

Wood decomposition is more rapid on than off termite mounds in an African savanna

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Abstract. Decomposition is important for nutrient cycling and the dynamics of soil organic matter. The factors that influence local decomposition rates in savannas dominated by *Macrotermes* mounds remain uncertain. Here, we experimentally assessed the effects of macro- and micro-detritivores, active and inactive mounds, and vegetation cover on wood decomposition rates for eight common woody plant species in Lake Mburo National Park, in Uganda. Five pairs of *Macrotermes* mounds, one active and one inactive per pair, were selected. Each mound provided two sample locations, one, the most shaded (with canopy cover), and one, the most open (without canopy cover) edge of mound. In addition, for each mound pair, one additional sample location was located off-mound, in an open level area between the mounds. After one, three, and 12 months, protected (wrapped in 1-mm mesh fiber-glass excluding macrodetritivores) and unprotected wood samples from each location were retrieved, brushed clean, oven-dried, and weighed. After 12 months, mean percentage mass loss was four times higher for unprotected than protected wood samples across all species located on mound sites (when decomposition in shaded and open microhabitats was combined). Mean percentage mass loss across all species combined was 1.2 times higher on active than inactive mounds. Across all mounds, decomposition was on average 1.1 times more rapid in the shaded than open mound parts. These differences were more pronounced on inactive mounds (1.3 times more rapid in the shaded than open parts). Percentage mass loss was markedly lower off-mound ($12.6 \pm 0.8\%$) than on active ($25.9 \pm 1.5\%$) or inactive mounds ($19.7 \pm 1.2\%$). Proportional mass loss for unprotected wood decreased with increasing wood density, but proportional mass loss of protected wood samples was not detectably influenced by wood density. Our study highlights the strong and locally contingent influence of termite mounds, termite activity, vegetation, and their interactions on wood decomposition rates within a savanna landscape. Furthermore, variation in per-species wood decomposition rates, including the negative correlation with wood density, depends on accessibility to macrodetritivores.

Key words: ecosystem engineers; ecosystem processes; heterogeneity; *Macrotermes* mounds; nutrient cycle; soil fauna; Uganda.

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INTRODUCTION

Decomposition determines soil organic matter, mineralization of organic nutrients, and the terrestrial carbon cycle (Knops et al. 2002, Mackensen et al. 2003). While climate is an important influence on decomposition rates,

biota, particularly detritivores, can also play a major role, though many such determinants remain poorly characterized (Lavelle et al. 1993, Andr n et al. 1995, Bradford et al. 2014).

Termites are important wood feeding detritivores within the savannas of Africa and Asia (Buxton 1981, Collins 1981, Cornwell et al. 2009).

Studies have found considerable local variation in the influence of these organisms: For example, one assessment in a savanna in Botswana reported a sixfold variation in decomposition rates that was attributed primarily to the local dominance of different termites (Schuurman 2005). A recent study from South Africa found that fungus-growing termites (*Macrotermes*) maintained high levels of decomposition even when moisture was scarce thus decoupling decomposition rates from rainfall (Veldhuis et al. 2017). Mound-building termites occur throughout the ~10 million square kilometer African savanna (Riggio et al. 2013, Bonachela et al. 2015, Davies et al. 2016). Despite our awareness that mound-building termites play a major role in determining decomposition rates, the factors that influence these rates and their local variation remain uncertain.

In the African savanna, *Macrotermes* mounds are conspicuous, often long-lived structures (Korb and Linsenmair 2001, Levick et al. 2010, Erens et al. 2015). At any time, such mounds may be occupied by fungus-growing *Macrotermes* (active) or abandoned (inactive), though any such abandoned mound is liable to be recolonized (to become active again; Pomeroy 2005, Erens et al. 2015). Therefore, the abundance of *Macrotermes* in the landscape cannot be simply inferred from the number of their mounds. At the same time, variation in *Macrotermes* abundance and activity is likely to influence wood decomposition across the landscape.

Macrotermes mounds typically support dense and diverse tree communities relative to the adjacent sparsely wooded off-mound areas (Traoré et al. 2008, Sileshi et al. 2010). Termites process soil, altering its properties and associated woody vegetation (Moe et al. 2009, Jouquet et al. 2011). *Macrotermes* mounds possess distinct clay-rich soils that enhance water available to plants and ensure high cation exchange capacity and a greater availability of plant nutrients than occur in the surrounding soils (Sileshi and Arshad 2012). As elevated sites, *Macrotermes* mounds also protect plants from fires and floods (Jouquet et al. 2011, Joseph et al. 2013). These mound properties result in a distinct suite of trees growing on-mound relative to off-mound sites (Traoré et al. 2008). The tree cover on mounds also creates cooler microclimates within the warmer

landscape that can facilitate the persistence of heat sensitive organisms (Duffy et al. 2015, Joseph et al. 2016).

Studies suggest that much of the variation in wood decomposition rates reflects properties of the wood itself (Cornwell et al. 2008, Weedon et al. 2009). Typically, higher density woods have slower decay rates than lower density wood (Chambers et al. 2000, Chave et al. 2009). Thus, we anticipated that the local turnover of woody debris would reflect properties of the wood as well as the activity of decomposers.

In this study, we experimentally assessed wood decomposition in Lake Mburu National Park, in Uganda, where *Macrotermes* mounds are locally abundant (typically 4–8 mounds/ha, Pomeroy 1977). We assessed wood decomposition for eight common tree species using five paired replicates of active and inactive mounds, each with an open (without tree canopy cover) and shaded (with vegetation cover) microhabitat location, and in the open area between each pair of mounds. We assessed percentage mass loss as the measure of wood decomposition for the eight woody plant species. Four of these woody species are typically observed growing in the open areas between termite mounds, and the other four are commonly seen growing on-mound. Six wood sample-sets consisting of a piece of wood from each of the eight species were placed on the open and shaded locations of active and inactive mounds, and in an off-mound location between each active and inactive mound pair. To evaluate the role of macrodetritivores, we replicated our samples with and without a 1-mm double-layered fiber-glass mesh. Mass loss was assessed after one, three, and 12 months.

We addressed the following questions: (1) How does decomposition vary on active and inactive mounds? We expected higher decomposition rates on active mounds because of greater termite activity. (2) How do rates of decomposition vary between mounds and adjacent off-mound areas? We expected decomposition rates to be higher on- than off-mound, because mound microenvironments seem likely to facilitate decomposition and host more detritivores. (3) How does decomposition vary on mounds with shaded and open microhabitat locations? We expected decomposition rates to be higher in the shaded microhabitat because of enhanced

moisture availability (Gliksman et al. 2017). (4) Does wood density influence decomposition? We predicted that the wood from species possessing lower density wood would decompose faster than that of species possessing higher density wood under all otherwise equal conditions (Chambers et al. 2000, Chave et al. 2009).

METHODS

Study site

We conducted our experiment within the 260-km² Lake Mburo National Park in southwestern Uganda. The elevation of the park ranges between 1200 and 1300 m above sea level and receives about 865 mm of rainfall annually within two rainy seasons between February and May and between September and November. June and July are the driest months. Average monthly temperatures range from 19.8° to 20.9°C (www.climate-data.org). The vegetation consists of mound-associated thickets, mixed woodlands, forest patches, and swamps (Bloesch 2008). Large mounds (5–10 m in diameter) constructed by *Macrotermes subhyalinus* (Rambur) are conspicuous features in much of the park covering about 5% of the landscape (Moe et al. 2017). The tree communities on these mounds differ from those off-mound, and tree densities and diversity are higher (Støen et al. 2013, Acanakwo et al. 2018). The common tree species growing on-mound include *Rhus natalensis* Bernh. ex C.Krauss, *Grewia* species, *Teclea nobilis* Del., *Allophylus africanus* P. Beauv., while *Acacia* species such as *A. gerrardii* Benth., *A. sieberiana* DC., *A. hockii* De Willd., and *Dichrostachys cinerea* (L.) Wight & Arn dominate in off-mound areas (Moe et al. 2009, Acanakwo et al. 2018). Woody cover on vegetated mounds is typically clumped and uneven typically creating both shaded and exposed areas.

Experimental design

We conducted the experiment in Lake Mburo National Park, Uganda. We located five active mounds, each of which was paired with the nearest inactive mound located between 20 and 80 m away in any compass direction and having no other closer mound between. To distinguish active from inactive *Macrotermes* mounds, we checked for new constructions on mounds by looking for fresh soil deposition. When no new

constructions were observed, we punctured the mound with a sharp iron rod to a depth of ~50 cm and checked for repairs five days later. A mound was considered active if it bore new constructions or if the puncture hole was repaired; otherwise, it was considered inactive.

At each mound (active and inactive), we sited two experimental stations: one in the most open area we could find at the base of the mound (i.e., by the lowest slope with no tree or shrub canopy cover) and the other in the most shaded part. At the mid-point between each pair of active and inactive mounds (i.e., in the adjacent, off-mound area), an additional station was sited (all these areas bore open vegetation). All stations were set on bare ground with loose litter removed.

Wood samples

We assessed eight common woody plant species. We selected *R. natalensis* Bernh. ex C.Krauss, *Grewia similis* K.Schum., *T. nobilis* Del., and *A. africanus* P. Beauv., as species that are common on-mound, and *A. gerrardii* Benth., *A. sieberiana* DC., *A. hockii* De Willd., and *D. cinerea* (L.) Wight & Arn as species that are common off-mound. For each species, we selected and cut ten stems that were relatively straight, at least 2 m tall, with diameter at breast height (dbh) between 5 and 10 cm. The cut stems were debarked and sun-dried for seven days. The sun-dried stems were then cut to pieces measuring 10 × 2 × 2 cm. Since we did not see any clear distinction in coloration or texture to indicate heartwood, we used whole stems to make samples and we assumed that all our samples are entirely sapwood. The wood pieces were numbered, oven-dried for 72 h at 80°C, and then weighed to obtain an initial weight. A set of wood pieces comprising one from each of the eight species were tied together using a twisted wire so as to sit about 0.5 cm apart.

To separate the contribution of macrodetritivores from microbes and other smaller soil fauna on the rates of wood decomposition, we wrapped half of the wood sample-sets in 1-mm fiber-glass meshes. We refer to these wrapped sample-sets as protected, and the others as unprotected.

We placed six unprotected and six protected wood sample-sets at each of the 25 stations in June 2015. We recorded the number-codes of each species in the sample-set and the location of the sample-set in the station in order to readily

identify and distinguish the wood samples later. After one, three, and 12 months, two unprotected and two protected sample-sets were retrieved from each station. These were cleaned with a brush to remove loose soil and then oven-dried for 72 h at 80°C and weighed. The difference between the initial and final dry weights provided our measure of analyses: (1) including lost samples as 100% decomposed and (2) summarizing the data for only the remaining samples.

Wood density

We derived wood density for our selected tree species following procedures from Grundelius (1990). For each species, we cut five $2 \times 2 \times 2$ cm wood chips from roughly sized sun-dried wood samples. The wood chips were soaked in distilled water for 24 h. Taking one chip at a time, chip surfaces were dried then placed in a sample-holding bag of known mass and immersed in a jar of water that stood on a digital weighing scale. Sample chips for all eight species floated on water, so they displaced the volume of water equal to their own weight which we recorded as green mass. We obtained this value from the following formula: $\text{green mass} = (\text{Mass of chip and bag} - \text{mass of empty bag}) / \text{density of water surrounding the bag in the jar}$ (1.000 g/cm^3). The wood chips were then oven-dried until a constant mass was obtained, providing oven-dry mass. Wood density was derived as oven-dry mass divided by green mass.

Analyses

We explored the data using scatter plots of percentage mass loss against explanatory variables, that is, mound status (active, inactive, and off-mound), mound microhabitat (open, shaded), and time (1, 3, 12 months) to check for outliers. Mound sites had two microhabitat locations (open and shaded), while off-mound sites were all open. For this reason, we used separate models to examine the effect of (1) microhabitat locations on mounds, and (2) on-mound vs. off-mound habitats (open sites only).

Model 1: To assess wood decomposition rates in on-mound locations, we tested the effects of woody plant species, mound status (active vs. inactive), mound microhabitat (open vs. shaded), duration of exposure, and access to wood samples by large macrodetritivores (unprotected vs.

protected). To avoid pseudo-replication within decomposition stations, we used average mass values for each species of the remaining wood samples from the two protected and unprotected sample-sets after a particular duration. We constructed linear mixed effects models (LMM) with mean percentage mass loss as response variable using the lmer function within the lme4 R package (Bates et al. 2015). To approximate a normal distribution, the mean percentage mass loss was arcsine square-root transformed prior to analysis (McDonald 2014). Since we took samples three times from each sample station, we used decomposition station identity as a random factor in our models (Crawley 2013).

Model 2: To assess wood decomposition rates on- and off-mound, we tested the effects of woody plant species, mound status (considering only locations on active and inactive mounds that were open, i.e., with no canopy cover, and off-mound sites), duration of exposure, and access to wood samples by large macrodetritivores. We constructed LMM with arcsine square-root transformed mean percentage mass loss as response variable using the lmer function within the lme4 R package (Bates et al. 2015). We used decomposition station identity as a random factor.

For both models, we first fitted saturated models with all the main terms and their interactions. We subsequently reduced the model by removing non-significant ($P > 0.05$) interactions followed by non-significant terms, until we obtained the model with only significant interactions and their terms (Crawley 2013). We validated the models by visually investigating assumptions of normality and equal variances by residual plots, with no apparent violations. All analyses were run using R statistical software (R Core Development Team 2017).

RESULTS

Overall, wood from all species showed progressively greater losses over the 12 months. On average, unprotected wood mass lost was $24.7 \pm 1.0\%$ in the first month, $36.0 \pm 1.3\%$ in the third month, and $63.6 \pm 1.6\%$ after 12 months (Fig. 1). Wood mass loss was consistently higher, on average about four times (about 342%) greater, for samples exposed to macrodetritivores than those that were protected.

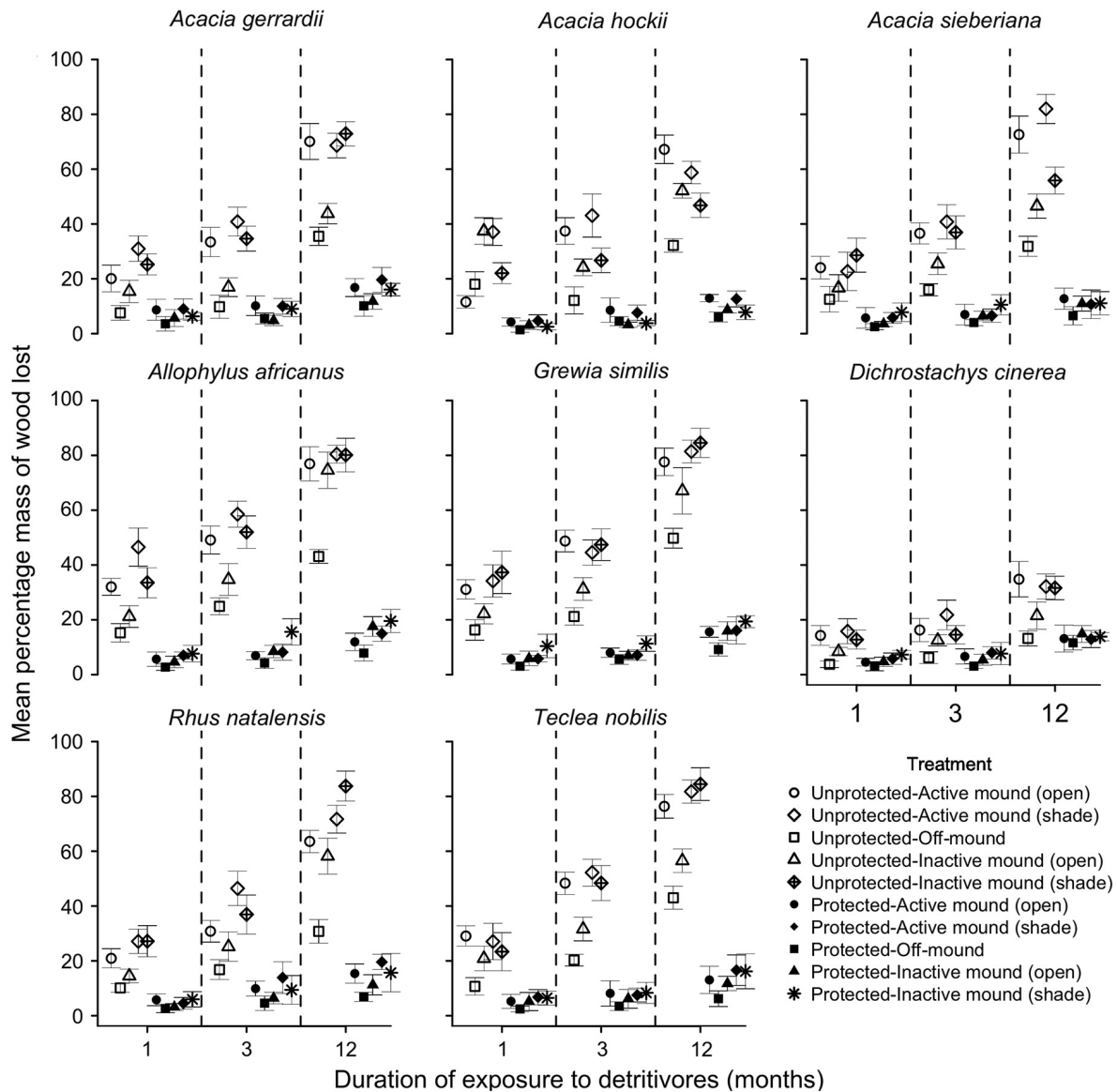


Fig. 1. Mean (\pm SE) percentage wood mass loss by eight wood sample species common within Lake Mburo National Park, Uganda. The experiment was replicated five times, with all detritivores having access to six (half) of the wood sample-sets (unprotected), whereas only micro-detritivores accessed the 1-mm mesh-bound sample-sets (protected). The sample-sets were placed in the shaded and open locations of mounds, and in an open off-mound location between the active–inactive mound pairs.

After 12 months, mean (\pm SE) percentage mass loss was $63.6 \pm 1.6\%$ for unprotected wood samples and $14.4 \pm 0.6\%$ for protected wood samples across all tree species located on mound sites (when decomposition rates in shaded and open microhabitats was combined; Figs. 1, 2). In the adjacent off-mound sites, unprotected samples lost a mean percentage mass of $35.1 \pm 2.1\%$,

while protected samples lost $8.10 \pm 0.95\%$ (Figs. 1, 3).

Species associated with off-mound environments typically had higher wood density than those growing on-mound. Densities ranged from 0.559 to 0.987 g/cm^3 , and 0.515 and 0.650 g/cm^3 for off- and on-mound species, respectively (Appendix S1: Table S1).

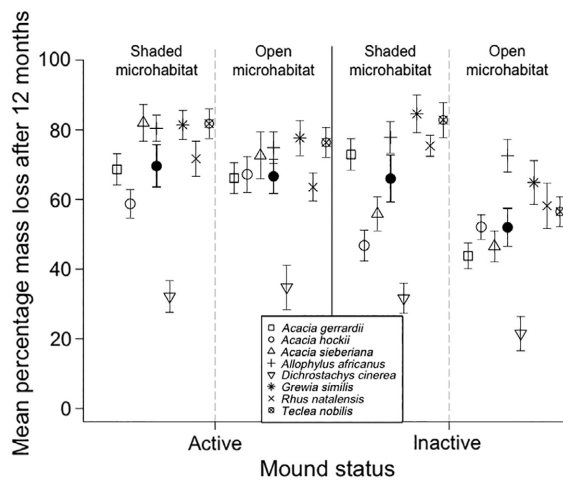


Fig. 2. Mean (\pm SE) percentage wood mass loss by unprotected species in the shaded and open microhabitat locations of active and inactive *Macrotermes* termite mounds in Lake Mburo National park, Uganda. Open characters and symbols are mean values for individual species, while the filled circles are the overall mean (\pm SE) values for species per microhabitat.

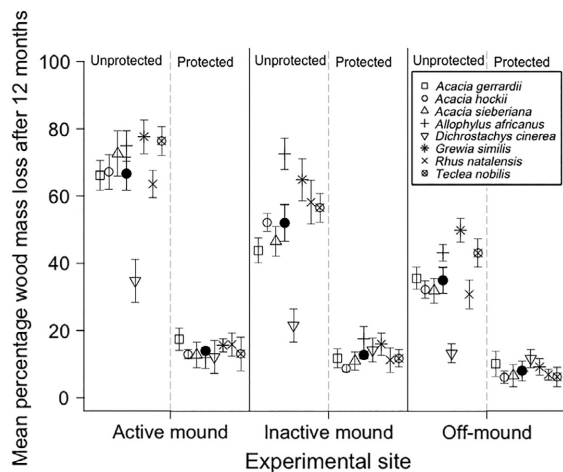


Fig. 3. Mean (\pm SE) percentage wood mass loss from protected and unprotected wood species on active mounds, inactive mounds, and off-mound sites in Lake Mburo National Park, Uganda. Open characters and symbols are mean values for individual species, while the filled circle is the overall mean values for species per microhabitat.

We lost five wood samples after three months and 12 samples after 12 months. The coefficient of variance for the dataset including lost samples (i.e., 100% mass loss) and the dataset without the

lost samples was similar (63.8% and 62.2%, with and without lost samples, respectively). The estimated per-species mean percentage mass loss including and excluding these lost samples differed by <1.0 (Appendix S1: Table S2).

After 12 months, mean percentage mass loss for unprotected wood samples, across all species combined was higher on active ($68.1 \pm 2.0\%$) than on inactive mounds ($59.1 \pm 2.3\%$), whereas mean percentage wood mass loss for protected samples on active mounds was $14.8 \pm 0.9\%$ vs $14.0 \pm 0.91\%$ on inactive mounds (Fig. 2, Appendix S1: Table S3). Overall, mean percentage mass loss from unprotected samples was 1.1 times (about 14.0%) higher in the shaded than the open mound locations ($67.8 \pm 4.4\%$ vs. $59.3 \pm 4.0\%$). However, this difference was most pronounced on inactive mounds ($66.7 \pm 4.9\%$ shaded vs. $52.0 \pm 5.5\%$ open; Fig. 2, Appendix S1: Table S3). A similar pattern was observed for the protected wood samples. Wood mass loss across species was also 1.1 times (about 13.5%) higher in the shade than in the open-canopy parts of mounds ($15.29 \pm 1.0\%$ vs. $13.47 \pm 0.8\%$). On active mounds, mean percentage mass loss across species was marginally higher in the shaded parts of mounds ($15.46 \pm 1.4\%$) than in the open ($14.08 \pm 1.2\%$). Similarly, on inactive mounds, wood mass loss across species was marginally higher in the shaded ($15.12 \pm 1.5\%$) than open ($12.84 \pm 1.1\%$) mound locations.

After 12 months, across all species combined, decomposition rates of unprotected wood were significantly lower in off-mound sites ($34.9 \pm 3.9\%$) relative to on-mound sites within the open microhabitats (see Fig. 3, Appendix S1: Table S4).

The wood decomposition rates for species by microhabitat location for unprotected samples after 12 months spanned a 6.4-fold range (Fig. 1, Appendix S1: Table S3). The highest mass losses ($>80\%$) were experienced by *Rhus natalensis* ($81.8 \pm 3.5\%$), *Teclea nobilis* ($82.8 \pm 5.0\%$), and *Grewia similis* ($84.5 \pm 5.4\%$) in the shaded location of inactive mounds, while *Allophylus africanus* ($80.4 \pm 3.8\%$) and *Acacia sieberiana* ($82.0 \pm 5.3\%$) experienced the highest mass losses in the shaded locations of active mounds. The lowest mass losses ($<7.0\%$) were recorded in off-mound sites for *Acacia hockii* ($6.1 \pm 1.8\%$), *A. sieberiana* ($6.6 \pm 3.3\%$), *T. nobilis* ($6.2 \pm 2.9\%$), and

R. natalensis ($6.9 \pm 1.6\%$) (Figs. 1, 2, Appendix S1: Table S3).

Of the protected wood samples, after 12 months, decomposition rates spanned a 3.5-fold range. Losses were highest for *Acacia gerarrdii* ($21.1 \pm 3.7\%$) and *R. natalensis* ($19.6 \pm 2.7\%$) in the shade of active mounds, and *G. similis* and *A. africanus* in the shade of inactive mounds ($19.4 \pm 4\%$ and $19.5 \pm 4.2\%$, respectively). The lowest losses after 12 months were all experienced off-mound where *A. hockii*, *A. sieberiana*, *T. nobilis*, and *R. natalensis* lost $6.1 \pm 1.8\%$, $6.6 \pm 3.3\%$, $6.1 \pm 2.9\%$, and $6.9 \pm 1.6\%$, respectively.

The relative wood decomposition rates in unprotected samples appeared greater for species with lower wood density, with the dense-wooded *Dichrostachys cinerea* proving more durable than the other species. After 12 months, percentage mass loss across species reduced with increasing wood density both in open on-mound locations (lm: Estimate = -38.331 , $t = -4.931$, $R^2 = 0.802$, $P = 0.003$) and in shaded locations (lm: Estimate = -51.77 , $t = -3.1$, $R^2 = 0.616$, $P = 0.02$; Fig. 4). We did not detect any relationship between mass loss and wood density among the unprotected samples

when *D. cinerea* was excluded from the analyses (Appendix S1: Fig. S1). No relationships between mass loss and wood density were detected for protected samples either in open (lm: Estimate = -2.25 , $t = 0.53$, $R^2 = 0.045$, $P = 0.61$) or shaded locations (lm: Estimate = -6.424 , $t = -0.753$, $R^2 = 0.086$, $P = 0.48$; Fig. 4).

DISCUSSION

Overall, our results highlight the key role of macrodetritivores in governing wood decomposition rates within the landscape. Decomposition progressed typically about 342% more rapidly when macrodetritivores had access to the wood samples vs. when they did not. Macrodetritivore decomposition was higher on *Macrotermes*-occupied (active) mounds, but the difference between occupied and unoccupied was only about 11% for the unprotected (fully accessible) samples. Altogether, wood decomposition was higher on- than off-mound and on shaded vs. open microhabitat. The results indicate that macrodetritivores are the main agents of decomposition and that mound status (active or inactive), shade

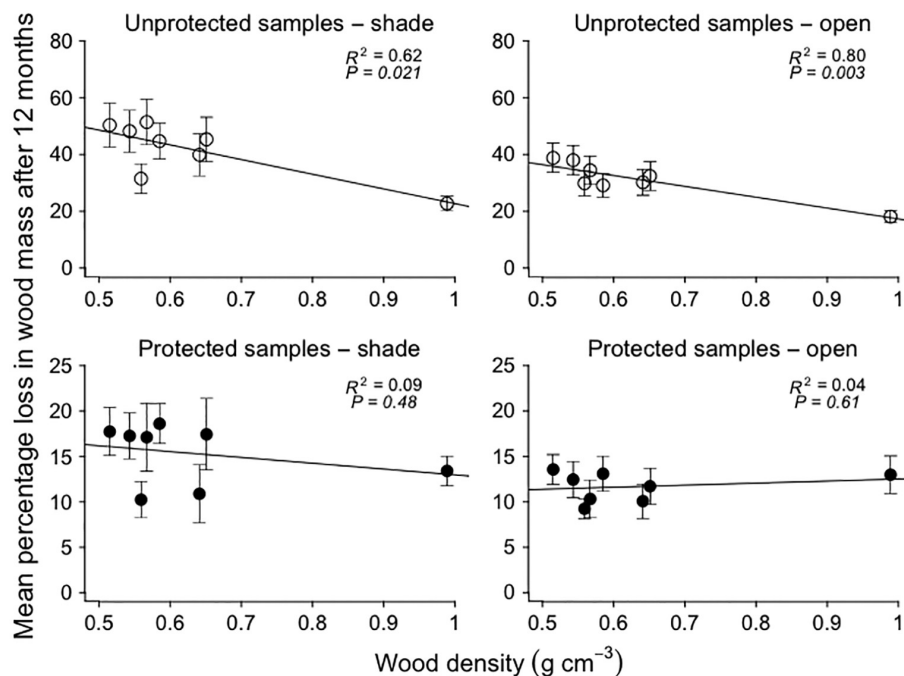


Fig. 4. Relationship between mean percentage mass loss and wood density for unprotected and protected wood samples in the shaded and open parts of the mounds.

locations, and the tree species influence local rates.

We predicted that decomposition rates would be higher on active than inactive mounds due to greater *Macrotermes* activity. Our results supported this prediction, with mass losses proceeding about 15% faster on active compared to inactive mounds for samples exposed for 12 months. This suggests that the occupancy of mounds influences how decomposition rates vary across the landscape. Our result (greater decomposition rates on active > inactive > off-mound) highlights the ecological importance of *Macrotermes* mounds in facilitating decomposition within the savanna landscape.

Macrodetritivores were also the main agents of decomposition on inactive mounds and in off-mound locations. *Macrotermes* termites may still play a role in these locations since the mean distance between our active–inactive mound pairs was 36.7 ± 2.4 m which is only marginally greater than their recorded foraging distance of 35 m (Darlington 1982). We did not assess the status of all the other mounds within the study neighborhood. Veldhuis et al. (2017) used earth tunnels left by *Macrotermes* (protection against predators) to differentiate *Macrotermes* activity from other macrodetritivores like millipedes, cockroaches, and non-*Macrotermes* termites. We did not record earth tunnels, as they are too readily damaged by animals or rain. In any case, as decomposition remained relatively high on inactive mounds, we suspect that other macrodetritivores play a role.

After 12 months of complete exposure of wood samples to decomposer organisms, mass loss was lower (90%, lower) from off-mound sites relative to mass loss from sites on active mounds, and (48.1%, lower) from off-mounds relative to sites from inactive mounds. The adjacent off-mound sites were established in the open (with no tree canopy). A number of abiotic and biotic factors, typically operating in concert, determine decomposition rates in such open sites. Lignin can be degraded by sunlight, for example, boosting subsequent microbial degradation particularly in wet periods (a process termed “photoprimering,” see, e.g., Austin et al. 2016). Nonetheless, if this was a dominant process, we might expect that samples exposed to direct sunlight would decompose faster than those in shaded sites, which was not the case. Although arthropod decomposers are able to forage and decompose wood in open off-

mound locations, they likely experience higher predation risk (Pringle et al. 2010). In addition, moisture is an important requirement for decomposition in dry environments (Gliksman et al. 2017). The strong sun and dry conditions in our open sites likely impede the microbial process that would facilitate decomposition.

Our prediction that mass loss rates would be higher in the shaded than in the open microhabitat locations was supported. Decomposition proceeded about 14% faster in the shaded than open locations of termite mounds. We believe that this reflects the positive influence of greater moisture availability. Interestingly, the effect of shade strongly interacted with *Macrotermes* termite presence: The effect of shade was minor on active mounds, while on inactive mounds, mass loss from unprotected samples in the shaded location proceeded at about 28% faster than in the open location. It seems the decomposition rates associated with active *Macrotermes* mounds are not dependent on moisture, consistent with Veldhuis et al. (2017). On a larger scale, Leitner et al. (2018) showed that shade, resulting from increasing tree cover, was associated with reduced decomposition. This was attributed to reduced termite activity in the wooded areas. Even when all organisms larger than 1 mm were excluded, decomposition rates were greater in shadier than open mound locations. Decomposition rates were also higher on- than off-mound in the absence of macrodetritivores. We speculate that the soil biota and other soil properties play some role in these differences. Provisional analysis of genetic material found in soils on and off *Macrotermes* mounds in Lake Mburo reveals a much smaller number of common genetic sequences in mound soil than in the neighboring, relatively sequence-rich off-mound locations indicating a highly modified microbial community in the termite-processed soils (Peter Alele and Douglas Sheil, *unpublished data*). The microbial metabolism of lignin is specialized and depends on specific enzymes in specific bacteria and fungi (Datta et al. 2017). Decomposition depends on these organisms being present under suitable conditions. Even if suitable organisms are present, evidence shows that nutrient availability can limit decomposition in many settings (e.g., Kaiser et al. 2014, Bonanomi et al. 2017). Though not yet studied in tropical savannas, experiments on wood decomposition frequently indicate

sensitivity to scarce or unavailable nutrients (notably nitrogen and phosphorus, e.g., Bebbler et al. 2011, Gora et al. 2018). This suggests that, aside from the microbial benefits gained from increased humidity under mound vegetation, the greater nutrient concentrations found in the soils of mounds (Okullo and Moe 2012, Sileshi and Arshad 2012, Seymour et al. 2014) may influence the decomposition rates of any wood samples placed on them. Accessibility to, and colonization by these microbial organisms either from the soil, or via other organisms (macro- or micro-) may also play an important role as priority effects can be influential (Leopold et al. 2017). Further experiments would be needed to clarify such effects.

Across the eight-tree species, percentage mass loss rate from unprotected wood samples slowed with increasing wood density regardless of microhabitat type, although in the absence of *Dichrostachys cinerea*, we did not detect any relationship between decomposition rates and wood density. It is surprising that the relationship between denser wood and slower decomposition does not hold when macrodetritivores are excluded. Other traits, such as wood nutrient concentrations, can also influence decomposition rates (Hu et al. 2018). Studies in the wet tropics have shown considerable variation in wood nutrient concentrations among and within species and have indicated that these species and site-determined variables can dominate variation in decomposition rates (e.g., Heineman et al. 2016). Several of our study species, including the dense-wooded *D. cinerea*, are nitrogen fixing species, and those that grow on termite mounds likely have access to various other nutrients like Calcium (Ca) and Magnesium (Mg) that are known to be enriched in these soils (Okullo and Moe 2012). Though further study is required, we speculate that variation in wood nitrogen or other nutrients may overshadow any effect of wood density when macrodetritivores are excluded. In any case, our results indicate that the influence of wood density in determining decomposition rates depends on the organisms involved.

Overall, our results showed that in 12 months, wood decomposition rates were 342% greater in the presence of macrodetritivores (unprotected) than in their absence (protected with 1-mm double-layered mesh). Decomposition proceeded at 15.2% faster on active than inactive mounds; 14%

faster in the shaded than open mound microhabitat locations, but about 28% faster in the shaded than open locations of inactive mounds. These results suggest implications pertinent to many national parks in Africa where large mammalian herbivores influence vegetation canopy on *Macrotermes* mounds. Nonetheless, the effect of large mammalian herbivores on wood decomposition has not been examined.

We have shown that the presence of termites, their mounds, and constituent vegetation influence wood decomposition rates in a savanna landscape. Wood decomposed more rapidly on-mound rather than off-mound and on active vs. inactive mounds. Wood mass loss was little affected by vegetation cover on active mounds, but on inactive mounds mass loss was 28.3% greater in the shaded than open microhabitat locations. The marked spatial variation in decomposition rates found in this landscape underlines the important direct and indirect role of *Macrotermes*.

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LITERATURE CITED

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Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2554/full>