then weighed. For each log, we recorded the presence/absence of ongoing or past termite (Reticulitermes spp.) activity. We also recorded the presence/absence of feeding galleries created under the bark by cerambycid larvae. Some cerambycid larvae were collected and reared to adulthood for identification. Cerambycids were only observed in logs with bark which is consistent with the life history characteristics of the family (eggs are typically laid on the bark and larvae, upon hatching, bore through the bark and feed within the underlying phloem layer). Observed cerambycid galleries were limited to the phloem and outermost layers of sapwood, i.e., tunnels bored into the wood were not observed. Because other invertebrate species were less regularly observed, or caused less recognizable damage, our analysis of invertebrate activity was limited to termites and cerambycids. The logs were dried to a constant weight at 65 °C and those exhibiting heavy termite damage were burned to isolate termite-imported soil, i.e., to correct for this in the final dry weights (Ulyshen and Wagner, 2013). Prior to burning, all logs were cut in half and photographs were taken of the resulting cross-sections. A grid was superimposed on these images to calculate the area of visible termite damage. These data were compared between logs assigned to the "open pan" and "no pan" treatments to determine if termite activity within logs placed in open pans is representative of that occurring naturally. Wood samples were collected from the centers of these logs using an electric drill. One hole (~1 cm diameter × 9 cm deep) was drilled lengthwise into the center of one half of each log. The wood shavings were ground into a fine powder using a Wiley mill and these samples were submitted to the Agricultural and Environmental Services Laboratories at the University of Georgia for determination of percent lignin. The final response variables were termite incidence (evidence of past or current activity), cerambycid incidence (presence of past or current activity), termite damage (% of grid cells with visible damage in cross section), mass loss (initial wood weight − final wood weight/ initial wood weight), percent water (wet wood weight − dry wood weight/dry wood weight) and percent lignin.

2.3. Data analysis

We first sought to determine whether the open pans measurably affected termite activity or water content relative to logs placed in direct contact with the forest soil. We compared the following variables between the "open pan" and "no pan" treatments in preliminary models from which the "closed pan" treatment was excluded: termite incidence (presence/absence), termite damage visible in cross section (limited to logs with termite activity) and water content (dry weight basis). Termite incidence was compared using Fisher's exact test. Termite damage visible in cross section was compared using ANOVA (limited to logs

Fig. 1. (A) One replicate location after installation. (B) Examples of insect damage visible at the end of the experiment. The top log in this image was assigned to a closed pan and had visible cerambycid damage beneath the bark. The log below was assigned to an open pan where it was heavily attacked by termites (the inset shows damage visible in cross-section).

with visible termite activity, no transformations were necessary to satisfy assumptions). Water content (dry weight basis) was compared using ANOVA on log-transformed data. Because no significant differences were detected between the open pan and no pan treatments (see Section 3), they were combined into a single "unprotected" treatment for all subsequent analyses. As intended, the "closed pans" were successful at excluding termites (see Section 3) so logs assigned to this treatment were effectively "protected" from these insects.

We analyzed the dataset in three different ways to explore the effects of insects on decomposition. The first consisted of comparisons between termite protection treatments (protected vs. unprotected), irrespective of visible insect activity, as defined above. The response variables were mass loss, percent lignin and water content (dry weight basis). Data were analyzed using the proc mixed procedure of SAS (SAS Institute, 1999) with termite protection, bark (with vs. without) and ends (sealed vs. unsealed) as fixed effects. Location and location × protection × bark were treated as random effects to account for the fact that logs belonging to each of the end treatments were grouped together by protection/bark combination (Fig. 1A). The complete initial model included initial specific gravity and initial cross-sectional area as potential covariates but these terms were dropped when insignificant.

Because 16.7% of unprotected logs were not attacked by termites over the course of the study, we also used ANOVA to compare mass loss and lignin content between logs with and without visible termite activity. These models consisted of termite incidence, bark treatment, end treatment, all interaction terms and the same covariates as listed above. Finally, we repeated these analyses to compare mass loss and lignin content between logs with and without visible cerambycid activity. Because cerambycids were excluded from logs without bark by their biology, only logs with bark were included in these analyses. In total, 33.3% of these logs were colonized by cerambycids. These models consisted of cerambycid incidence, termite incidence, end treatment, interaction between cerambycid incidence and end treatment and the same covariates as above (which, again, were dropped when insignificant).

We also analyzed reduced datasets to determine how (1) termite incidence and (2) the amount of termite damage visible in cross section varied with bark and end treatments. This first analysis was limited to unprotected logs whereas the second was further limited to unprotected logs with visible evidence of termite activity. Fisher's exact test was used to compare incidence and ANOVA was used to compare damage. The ANOVA model consisted of bark and end treatments, their interaction and the same covariates as listed above. Both covariates were found to be insignificant and were therefore dropped from the final model.

LS-means (i.e., least squares means, or marginal means in SAS terminology) were calculated when a model contained significant covariates or when data were unbalanced (this happened, for instance, when limiting the analysis to only logs with visible termite activity). By adjusting for other effects in the model, LS-means estimate the marginal means for a balanced population (SAS Institute, 1999). Where applicable, LS-means and standard errors are presented in the figures or within the text (as indicated) but raw values are available in the Supplementary materials.

3. Results

A complete set of logs was recovered at the end of the experiment. The closed pans successfully excluded termites, without a single treatment failure. By contrast, 79.2% and 87.5% of logs assigned to the open pan or no pan treatments, respectively (or 83.3% of all 48 unprotected logs), were attacked by termites

over the course of the study (Fig. 1B). Among logs assigned to open pan and no pan treatments that were attacked by termites, termite damage accounted for an average of $15.2 \pm 4.6\%$ (range: 0–62.4%) and $15.0 \pm 3.4\%$ (range 0–66.9%) of cross-sectional area, respectively. Because no significant differences were detected between open pan and no pan treatments in termite incidence (p = 0.70), termite damage ($F_{1,13} = 0.01$, p = 0.93) or water content ($F_{1,15} = 0.00$, p = 0.94), they were combined into a single "unprotected" treatment for all subsequent analyses. Whereas termites were successfully excluded by closed pans, all logs were readily colonized by flying insects. Among the 12 logs with bark assigned to each of the closed, open and no pan treatments, for example, 41.7%, 25.0% and 33.3%, respectively, showed signs of cerambycid activity (larvae reared to adulthood were identified as *Aegomorphus quadrigibbus* (Say)) (Fig. 1B).

Overall, bark treatment, end treatment and initial cross-sectional area (a covariate) were the only significant sources of variation for mass loss (Supplementary Table 1). Logs with bark lost significantly more mass than those from which bark had been removed, a 2.37-fold difference based on LS-means ($33.0\% \pm 1.6$ vs. $13.9\% \pm 1.6$, respectively). Logs with unsealed ends lost significantly more mass than those with sealed ends, a 1.33-fold difference based on LS-means ($26.8\% \pm 1.6$ vs. $20.1\% \pm 1.7$, respectively). Mass loss generally decreased as initial cross-sectional wood area increased (results not shown). Only the bark treatment and initial wood specific gravity (a covariate) were significant sources of variation for water content (Supplementary Table 1). Logs without bark were drier than those with bark (Fig. 2) and water content decreased with increasing specific gravity (results not shown). There were no significant effects in the model for percent lignin (Supplementary Table 1).

While we detected no significant insect effect on mass loss, water content or lignin based on the inclusion of pan treatment (protected vs. unprotected) in the models, we did detect significant insect effects in models containing termite or cerambycid incidence (presence vs. absence). We found greater mass loss from logs with visible termite activity compared to logs without
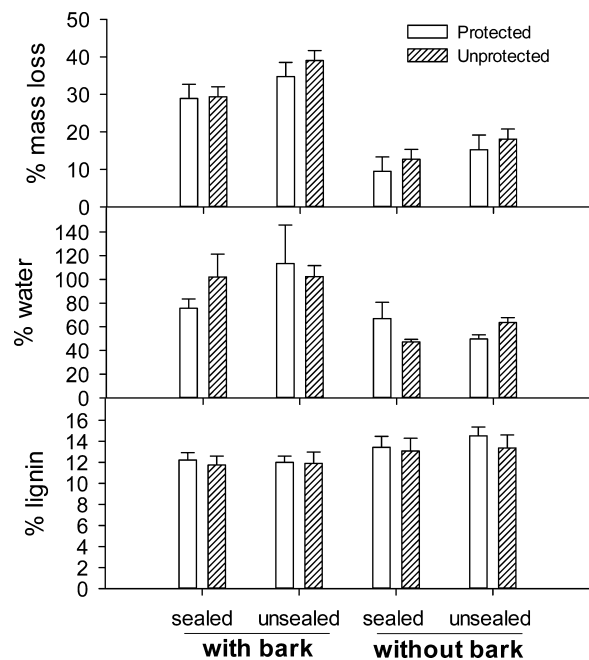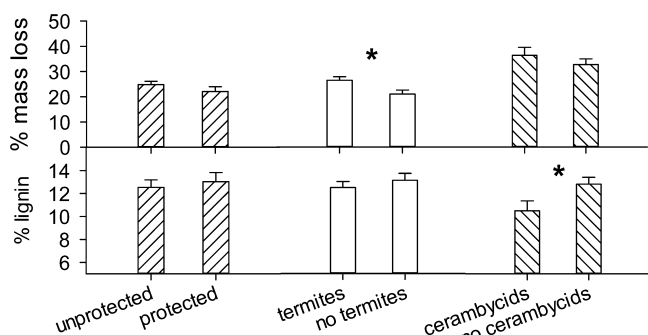
Fig. 2. Mean ± SE % mass loss, % water content and % lignin from logs with and without bark, with sealed or unsealed ends and protected or unprotected from termites. *Note*: LS-means ± SE are given for mass loss, see Supplementary materials for raw means.

Fig. 3. Percent mass loss and percent lignin (LS-means ± SE) for (1) unprotected vs. protected logs (left), (2) logs with vs. without termites (center) and (3) logs with vs. without cerambycids (right, note that only logs with bark are included here). Asterisks denote significant differences (α < 0.05).

termites, about a 1.26-fold difference based on LS-means (26.3% ± 1.4 vs. 20.9% ± 1.6, respectively) (Supplementary Table 2, Fig. 3). Cerambycid activity had no significant effect on mass loss but did result in significantly lower lignin values compared to logs without cerambycids, about a 0.82-fold difference based on LS-means (10.4% ± 0.8 vs. 12.7% ± 0.6, respectively) (Supplementary Table 3, Fig. 3).

Finally, we found no difference in termite incidence among logs with or without bark (p = 1.0) or among logs with sealed vs. unsealed ends (p = 0.7). Among unprotected logs with visible termite activity, however, we found termite damage visible in cross section to exhibit a significant bark × end interaction ($F_{1,16}$ = 10.0, p < 0.01). Logs with bark and with unsealed ends had significantly more termite damage than the other treatments (Fig. 4).

4. Discussion

Insects significantly affected wood decomposition in this experiment. Mass loss was 26% greater when termites were present and cerambycids resulted in an 18% reduction in lignin. Logs with unsealed cut ends decomposed more quickly than logs with sealed ends. Logs without bark contained less water, were not colonized by cerambycids, were less damaged by termites (relative to logs with bark and unsealed ends) and showed much lower rates of mass loss. Unlike most previous studies aimed at quantifying the contributions of insects to decomposition, these results are not confounded by differences in microclimate between treatments. Indeed, the open-topped pan design minimized differences in humidity while successfully excluding termites. Stoklosa et al. (2016) recently described a dowel method for quantifying the extent to which insect-exclusion methods affect microclimate and, in turn, decomposition. The utility of that approach is limited to
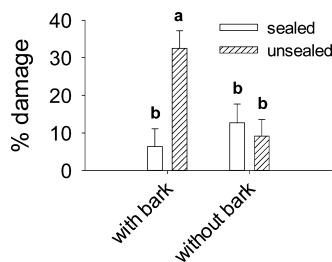
Fig. 4. Percentage of cross-sectional area damaged by termites (LS-means ± SE) for logs with vs. without bark and with sealed vs. unsealed ends. Bars with different letters are significantly different based on LS-means. Only unprotected logs with visible termite activity were included in these calculations.

short-term studies, however, as it only works when some dowels remain undamaged from insects. By contrast, the open-topped pan design used here is likely to work over long periods provided that the borders of the pans are kept free from fallen leaves and other plant material. This method may therefore help address the need for longer-term studies on wood decomposition and associated organisms (Seibold et al., 2015; Ulyshen, 2016).

Termites are thought to be among the most effective invertebrate consumers of dead wood in many tropical and subtropical forests (Ulyshen, 2016; Ulyshen et al., 2014) and may, in some cases, even exceed the importance of free-living microorganisms (Liu et al., 2015). Although most (83.3%) unprotected logs (i.e., those assigned to the open pan or no pan treatments) were attacked by termites in our study, we did not detect a significant difference in mass loss between protected and unprotected logs. When logs with or without visible termite activity were compared, however, those with termite activity lost significantly more mass than those without. We may therefore have seen significant differences between protected and unprotected logs if the study had extended long enough for all of the unprotected logs to be attacked by termites. In addition to directly damaging and consuming wood, wood-feeding insects can potentially have indirect effects on wood decomposition through interactions with the microbial community (Ulyshen, 2016). In the current study, one third of all logs with bark showed signs of cerambycid activity. Although there was no significant difference in mass loss between logs with and without cerambycid activity, logs with signs of these insects had significantly less lignin than those without. Because the degradation of lignin is thought to be driven largely by fungi and bacteria, including species found within the guts of wood-feeding insects (Bugg et al., 2011; Cragg et al., 2015; Geib et al., 2008), these findings suggest cerambycids exerted significant indirect effects on decomposition by promoting the activities of free-living and/or endosymbiotic microorganisms. Cerambycids may have facilitated the colonization of free-living fungi and bacteria, for example, by providing access through entry holes in the bark or by vectoring spores or mycelia (Leach et al., 1937; Persson et al., 2009; Strid et al., 2014). Moreover, wood-feeding insects are known to harbor diverse microbial assemblages within their guts and there are documented examples associating lignin degradation with the gut microbes of certain cerambycid species (Geib et al., 2008). Facilitating colonization by free-living microbes is more likely to account for our results considering that the wood samples were collected from the centers of the logs whereas cerambycid activity was limited to the outermost layers of sapwood.

To our knowledge, this is the first study to compare decay rates between logs with and without bark. We found the removal of bark to reduce how quickly wood decomposes by more than half. The fact that logs without bark were significantly drier than those with bark at the end of the study suggests that bark may have an accelerative effect on decomposition by enhancing moisture retention. The removal of bark may also reduce decay rates by excluding entire guilds of phloem-feeding and subcortical insects as well as their role as vectors of fungi. Although no effects on mass loss were detected, the fact that cerambycid activity reduced lignin content in logs with bark supports the notion that important players are excluded by the removal of bark. The contributions of other bark-associated insects were not quantified in this study. Termite incidence did not vary between bark treatments or end treatments. We did, however, find a significant interaction between bark and end treatments for termite damage. Termites caused more damage in logs with both bark and unsealed ends compared to the other treatment combinations. These findings suggest that termites benefit from bark coverage but only when this layer has been breached by some previous damage. Most termites, including the subterranean species studied here, require

shelter for foraging and will often build tubes or sheeting for this purpose (Eggleton, 2011). Bark may be of some advantage to termites by providing a protective covering. Our results suggest this may be true only when damaged areas provide easy access, however.

The role of insects in providing access to fungi may be more pronounced when bark is intact. For instance, Leach et al. (1937) reported a stronger effect of beetles on pine decomposition when the log ends were sealed. In that study, decay spread slowly into the heartwood of sealed logs except where beetle tunnels facilitated fungal penetration. Leach et al. (1937) found decay fungi to spread rapidly throughout the sapwood regardless of insect activity, however. In our study, logs with sealed ends decomposed significantly slower than those with unsealed ends. As there were no significant differences in water content between end treatments, this difference may be due to fungi more readily colonizing the exposed ends of unsealed logs. Our prediction that a greater insect effect would be detected from logs with sealed ends, however, was not supported. This may be due to the fact that small-diameter logs without heartwood were used in our study.

We conclude that rates of wood decomposition are greatly influenced by bark coverage and that insects also have significant direct (termites) and indirect (cerambycids) effects. Our findings underscore the importance of using naturally-occurring woody substrates as opposed to standardized wooden blocks in decomposition experiments. The open-topped pan design used here promises a way forward with respect to quantifying long-term effects of insects on wood decomposition while finally minimizing, if not eliminating, differences in microclimate among treatments.

Acknowledgement

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2016.03.017.

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