



Quantifying the role of termite decomposition in a mesic savanna

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Abstract

Savanna systems are among the most sensitive to future climate and land-use change, yet we lack robust, direct quantifications of savanna carbon cycling. Together with fire, decomposition is the main process by which the carbon and nutrients are recycled and made available again to plants. Decomposition is largely mediated by microbes and soil invertebrates. Using a novel large-scale termite suppression experiment, we quantify, for the first time, the relative contribution of microbes, termites, and other invertebrates to the decomposition of wood (fresh native and dry non-native), dry dung, and grass in a mesic savanna. We found that termites were responsible for two thirds of the mass loss from dry wood and a third of the mass loss from fresh native wood, dry dung, and dry grass. Microbes were wholly responsible for the difference as there was no evidence of other invertebrates contributing to decomposition, even with fresh wood. Using multiple substrates in savanna decomposition studies is important where a mixture of contrasting life forms occur because both the rates of decomposition and the dominant agent varied considerably. In addition, including both a dry non-native and fresh native wood cast light on possible explanatory variables such as wood density, green-ness and the presence of bark, and the necessity of teasing these variables apart in future studies. Termites stand apart from all other insects in their impact on decomposition within savannas and should be acknowledged alongside microbes and fire as the primary agents of wood, grass, and dry dung turnover in global carbon models.

KEYWORDS

decomposition, dung, global carbon models, grass, savannas, substrates, termites, wood

1 | INTRODUCTION

Savannas which cover 20% of the global land surface and approximately 50% of the African continent (Pennington et al., 2018) are defined by a dominance of C4 grasses in the understory with

a discontinuous stratum of disturbance-tolerant woody species in the overstory (Ratnam et al., 2011). These systems are anticipated to be among the most sensitive to future changes in climate and land use, yet we lack robust, direct quantifications of their carbon cycling (Stevens et al., 2022). Together with fire, decomposition is the main

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process by which the carbon and nutrients captured by savanna trees and grasses, are recycled through the biosphere and made available again to plants (Bishop et al., 2021; Griffiths et al., 2021; Pausas & Bond, 2020). Other than fire, the principal agents of decomposition are decomposer organisms—predominantly fungi, bacteria, and soil invertebrates (Lavelle et al., 1993)—although photodegradation is also responsible for the breakdown of dead plant material in some environments (García-Palacios et al., 2013; Wardle et al., 2004). Determining the drivers of decomposition is essential for predicting how ecosystem change will affect savanna functioning. Until recently, climate (rainfall and temperature) and litter quality were considered to be the dominant controls on decomposition rate while the effect of decomposer organisms was considered to be relatively modest (Swift et al., 1979). Yet recent studies, such as Bradford et al. (2017) suggest that differences in the decomposer organism populations can influence decomposition rates at the global scale.

While the importance of microbes (bacteria and fungi) as agents of decomposition has long been appreciated (Griffiths et al., 2021), invertebrate decomposers (termites, in particular) have only recently been recognized for their substantial contribution (Wall et al., 2008; Zanne et al., 2022). Termites feed on a wide range of plant material owing to their intimate association with microbial symbionts either in their gut or, in the case of Macrotermitinae (the fungus-growing termites) in their mounds (Bignell, 2016; Holt & Lepage, 2000). It is these microbial symbionts, in addition to a suite of cellulases, that have enabled termites to become one of the few animal groups capable of digesting lignocellulose (Cragg et al., 2015), resulting in their dominance in tropical soils (40%–60% of total soil macrofaunal biomass; Potapov et al., 2022; Rosenberg et al., 2023) and allowing them to wield a significant impact on ecosystem functioning (Jouquet et al., 2016). Using a large-scale manipulative experiment in a Malaysian tropical forest, Griffiths et al. (2019) demonstrated that termites are responsible for the majority of wood mass loss (in Malaysia: 58%–64% termite versus 36%–42% microbial decay).

Numerous studies from across African savannas suggest that termites are the principal decomposers of wood, grass, and dry dung (e.g., Buitenwerf et al., 2011; Buxton, 1981; Collins, 1981; Freyermann et al., 2008; Schuurman, 2006). In one such example, Wood and Sands (1978) estimated that in a Guinean savanna in Nigeria, termites consume up to 55% of total surface litter (wood, leaves, and grass including 20%–25% of the grass standing crop). They predicted that the consumption of the standing grass crop by termites roughly equates to the consumption attributed to mammalian herbivores. Fire, by comparison, consumes approximately 36% of all plant production in the same system (Bignell & Eggleton, 2000; Wood & Sands, 1978). Focussed only on woody litter, Collins (1981) found that termites removed 60% of annual wood-fall in the same Guinean savanna in Nigeria (equates to 835.5 kg ha⁻¹ yr⁻¹ of woody litter). In Tsavo National Park in Kenya, termites removed approximately 35% of elephant dung per month (87 kg ha⁻¹ yr⁻¹; Coe, 1977). Yet, despite these studies, the specific

contribution of termites and other invertebrates to decomposition in African savannas has not been quantified as there were no methods to separate the contribution of termites from that of other invertebrates.

Additionally, most decomposition studies use dry wood lacking a bark layer (for example *Pinus* wood blocks; Ulyshen et al., 2016; Zanne et al., 2022). Bark traps moisture within the wood allowing a different suite of decomposer organisms to become active. Thus, studies using only dry wood may overestimate the contribution of termites.

This study represents the first savanna quantification of the relative contribution of microbes, termites, and other macroinvertebrates to wood (*Pinus* and *Terminalia*), dung, and grass decomposition. Using a method that has recently been developed within tropical forests (Sabah, Malaysia) (Ashton et al., 2019; Griffiths et al., 2019), we suppressed termites at a large-scale and used macro-invertebrate accessible and macro-invertebrate inaccessible decomposition bags to partition out the biotic agents of decomposition. We predicted that termites make a larger relative contribution to the decomposition of wood than microbes as wood provides a safe foraging environment for termites and the lower surface: volume ratio (of either a cylindrical stem/trunk or wood block) favors termites over microbes. The surface-to-volume ratio influences the accessibility of the organic material to microbial colonization and enzymatic action (Zhou et al., 2007). Further, we expected that invertebrates other than termites would play a greater role in the decomposition of the native bark-covered fresh wood (*Terminalia*) as phloem- and dead-wood-feeding beetles are attracted to fresh wood while termites are attracted to dry wood (Grassé, 1937; Josens, 1972). Conversely, we expected that the contribution of microbes to dung and grass to be greater, relative to the contribution of termites, given the higher surface: volume ratio (of a flat spherical dung pat or of narrow cylindrical grass stems).

2 | METHODS

2.1 | Study site

The experiments were conducted at Wits Rural Facility (WRF), in the Limpopo Province, South Africa (−24.566, 31.098). The site is at an elevation of 580 m a.s.l. and the vegetation type is classified as Granite Lowveld Savanna (Mucina & Rutherford, 2006). Dominant tree species include *Terminalia sericea* (Burch. ex DC.), *Combretum collinum* (Fres.), *Sclerocarya birrea* (A.Rich.), and *Dichrostachys cinerea* (L.) Wight & Arn. Dominant grasses include *Panicum maximum* (Jacq), *Heteropogon contortus* (L.) Roem. & Schult., and *Themeda triandra* (Forssk). Seasonal rain occurs during the summer months (December–April), and mean annual rainfall is 652 ± 200 mm (1992–2018). Mean monthly temperature between 2016 and 2018 was 21.1 ± 0.6°C, with mean minimum and maximum temperatures of 14.0 ± 0.8°C and 28.3 ± 0.45°C, respectively. Mpuluzi granites form the major basement geology of the area. The granites weather into sandy soils in the uplands and clayey soils with a high sodium content in the lowlands (Mucina & Rutherford, 2006). The large mammal

density is estimated to be 0.4 animals/ha. The reserve is burnt infrequently (every 7–18 years).

2.2 | Experimental design and termite suppression

We established four exclusion and four control plots within the 350-ha WRF area. Plots were established in pairs (one exclusion and one control) with similar vegetation and topographic characteristics and spaced a minimum of 500m apart across WRF. Control plots were 0.25 ha in size, while our termite suppression plots were 1 ha (100×100m), with sampling restricted to the central 0.25 ha. The 25m encircling buffer zone surrounding the core sampling area on the termite suppression plots was created to reduce the risk of termites from outside the suppression zone foraging within the experimental plot. Large plot areas (1 ha) are necessary to understand termite decomposition as mound-building termites have an over-dispersed distribution (Davies et al., 2014).

2.3 | Chemical treatments

Following Ashton et al. (2019) and Griffiths et al. (2019), two synthetic insecticides were used to suppress termites on the exclusion plots: one to suppress mound-building termites and the other to suppress foraging termites. We used Premise 200SC (Bayer, Environmental Science), with the active ingredient Imidacloprid at 23ppm (0.00235) to suppress the mound-building termites. Imidacloprid is a neonicotinoid insecticide, based on the natural toxin nicotine, which binds to the nicotinic-acetylcholine receptors in the insect's nervous system (Yamamoto, 1999). See Supplementary materials for further details on the chemical treatments, non-target effects and poison residue analyses.

In the case of small mounds (e.g., *Nitiditermes*—older name, *Cubitermes*), the entire mound was broken into small pieces and removed from the plot. The exposed soil at the mound base was then sprayed with imidacloprid solution. Large mounds (e.g., *Macrotermes*) were broken open with the use of a skidsteer (Bobcat S175), and/or pick-axes. Where possible, the termite queen and fungal combs were removed. The area of soil disturbed was negligible (<0.2% of each plot: approx. Four mounds per plot with disturbance limited to the central 2×2m of each mound). Depending on the size of the mounds, 10–80L of imidacloprid solution was applied to the exposed interior of the mound. Large *Macrotermes* mounds at the edge of the 1 ha plot were sometimes removed as we found that termites extended their foraging range into the treatment plots following the removal of neighboring mounds.

The second insecticide, Agenda 20C (Bayer, Environmental Science), with the active ingredient fipronil at 5.7 ppm was used to suppress actively foraging termites, as well as any remaining mound-building termites. Fipronil is a phenylpyrazole insecticide that blocks gated-chloride channels resulting in central nervous system toxicity (Raymond-Delpech et al., 2005). Toilet paper

rolls (TPR), wood-shavings (WS) and rooibos tea bags ((TB) containing *Aspalathus linearis*) soaked in a fipronil solution at 6 ppm (0.0006) were used as baits for the subterranean termites. The TPR were sawn in half and dipped in the fipronil solution and then shade-dried for 2 days. On each treatment plot, 441 half toilet rolls were shallowly buried (5–10 cm depth) every 5 m in a 21×21 grid across the plot. In addition, a circle of TPRs were buried around each large *Macrotermes* mound that had had imidacloprid applied. The WS and TB were soaked in the fipronil solution for a minimum of 12 h. A cup of WS was buried in a similar configuration to the TPRs—at a depth of 5–10 cm, every 5 m in a 21×21 grid across the plot. A total of 500 TBs were scattered across each plot roughly every 3.5 m in a 22×23 grid. Each plot was monitored every 3 months for the presence of new mounds and, where found, these were removed and imidacloprid was applied locally. Additionally, fipronil-treated TPR, WS and TB were applied to the treatment plots every month. Termite suppression started in October 2017. Suppression was achieved by December 2018 (Figure 1, Figure S4) after which we began our decomposition experiment. Using a similar targeted approach to Ashton et al. (2019) and Griffiths et al. (2019), our suppression method was developed to limit adverse non-target effects. The use of TPRs, WSs and TBs enabled us to take a targeted baiting approach on our termite suppression plots as no other invertebrates consume cellulose in that form, and we were able to reduce termites without affecting other ecosystems components. There were no detrimental non-target effects: other than termites, the suppression treatment did not negatively affect the abundance of the seven most common invertebrate taxa (those with mean abundances of >1 individuals per soil monolith) ($F = 1.925$, $p = 0.17$; $DF = 1$, Table S1, Figure S5). In additional validation analyses, both imidacloprid and fipronil were successfully detected by Gas chromatography–mass spectrometry (GC–MS; Figures S6 and S7); however, neither chemical treatment (imidacloprid and fipronil) was detected in soil, grass, or leaves from any of the experimental plots (Figures S6 and S7) indicating no persistence in the environment.

2.4 | Termite activity monitoring

To ensure the suppression effect was maintained throughout the decomposition experiment we monitored termite feeding activity across the plots using whole untreated TPR (following Parr et al., 2016, Griffiths et al., 2019), and then reapplied the treatments when required. Monitoring with TPR provided a direct link between the termite suppression and termite resource use. Sixteen toilet rolls (unbleached, single ply and unscented) were placed on each plot in a grid of four-by-four baits, spaced 5 m apart. The baits were placed on the soil surface and secured using aluminium pegs placed through the center hole of the toilet roll. After 4 weeks each toilet roll was scored for termite attack on a 0 to 5 scale where 0=0% consumed, 1=1%–25% consumed, 2=26%–50%

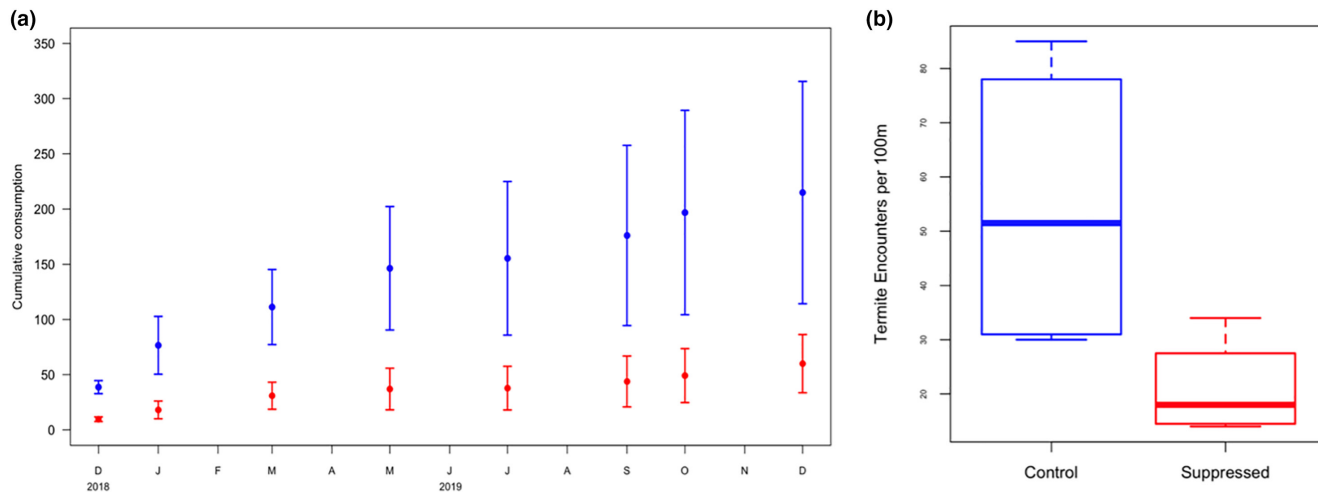


FIGURE 1 (a) Cumulative consumption of bait toilet paper rolls (TPR) by termites in control versus termite suppression plots over the period of the experiment (December 2018 to December 2019). Error bars are standard errors for replicate plots in each treatment group. (b) The number of termite encounters per 100m of active searching transect in control versus suppression plots. Error bars are standard errors for replicate plots in each treatment group.

consumed, 3=51%–75%, 4=76%–95%, and 5=96%–100% (Parr et al., 2016). After scoring, monitoring TPR were replaced with fresh ones to avoid saturation and have the same baseline for assessment in the following month.

2.5 | Decomposition assays

A combination of the open and closed decomposition bags on the termite suppression and control plots allowed us to determine the relative contributions of microbes, termites, and other macroinvertebrates to decomposition rates.

Decomposition rate was determined using decomposition bags with three substrates (grass, wood, and dung). *Themeda triandra* (Forssk) was chosen as the grass because it has a moderate to high palatability and has previously been used in savanna decomposition experiments in the same region (e.g., Davies et al., 2013; Leitner et al., 2018). *Themeda triandra* was harvested from within and around WRF. After harvesting, grass material was cut into segments of approximately 5 cm, mixing stems, inflorescences, green, and dried leaves. Pine (*Pinus radiata*) and *Terminalia sericea* were selected as the wood substrates. The pine (wood density: 0.39 g.cm⁻³) formed part of a global wood block study (see Zanne et al., 2022) and enables future cross-continental comparisons. *Terminalia sericea* was selected as it is the most common tree species across our plots (Figure S2) and within the context of our savanna it has medium wood density (0.715 g.cm⁻³; within WRF wood density varies from 0.51 g.cm⁻³ [*Sclerocarya birrea*] to 0.99 g.cm⁻³ [*Dichrostachys cinerea*]). Elephant (*Loxodonta africana*) dung was chosen owing to its abundance in savannas (a single elephant produces approx.150 kg of dung per day; Owen-Smith, 1988) and was collected in game reserves in the vicinity of WRF.

Decomposition bags (20×20 cm) were constructed from 300-micron nylon mesh (Plastok), with the edges double folded and closed with staples. Nine holes were punched on the underside of half of the bags allowing access by termites and other macroinvertebrates (i.e., the *open bag* treatment). The second half of the bags were left intact, precluding access by termites and other macroinvertebrates (i.e., the *closed bag* treatment). Grass bags contained 10 g of *T. triandra* oven-dried at 70°C for 48 h. Wood decomposition bags contained either one block of *Pinus radiata* (9×9×5 cm block, 405 cm³, hereafter referred to as *Pinus*) or one short length of a *Terminalia sericea* trunk (diameter approx. 8 cm with bark on; hereafter referred to as *Terminalia*). *Pinus* was oven-dried at 120°C for 48 h and these dry weight values were recorded. *Terminalia* wood lengths were not dried before being placed on our plots as we were interested in the fate of fresh wood and so fresh weights were recorded. Twenty-four pieces of fresh wood were weighed, oven-dried at 120°C for 48 h and then weighed again. A regression was performed between the fresh and dry weights ($R^2=0.989$) allowing us to estimate a starting dry weight (Figure S3). Dung decomposition bags each contained 20 g of elephant dung oven-dried at 70°C for 48 h. Each bag was pegged to the ground to secure it.

A total of 640 decomposition bags (80 per plot: 60 wood, comprising 20 pine and 20 *Terminalia sericea*, and 10 grass and 10 dung) were placed across a four by five grid (10 m spacing between bags) on each plot (8×0.25 ha) in December 2018 (Figure S1). Five open and five closed dung and grass litterbags were sacrificially removed from each plot at 56 and 112 days respectively. Twenty open and twenty closed wood decomposition bags were sacrificially removed from each plot after 12 months. These collection periods were deemed most appropriate as previous studies have demonstrated that dung and grass decompose over a period of months while wood decomposition occurs upwards of 6 months (Buxton, 1981; Coe, 1977;

Collins, 1981; Schuurman, 2005; Zanne et al., 2022). All twenty of the *Terminalia sericea* wood decomposition bags were removed from each plot after 24 months.

After harvesting, the decomposition bags were oven-dried at 80°C for 72 h. After drying the contents of the decomposition bags were removed. The original substrate was manually separated from any foreign plant material, soil, or gallery material (termite worked soil) taken into the bags by termites. The wood, dung, and grass were then weighed to determine the proportional mass lost. In addition, the termite sheeting and termite worked soil material was also weighed.

2.6 | Determining termite community composition

To quantify the effect of the suppression treatment on termite community composition, we sampled termites on suppression and control plots in February 2019 using the active searching transect method (Davies et al., 2013, 2021). A single transect of fixed area (200 m²) was established at each of the eight plots (four treatment and four control). Each transect measured 100×2 m and was subdivided into 20 contiguous sections each of 5×2 m. Ten minutes of sampling effort was spent in each section, giving a total of 100 min sampling effort for each transect. All microhabitats in which termites are known to occur were searched, including logs and twigs, dung, tree trunks up to a height of 2 m, termite mounds, soil beneath logs, the base of grass clumps and the base of trees. Specifically, each encounter with a population of termites was recorded and a sample of workers and where possible soldiers were collected. All termite encounters were recorded, and specimens collected, even if two or more of these in the same section were of the same species. Termite specimens were collected in February 2019. Both worker and soldier castes were collected where possible. Termites were identified at the University of Pretoria and the Natural History Museum, London (by KB and PE). Specimens were identified to genus, where possible, using soldier castes whenever available (when soldiers were not present, workers were used). Voucher specimens were lodged at the University of Pretoria, South Africa.

2.7 | Analyses

2.7.1 | Suppression effect

Cumulative mean attack curves were produced for termite suppression and control plots by summing the attack scores on the TPR across the four relevant plots for each monitoring event and then summing this over time. Using the mean scores from each monitoring event, we calculated a slope for the termite suppression and control line (using a regression through the origin for each). From this we estimated consumption rate per month across control and termite suppression plots. The difference between these allowed us to calculate the percent suppression achieved across the period. To test the difference in cumulative attack rate between termite suppression and control plots we performed linear mixed effects model

analyses (lmer in the “lme4” package in R statistical software; Bates et al., 2015) with the treatment, month and their interaction as explanatory variables, and square-root transformed cumulative TPR score as the dependent variable.

2.7.2 | Decomposition rates

There are inherent difficulties in doing large-scale manipulation experiments. The first of these obstacles was that termites from mounds >150 m from the outside edge of our plots began extending their foraging range into our termite suppressed plots where all resident colonies were suppressed. This was presumably because of ecological release from interspecific competition and this phenomenon was observed on numerous occasions. To counter this we targeted a selection of mounds outside our 1 ha plots that we identified was the source of a few sets of foraging termite parties for suppression. As termite foraging is ephemeral and patchy it was impossible to completely curb it. Consequently, we followed Zanne et al. (2022) and removed the open bags on the termite suppression plots that had been discovered by termites (i.e., bags that contained termite sheeting or termite-worked soil—Figure S9).

Proportion of mass loss from each decomposition bag was logit transformed (as the data were bounded continuous proportions; Warton & Hui, 2011) prior to performing linear mixed effects model analyses (lmer in the “lme4” package in R statistical software; Bates et al., 2015) to evaluate if the interaction between plot treatment (termite suppression versus control) and bag type (open and closed) affected the proportional mass loss from decomposition bags. In these models, plot was included as a random factor.

2.7.3 | Agents of decomposition

We calculated the mean absolute percentage of each substrate that was decomposed by termites, microbes, and other invertebrates for each substrate type (*Pinus*, *Terminalia*, dung, and grass) following Ashton et al. (2019) and Griffiths et al. (2019). For each substrate, the percentage decomposed by microbes was taken to be the mean percentage of mass lost from the closed bags on the control plots. The termite contribution (%) was calculated by subtracting the mean percentage of mass lost from the open bags on the termite suppressed plots from the mean percentage of mass lost from the open bags on the control plots. Subtracting both the microbe and termite contribution from the mean percentage of mass lost from the open bags on the control plots enables the contribution of other invertebrates to be estimated (%). In addition, we calculated the relative contributions of termites, microbes, and other invertebrates to decomposition for each substrate type (*Pinus*, *Terminalia*, dung, and grass). To do this, we used the termite contribution (%), microbe contribution (%) and other invertebrate contribution (%) as described above, expressing these as a percentage of total decomposition.

3 | RESULTS

3.1 | Termite suppression

Termite suppression reduced feeding activity on treatment plots by 72% (Figure 1). Average TPR consumption across the plots at each sampling interval was 26.9% on control plots and 7.5% on suppression plots (Figure S4). Termite feeding activity varied seasonally with very low consumption rates in winter (July, Figure S4) and particularly high levels of consumption from December to May (Figure S4).

Suppression resulted in a significant reduction in total termite encounters ($df=35$, $t=-2.279$, $p=0.03$; Figure 1b). Eleven genera of termites were found at WRF (Table S2) with no one genus making up more than 50% of the termite community. At the genus level, *Nitiditermes* (z -value=6.8; $p<0.0001$), *Ancistrotermes* (z -value=-2.0; $p=0.04$), *Macrotermes* (z -value=-2.4; $p=0.02$) and *Odontotermes* (z -value=-2.0; $p=0.02$) were all significantly reduced across collections, that is, before to after suppression (Figure S8).

3.2 | Trends in decomposition

Overall, dung decomposed the fastest, followed by grass, with wood (*Pinus* and *Terminalia sericea*) decaying the slowest (Figure 3). The *Terminalia* wood decomposed twice as slowly as the *Pinus* wood. For all substrates, mean mass loss from open bags (macroinvertebrate accessible) in control plots was significantly higher, than mass loss

from closed bags (macroinvertebrate inaccessible) (*Pinus*: $z=3.6$, $p=0.002$; *Terminalia*: $z=2.8$, $p=0.03$; dung: $z=3.3$, $p=0.005$; grass: $z=4.2$, $p=0.002$; Figures 1 and 2, Table S3). In contrast, there was no significant difference between mass loss from open versus closed decomposition bags in suppression plots ($z=-0.6$, $p=0.9$; $z=-0.9$, $p=0.8$; $z=1.1$, $p=0.7$; and $z=0.2$, $p=1.0$ for *Pinus*, *Terminalia*, dung and grass respectively, Figures 1 and 2, Table S3), confirming the effect of suppression.

3.3 | The agents of decomposition

For *Pinus*, the major decomposition agent was termites that were responsible for 65.7% of mass loss, while 34.3% was due to microbes (Figure 3, Table S3). In contrast, for *Terminalia*, the major decomposition agent was microbes that accounted for 63.1% of mass loss while 36.9% was attributable to termites. For dung, the major decomposition agent was microbes that accounted for 52.9% of mass loss, while termites accounted for 39.9% and other invertebrates for 7.2%. For grass, the major decomposition agent was microbes that were responsible for 61.1% of mass loss while 38.9% was due to termites (Figure 3, Table S3).

4 | DISCUSSION

Over the course of our study, we suppressed the activity of termites by an average of 72%. In so doing, we performed the first large-scale

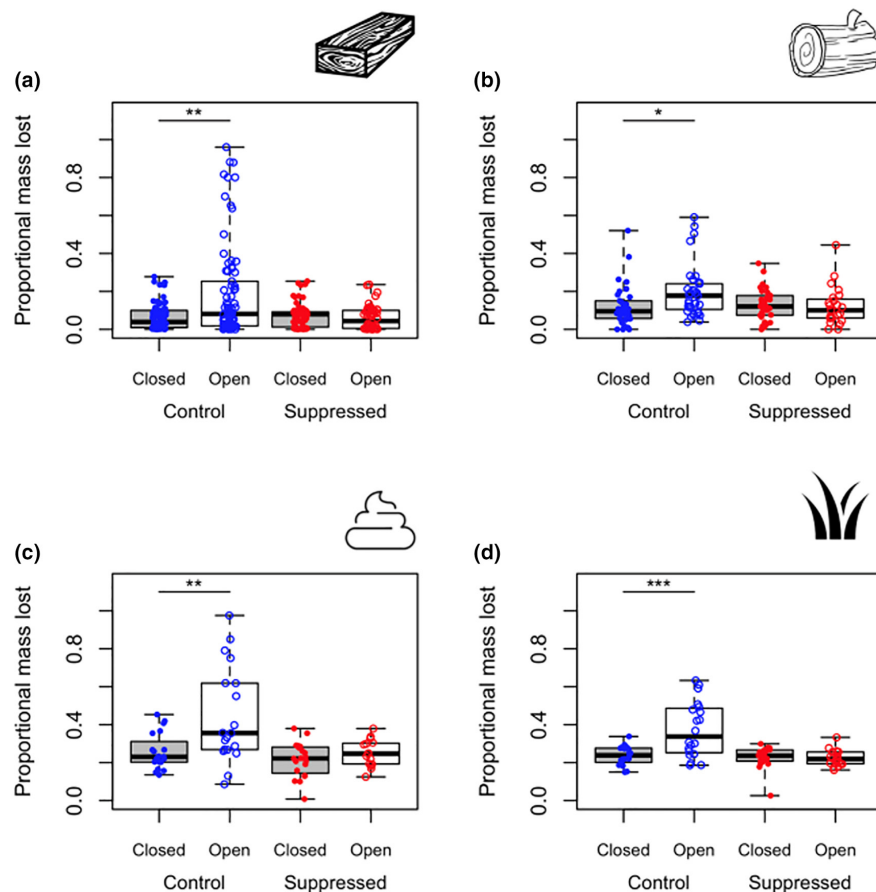
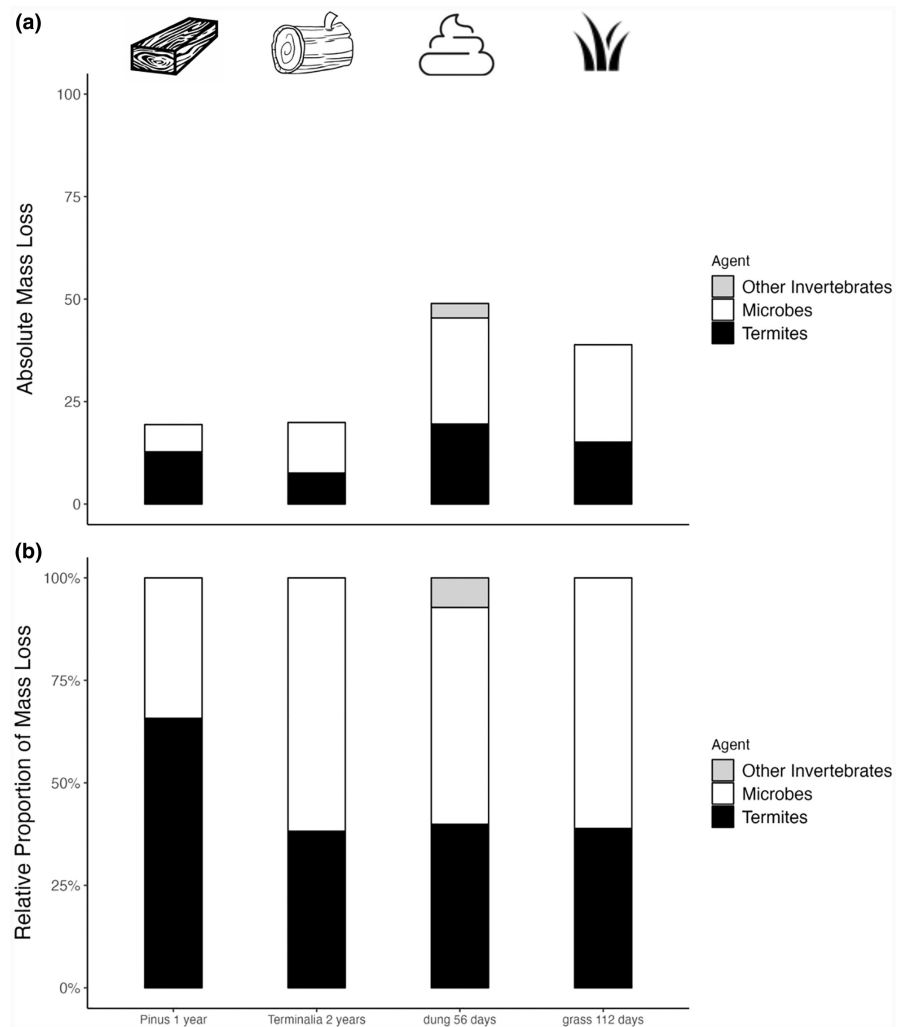


FIGURE 2 The median plus interquartile range for mass lost from open (O) and closed (C) decomposition bags for (a) *Pinus* wood blocks at 1 year; (b) *Terminalia* wood at 2 years (c) dung at 56 days and (d) grass at 112 days within control and termite suppression plots at Wits Rural Facility, 650mm Pa savanna. Level of significance (Tukey test results (z -values): ***, 0.001; **, 0.01; *, 0.05) displayed above solid lines where applicable.

FIGURE 3 The absolute (top) and relative contributions (bottom) of microbes, termites, and invertebrates to decomposition of wood (*Pinus* 1 year; *Terminalia* 2 years), dung (56 days) and grass (112 days) at Wits Rural Facility, 650mm Pa (mesic) savanna. The absolute contribution of microbes was calculated as the mean mass loss across the control closed and treatment closed bags. The absolute contribution of termites was calculated as the control open minus the treatment open while the absolute contribution of other invertebrates was calculated as the treatment open minus the treatment closed bags (Table S2). The relative contribution of each agent is the absolute decomposition value (Figure 2, Table S3) taken as a percentage of the total decomposition.



termite manipulation experiment conducted in savannas. It allowed us to partition the relative contribution of termites, microbes, and other invertebrates to wood, dung, and grass decay, letting us tease apart the key elements of the savanna carbon cycle. As expected, we found that termites are the major decomposers of *Pinus* wood, while microbes are the major decomposers of dung and grass. Contrary to expectation, we found that the decomposition of fresh *Terminalia* wood was dominated by microbes rather than termites or other invertebrates.

There are very few decomposition studies, including those conducted in savannas, that use more than a single substrate type (with the exception of Veldhuis et al., 2017, Dangerfield & Schuurman, 2000). The use of multiple substrates in savanna decomposition studies is essential as savannas are characterized by a mixture of contrasting life forms (trees and grasses) and a strong alternation of wet and dry seasons (Scholes & Archer, 1997). Consequently, the key decomposition substrates—wood, dung, and grass—are spatially and temporally variable. The amount of dead wood is clearly linked to tree cover and is available throughout the year, except after intense fires. In contrast, grass is a seasonal resource which is frequently in short supply later in the dry season. The scarcity of grass is either the result of fire or during prolonged

droughts due to competition with grazing mammals (Lepage, 1981). Dung is both a patchy and ephemeral resource that varies with season. There is likely to be less dry dung available in the wet season, as dung beetles are active and remove most of it (Ferrari & Watson, 1970; Freyermann et al., 2008). Furthermore, in areas, such as the Okavango, where elephants range increasingly further from permanent water sources during the wet season there are large differences in seasonal dung input across the landscape (Buchholtz et al., 2019). Using multiple substrates in our study was especially informative: not only did the rates of decomposition differ widely, but the dominant agent of decomposition also varied.

4.1 | The agents of decomposition

4.1.1 | Wood

We expected termites to dominate both *Pinus* and *Terminalia* wood decomposition. This held for *Pinus* where termites were responsible for two thirds of mass loss but in the case of *Terminalia*, termites were responsible for ~40% of mass loss while microbes accounted for the other ~60%.

This difference might, in part, be attributable to the greater density of *Terminalia* wood (relative to *Pinus*) that slowed termite decomposition. Behr (1972) demonstrated that termites preferentially consume lower density wood. This they hypothesized, was because wood density affects the fragmentation process by termites. In addition, termites have been shown to prefer dry wood over fresh wood (Lamto savannas, Ivory Coast; Josens, 1972 and Grassé, 1937) although very few studies have examined this in savannas. Furthermore, wood decomposition does not proceed linearly. It involves a succession of decomposer organisms and a changing substrate over time (Ulyshen et al., 2016). Despite this, almost all previous decomposition studies have exclusively used dried wood that lacks a cambium and bark layer (Ulyshen et al., 2016); this may be problematic because it excludes the initial suite of decomposer organisms, for example the phloem- and wood-feeding insects that use the cambium and bark layers as a food resource and oviposition substrate (Stokland et al., 2012). Through their tunneling activities these taxa can play an important role in facilitating fungal colonization (Weslien et al., 2011). However, we found no evidence of any other invertebrates in either the *Pinus* wood blocks or the *Terminalia* wood lengths—no holes in the wood or evidence of the insects themselves. As an alternative, Cornwell et al. (2008) have suggested that bark may limit microbial access to the wood during the initial stages of decomposition but may ultimately have a positive effect by enhancing moisture retention. It seems likely that the microbial decomposition of the *Terminalia* wood was enhanced by both the presence of a bark layer and because the wood was wet (fresh) when placed on the plots and available first in the wet season when moisture levels would have been highest.

We are unable to disentangle whether the lower rate of *Terminalia* wood decomposition was due to it being a higher density wood, possessing a bark layer or the fact that the wood was fresh when placed on the plots. Nevertheless, such large differences in decomposition (both the rate and contribution across agents) between the two species of wood is an important finding, as the choice of species can clearly influence the conclusions drawn about wood decomposition more broadly. To our knowledge this is the first time that this phenomenon has been investigated in a savanna. Furthermore, our findings demonstrate the pivotal role of termites and the apparently inconsequential role of other invertebrates in savanna wood decomposition.

4.1.2 | Dung and grass

The half-life of the elephant dung in our study site was 90 days (0.24 years; k -value=1.27; Table S4). In a study conducted in Tsavo National Park, Kenya (500 mm Pa), Coe (1977) found that elephant dung decomposed completely within 80–85 days. The higher rate of dung decomposition observed by Coe (1977) is expected as their study was conducted in the dry season when termites are known to remove higher quantities of mammalian dung, while our study was

carried out in the wet season (Freymann et al., 2008). As we focussed on dry dung, we have excluded the role of dung beetles in dung removal and decomposition. Dung decomposed at a higher rate than grass. Dung decomposition bags saw greater mass loss in 56 days than grass decomposition bags did in 112 days. Elephant dung is a higher-quality litter substrate than dead *Themeda* grass owing to its lower C:N ratio (21:1 versus 37:1; Stanbrook, 2018; Osanai et al., 2012). Thus, elephant dung likely has a higher nutritional value, palatability, and digestibility than *Themeda* grass (Barbe et al., 2017). In addition, the high rate of decomposition may be because dung has been primed both mechanically through fragmentation and biochemically by mammalian herbivores and their endosymbionts (e.g., gut bacteria; Freymann et al., 2008). The rapid rate of dung decomposition emphasizes the importance of termites in dry dung decomposition. The dearth of studies examining the role of termites in dung feeding and decomposition is in strong juxtaposition to the large number of studies on the role of dung beetles in decomposition and nutrient cycling (Freymann et al., 2008; Hanski & Cambefort, 1991). Across all four substrates, dung is the only substrate where substrate loss was attributed to other invertebrates in addition to termites. However, while we noted the presence of predatory staphylinid beetles that consume fly larvae living in animal dung we observed no other invertebrates. It is likely therefore that, rather than other invertebrates playing a role in decomposition, there was a small leaching effect from our dung bags. Following drying, a tiny fraction of the elephant dung formed a powdery residue which, in a few instances, we observed falling through the decomposition bag holes (in the macro-invertebrate accessible bags). This effect might have been exacerbated by the fact that these bags were put out during the wet season. The bulk of elephant dung was very coarse (Owen-Smith & Novellie, 1982) the leaching effect was small (<7%).

It is also possible some photodegradation may have occurred within the dung and grass decomposition bags; however, as the top panels of both bag types were identical in design, all bags were subject to a similar degree of photodegradation so our results will not be biased. Additionally, the fine mesh of the decomposition bags is likely to offer the substrates some shade from radiation, so we expect photodegradation to be low (in keeping with Acanakwo et al., 2019).

4.2 | Suppression and the termite community

We significantly reduced the number of termites on our suppression plots. While suppression reduced the number of encounters across all genera our treatment reduced only a subset of genera. Specifically, we managed to significantly reduce *Macrotermes*, *Nitiditermes*, *Odontotermes*, and *Ancistrotermes* numbers. The marked reduction in abundance across the other genera ($n=3$) suggests that these too were suppressed but the power of these statistical tests was low due to a low sample size. *Macrotermes* and *Nitiditermes* are the only two genera where the epigeal mounds were both mechanically

transformed/removed, and a suppression treatment was applied. Over the course of the experiment, it was evident that the mounds of *Macrotermes* were no longer active and no *Nitiditermes* mounds remained.

5 | CONCLUSION

By performing a suppression experiment that allowed us to partition the relative contribution of termites, microbes, and other invertebrates to decomposition we were able to determine that termites are the only invertebrate group that contributes significantly to the decomposition of wood, dry dung, and grass in savannas. Global decomposition studies (e.g., Zanne et al., 2022) assume that decomposition is carried out exclusively by either by microbes or termites. This study demonstrates that, particularly in the case of savannas, this is a reasonable assertion notwithstanding the role of dung beetles in wet dung. Within reasonable timeframes, we found that termites were responsible for two thirds of the mass loss from dry wood and a third of the mass loss from fresh native wood, dry dung, and dry grass while microbes were responsible for the difference. Global studies have established that decomposition is exceedingly climate-sensitive and driven by the complex interplay between temperature and precipitation (Siebold et al., 2021; Zanne et al., 2022). In their global decomposition study across all biomes Zanne et al. (2022) found that termite-mediated wood decomposition peaks in tropical semi-arid areas. A connected study we conducted along a savanna rainfall gradient (380–650 mm; Bunney, 2023) supported this finding for wood but found the inverse for dung and grass decomposition—absolute dung and grass decomposition increased with increasing rainfall. Therefore, in drier savannas, we would expect the absolute decomposition of wood by termites to increase while the absolute decomposition of dung and grass by termites we would expect to decrease. In wetter savannas we would expect the inverse. Termites stand apart from all other insects in their impact on decomposition within savannas and should be recognized alongside microbes and fire as the primary agents of wood, grass, and dry dung turnover in global carbon models.

AUTHOR CONTRIBUTIONS

CLP, MR, PE, and WT conceived the ideas and designed the methodology; KB collected the data; KB and MR analyzed the data; KB, CLP, and MR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.stjq2c7t>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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