Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2018:71

How termites and large mammalian herbivores influence tree communities, seed removal and wood decomposition in an African savanna

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Ås (2018)

Thesis number 2018:71
ISSN 1894-6402
ISBN 978-82-575-1539-3

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Acknowledgements

My journey of the Ph.D education has been a thrilling experience. Many people made invaluable contributions along the way. I wish to most sincerely thank my supervisors who have been my most important guides. I am grateful to Stein who took me on as a Ph.D. student and gave me unreserved supervisory support all through the four years; during field work, data analysis and write-up. Stein stirred optimism in me at moments when morale was low. His enthusiasm for my work was reassuring; it meant I was never alone in the quest to understand the concepts of savanna ecology. Douglas helped me to interpret, write and communicate ecological results better. I am not yet at my best, but I am now convinced that a good sentence should indeed be short and clear! I also wish to thank Douglas for correctly judging appropriate moments when breaks were due. The weekend walks to Lake Årungen, the water falls, and the walks through the forest in the company of Miriam, Kila, Fredrick and Miguel were always revitalizing.

The Norwegian State Educational Loan Fund (Lånekassen) sponsored the study for which I am thankful. I am grateful to the Uganda Wildlife Authority (UWA) who made it possible to conduct the experiments in the field. UWA granted me research permits to access Lake Mburo National Park.

I wish to express my gratitude to the leaders and members of the Ecology Group for the Monday lunch meetings, ecology excursions and parties. It was always nice to know more about other ecologists and fun to learn about the different topics they were working on.

The administrators of the Faculty of Environmental Sciences and Natural Resource Management (MINA) made studying at the department an enjoyable experience. I would like to thank Kari, Grethe, Ole-Wiggo, Stig and all the others in the administration team who did all in their means to make my stay at the department hassle free.

I wish to thank my mentors at Makerere University, World Agroforestry Center - Uganda office, and the National Forestry Resources Research Institute for their support and interest in my studies. I am grateful to Prof. Fred Babweteera, Prof. Jacob Agea, Prof. Mnason Tweheyo, Prof. Joseph Obua, Prof. JBL. Okullo, Prof. Gerald Eilu, Prof. Tom Otiti, Dr. Paul Okullo and Dr. Clement Okia who cared to check on my progress and spoke words of encouragement.

Thank you, Fredrick for sharing an office with me and for being a good friend. Thank you, Mari for helping with course registration when my inability to comprehend instructions written in Norwegian limited my options of action. Thanks to Marte, Rafael, Solrun, Miguel, Yennie, David, Dennis, Saeed, Nathan, Mekdes, Dawit, Mengesteab, Mahdieh and Ehsan for the laughter and little chats in the corridors and at the Ph.D. cake breaks. Sam and Sjur passed by our office regularly for brief chats; thanks for the thoughtfulness.

Finally, I wish to thank my mother, brothers and sisters, plus my entire extended family for being patient and supportive of my studies. I was always sure that one day the studies would be over, and I would return to meet you all.

Ås, July 2018

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Summary

The heterogeneity and extent savannas makes them resilient, diverse and socioeconomically important. Abiotic factors determine large-scale variation on a, but biotic factors matter at small-scales. In the African savannas, termites and ungulates contribute to spatial heterogeneity. Although we know that termites and ungulates influence savanna ecosystems, their combined influence on woody plant communities is uncertain. Despite a near global decline in wild mammalian herbivore population, it remains unclear how woody plant communities respond to such losses. The interactions between termites and ungulates are likely to influence the ecological process of post-dispersal seed removal. Termite activity is also likely to influence wood decomposition, but these effects remain poorly characterized.

The aim of this study was to experimentally investigate the influence of nutrient-rich termite (*Macrotermes*) mounds and their interactions with ungulate presence and absence on woody vegetation and on seed removal. We also assessed how wood decomposition varied across the landscape, on- and off-mound. We postulated that; a) interactions between termite mounds and ungulates influence woody plant community properties, which would in turn influence seed removal rates; b) the activity of termites determine wood decomposition rates. To discern the effects of termites and ungulates on woody plant community dynamics and seed removal rates, we assessed woody plants on mound and adjacent off-mound plots (with and without ungulates). In addition, we considered the effect of *Macrotermes*-occupied (active) and non-occupied mounds (inactive) on seed removal. We assessed rates of wood decomposition on five pairs of active-inactive mounds, each with shaded (with canopy cover) and open (without canopy cover) locations, in addition to sample locations off-mound in open level areas between each active-inactive mound pair.

We found that woody stem density and basal area were higher on- than off-mounds and each supported distinct woody vegetation. Species richness and plot level diversity were greater on- than off-mound. Ungulate exclusion had little detectable effect on composition either on or off-mound. However, while ungulate exclusion by fencing resulted in an increase in woody plant species richness and diversity off-mound, there was little effect on-mound. Although seed removal rates were higher on- than off-mound, ungulate exclusion markedly reduced removal rates on-mound, but not off-mound. Seed removal rates were higher on *Macrotermes*-occupied (active) mounds (30.9% per three days) than unoccupied (inactive) mounds (26.7% per three days). Wood decomposition rates across all selected common species in the landscape proceeded at 1.2 times faster rates on active than inactive mound. Wood decomposition was higher in the shaded than in the open locations. After 12 months, wood mass loss was markedly lower off-mound (12.6 ± 0.8%) than on inactive (19.7 ± 1.2%) and active mound (25.9 ± 1.5%). Mass loss rates reduced with increase in wood density.

These findings indicate that *Macrotermes*-mound induced habitat heterogeneity is an important determinant of woody plant community dynamics. In addition to the effects of mound, the active *Macrotermes* themselves influenced rates of seed removal (even though they do not consume them) and wood decomposition rates. Ungulate effects on species richness and diversity measures were stronger in the nutrient-poor off-mound than on-mound sites. Greater stem density and diversity of woody plants on mounds relative to off-mound areas, coupled with their resistance to change in composition with reducing ungulate abundance suggests that mounds support distinct woody plant communities relative to off-mound sites. The increased rates of wood decomposition on mounds point to positive feedback effects for tree regeneration and recruitment. We conclude that the effects of the interaction between ungulates and termites on woody plant community properties and ecosystem processes are context dependent.

List of Papers

Paper I

Acanakwo, E.F., Okullo, P., Sheil D., and Moe, S.R: Termites confer resistance to changes in tree composition following reduced browsing in an African savanna. *Submitted*

Paper II

Acanakwo, E.F., Okullo, P., Sheil D., and Moe, S.R. Exclusion of ungulates increases woody plant diversity in a low nutrient savanna landscape, but not on nutrient rich termite mounds. *Submitted*

Paper III

Acanakwo, E.F., Sheil, D., Moe, S.R. (2017). Termites and Large herbivores influence seed removal rates in an African savanna. Ecology 98:3165-3174.
https://doi.org/ 10.1002/ecy.2038

Paper IV

Acanakwo, E.F., Sheil, D., Moe, S.R. Wood decomposition is more rapid on- than off-termite mounds in an African savanna. *Submitted*

1.0 Introduction

Savannas are characterized by co-dominance of trees and grasses, of which the former are discontinuous while the latter are continuous (Scholes and Archer 1997, Sankaran et al. 2005, Bond 2008). Savannas cover more than 10% of the world´s land surface and more than 50% of the African continent (Scholes and Archer 1997). The tree-grass balance of the savannas make them socioeconomically important for the large human populations that live within and earn a livelihood by exploiting them (Frost et al. 1986, Archer et al. 2001).

Savannas are maintained and regulated by factors including rainfall, soils, herbivory and fire (Scholes and Archer 1997, Sankaran et al. 2005, Sankaran et al. 2008). These factors can create communities of varying sizes and patterns of arrangement, exhibiting structural and functional heterogeneity at multiple spatial and temporal scales (Frost et al. 1986, Picket et al. 2003). Ultimately, landscape heterogeneity results in multiple habitat types enabling a relatively large number of species and contrasting life forms to coexist (Tews et al. 2004, Eilts et al. 2011). Consequently, landscape heterogeneity coupled with their considerable extent, makes the savannas one of the most ecologically resilient, biologically diverse and socioeconomically important ecosystems (Frost et al. 1986, Du Toit and Cumming 1999).

Climate is considered the primary determinant of vegetation cover on a large-scale, within the savannas. However, despite efforts to separate the processes that yield patterns of woody plant distribution in the savanna landscape, realized vegetation patterns differ considerably from those predicted by climate alone (Sankaran et al. 2005, Sankaran et al. 2008, Lehmann et al. 2014). There is still an inability to predict, to any satisfactory degree, the structure of the savanna tree layer (Staver 2018). Nonetheless, biodiversity and traits of organisms in the savanna have been linked to spatial heterogeneity in environmental resources (e.g. mineral, nutrient and water levels) and habitat types. The heterogeneity arises mainly from spatial differences in soil physical and chemical states and their interactions with other factors such as fire and herbivory (Du Toit and Cumming 1999, Okullo and Moe 2012, Young et al. 2013, Seymour et al. 2014, Pringle et al. 2016).

Spatial heterogeneity is exhibited at varying scales. On a coarse scale, factors such as tectonic uplifts or subsidence, geology, climate and geomorphology determine heterogeneity (Picket et al. 2003). At finer scales, nested within large scale determinants, slope geomorphology determines the form, length and steepness of land units and thus govern gradients that drive local scale distribution of water, nutrients, toxics and organisms.

Landscape heterogeneity is a key determinant of biodiversity (Tews et al. 2004, Fahrig et al. 2011). It can influence biodiversity through effects on survival and growth rates (Beckage and Clark 2003), dispersal success (Valiente-Banuet et al. 1991), resource availability (Konaté et al. 1999, Sileshi et al. 2010, Seymour et al. 2014) and disturbance regime (Turner 1989, Clarke 2002).

At large scale, heterogeneity is mainly determined by abiotic factors (Picket et al. 2003). At small scales however, heterogeneity may be determined by biotic factors, such as large mammalian herbivores (Augustine et al. 2003, van der Waal et al. 2011) and termites (Sileshi et al. 2010, Jouquet et al. 2011). While the physical environment is crucial to the generation of heterogeneity, organisms are especially important because they react to and amplify physical components of heterogeneity (Picket et al. 2003). Studies show that organisms which cause changes in the physical state of abiotic materials in the different biomes through “ecosystem engineering” (Jones et al. 1994) can cause an overall positive and significant effect on species richness, and consequent implications for vegetation and animal distribution (Romero et al. 2015).

1.1 Large mammalian herbivores as drivers of heterogeneity of woody vegetation

Large herbivores exert strong impacts on plant communities through consumption, deposition of urine and dung, soil compaction, erosion as a consequence of trampling and dispersal of plant seeds on fur or dung (Smit and Putman 2010). These impacts ultimately influence species composition, richness and diversity, thus inducing vegetation heterogeneity (Olff and Ritchie 1998, Knapp et al. 1999, Bakker et al. 2006). Nonetheless, the effects of large herbivores on plants vary depending on their feeding guild as grazers, mixed feeders or browsers (Moe et al. 2014). For example, the effect of grazers on seedling establishment is indirect but their effects are positive. Grass can compete strongly with tree seedlings for light and soil nutrient resource. When grazers reduce herbaceous cover, rodent densities reduce (Goheen et al. 2004, Saetnan and Skarpe 2006). Rodents can directly and negatively affect seedlings through consumption of seeds. In addition, grazing suppresses the accumulation of grass biomass and consequently the destructive effects of fire on seedling regeneration (Holdo et al. 2012).

Mixed feeders which predominantly feed on grass, but resort to woody plants when the quality of grass reduces during dry conditions, can affect plant seedling establishment negatively through seed (Goheen et al. 2004) and seedling (Moe et al 2009b) predation, or positively through seed dispersal (Miller 1996, Milton and Dean 2001).

Browsers which forage on woody plants may affect tree regeneration positively through seed dispersal, but predation of seeds and seedlings suppresses tree establishment and growth (Moe et al. 2014). The increase of woody plants into higher height classes to attain physiological maturity e.g., reproductive capacity, may be suppressed by browsers which impose height-structured recruitment limitation (Fornara and du Toit 2007, Staver and Bond 2014).

African savannas support diverse species of abundant large mammalian herbivores (Du Toit and Cumming 1999). The impacts of these herbivores on tree-grass balance may therefore, be determined by the dominant herbivore guild, whose impact will depend on biomass densities of the guild members (Barnes 2001, Moe et al. 2014).

1.2 Termite ecology and biology

Termites are eusocial insects belonging to the blattodea order (Eggleton and Tayasu 2001). They are predominantly a tropical group with the highest diversity in the Afrotropics followed by Neotropics and Asian tropics (Eggleton 2000). They form a dominant group of invertebrate decomposers of dead organic matter (Bignell and Eggleton 2000). Termites can be divided into three groups based on their habitats as; damp wood, drywood and subterranean, or into "lower" (for all families except Termitidea) and "higher" termites (mostly Termitidea), based on microbial association (Ahmad et al. 2018).

Termites of the Macrotermitinea subfamily grow fungus with which they have a symbiotic relationship, in their nests. The fungus break down lignin in the plant material fed to them by termites (Jouquet et al. 2011, Poulsen et al. 2014). Old fungal bodies are then eaten by termites which further disperse their spores (Poulsen et al. 2014). While many *Macrotermes* species have a narrow range, some e.g., *Macrotermes bellicosus*, *M. falciger*, *M. michalseni* and *M. subhylinus* occur throughout the African savanna.

Termites induce heterogeneity in floristic composition and vegetation patterning in the African savannas (Sileshi et al. 2010). Heterogeneity is created via two mechanisms; mound building activities and foraging (Sileshi et al. 2010). Through mound building, *Macrotermes* translocate and mix huge volumes of soil vertically and horizontally. Because they use fine clay particles in mound construction, mound soils contain higher soil moisture, nutrients and mineral levels relative to the adjacent inter-mound areas (Konaté et al. 1999, Sileshi and

Arshad 2012). These mounds create resource-rich spots which support tree regeneration and establishment (Traoré et al. 2008a). The trees associated with mounds differ from those growing off-mound (Joseph et al. 2014, Davies et al. 2016). Therefore, *Macrotermes* mounds increase the range of environmental conditions over small spatial scales thus allowing more plant species with contrasting niches to coexist.

Within the tropics, termites of the genus *Macrotermes* (Macroterminae family) occur within mainland Africa, Asia and Madagascar (Cornwell et al. 2009). In the African continent, *Macrotermes* are widely distributed from the rain forest to arid savannas (Sileshi et al. 2010). With live biomass densities estimated at 70 - 110 Kg ha^{-1}, *Macrotermes* densities are comparable to the biomass of ungulates and mega herbivores in African savannas (Loveridge and Moe 2004). These termites are large and build epigeal mounds, within which fungus bodies are cultivated for the exosymbiotic benefit of lignin digestion (Schuurman 2005, Joseph et al. 2018). Because *Macrotermes* cultivate fungus bodies in their nests by maintaining a constant temperature and moisture through all seasons, they are able to remain active in the process of decomposition during hot and dry seasons when the activity of most other soil macro-invertebrates is diminished or eliminated (Veldhuis et al. 2017, Joseph et al. 2018).

Termites make up 40-65% of the overall soil macrofaunal biomass and impact the soil physical and chemical properties considerably (Jouquet et al. 2011). By loosening soil and moving particles vertically and horizontally, *Macrotermes* concentrate fine sized soil particles used for mound construction. The accumulation of clay results in high cation exchange, high soil organic matter content and higher water retention on-mound relative to off-mound areas (Konaté et al. 1999, Sileshi and Arshad 2012). The higher mineral, nutrient and moisture levels on-mound relative to off-mound areas creates resource-rich patches which facilitate tree establishment and growth (Traoré et al. 2008, Moe et al. 2009). The resulting vegetation heterogeneity supports communities of other taxa including invertebrates and vertebrates (Fleming and Loveridge 2003, Pringle et al. 2010, Okullo et al. 2013). The variation in habitat qualities and their effects on the distribution of animal taxa can influence seed removal, an ecological process that can ultimately influence plant recruitment (Hulme and Borelli 1999, Linzey and Washok 2000).

1.3 Interactions between termites and large mammalian herbivores

Termites and large herbivores are two important functional groups, essential for the ecosystem functioning of the African savanna (Bonachela et al. 2015, Davies et al. 2016). They both contribute to nutrient redistribution across the landscape through different mechanisms, such as foraging, mound-construction and excretion (Augustine et al. 2003, Sileshi et al 2010; Veldhuis et al. 2018). In some savannas, ungulates are reported to feed more intensely on and around *Macrotermes* mounds (Loveridge and Moe 2004, Mobæk et al. 2005, Brody et al. 2010). The high intensity of selective ungulate feeding is likely to result in variation of vegetation structure and diversity measures.

1.4 Study aim and objectives

Although termite and ungulate ranges overlap, and their foraging activities known to exert influence on savanna vegetation and animal communities, only a few studies have considered their combined influence on woody plants (Støen et al. 2013, Joseph et al. 2015, Seymour et al. 2016, Davies et al. 2016). At a time when global large mammalian herbivore populations are declining, mainly due to anthropogenic activities (Collen et al. 2009, Dirzo et al. 2014), it is not clear how woody plant communities in the savannas would respond to the loss of ungulates. In addition, the interactions between termites and large herbivores are likely to influence ecological processes of seed removal and wood decomposition, but knowledge of the factors that determine the rates of these processes, across the landscape is currently limited.

The aim of this study was to experimentally investigate the influence of spatially explicit nutrient-rich mound patches attributed to *Macrotermes* activities, and their interactions with ungulates on tree community composition, diversity measures and on ecological process of seed removal and wood decomposition. We postulated that the interaction between termites and ungulates influence woody plant properties, which in turn influence rates of seed removal. We also postulated that wood decomposition rates vary with termite activity across the landscape (Fig.1). To ascertain the extent to which the interaction between termite mounds and ungulates influence woody plant community structure, patterns of native woody plant seed removal, and how termite activity influence wood decomposition rates, we addressed the following issues;

1. The influence of ungulate exclusion on tree species composition in a spatially heterogeneous landscape (**Paper I**)
2. The influence of resource variability in the landscape on diversity of woody plants in the presence and absence of ungulates (**Paper II**)
3. Variation in tree seed removal rates within the landscape in the presence and absence of ungulates (**Paper III**)
4. Variation in wood decomposition rates across the landscape and how the presence of termites influences these rates (**Paper IV**)

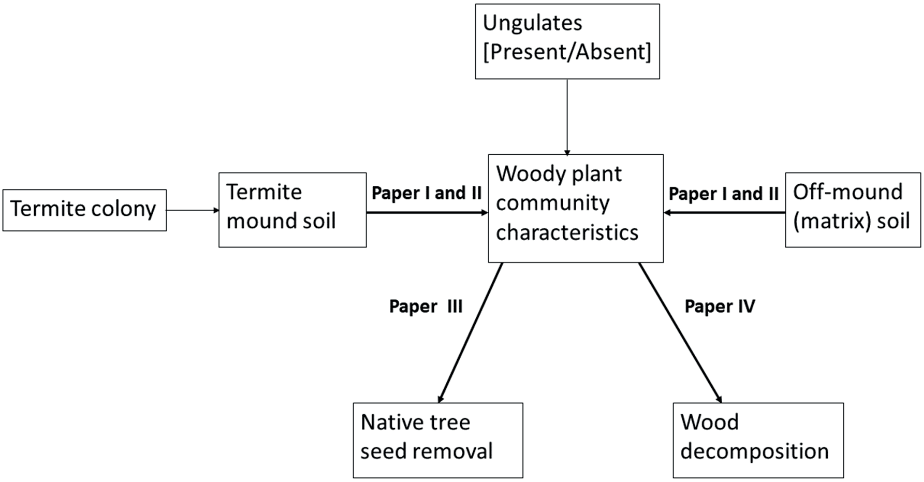

Figure 1. Conceptual framework showing the pathways of potential effects of biotic factors (termites and ungulates) on woody plant communities within the savanna landscape and subsequent effects on ecosystem services of seed removal and wood decomposition. The thick arrows indicate the interaction pathways that we experimentally assessed in this thesis.

2.0 Materials and Methods

2.1 Study area

The experiments for this study were conducted within the 260 km^2 Lake Mburo National park in south western Uganda (Fig. 2). 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-May and between September-November. June and July are the driest months. Average monthly temperatures range from 19.8 ºC to 20.9 ºC (www.climate-data.org). The vegetation in Lake Mburo National Park is mainly grass-dominated savanna, consisting of mound-associated thickets and scattered woody plants in off-mound areas and steep hills surrounding a perennial lake fringed by forest patches (Bloesch 2008, Moe et al. 2009a). Large mounds (5-10 m in diameter, Fig. 3) constructed by *Macrotermes subhyalinus* (Rambur) are conspicuous features in much of the park covering about 5% of the landscape (Moe et al. 2009, Moe et al. 2017). The woody plant community composition on these mounds differ from the community off-mounds and tree densities and diversity are higher on- than off-mound (Paper I, Støen et al. 2013). The common woody plant species growing on mound habitats include *Rhus natalensis* Bernh. ex C. Krauss, *Grewia* species, *Teclea nobilis* Del., *Allophylus africanus* P. Beauv., *Scutia myrtina* (Burm.f.) Kurz, and *Capparis* species, while *Acacia* species such as *A. gerrardii* Benth., *A. sieberiana* DC., *A. hockii* De Willd. and *Dichrostachsys cinereal* (L.) Wight & Arn dominate in off-mound areas (Paper I, Moe et al. 2009). Woody plant cover on vegetated mounds is not uniform. Most mounds have relatively dense shaded parts, covered by woody plant canopies and more exposed parts, without canopy cover (Fig. 3). The vegetation on the mounds have also been shown to be preferential feeding areas for large mammalian herbivores (Mobæk et al. 2005). Common ungulates in the landscape include impala -*Aepyceros melampus* (Lichtenstein, 1812), African buffalo – *Syncerus caffer,* waterbuck -*Kobus ellipsiprymnus* (Ogilby, 1833), bushbuck -*Tragelaphus* *scriptus* (Pallas, 1766), zebra -*Equus q. burchelli* (Gray, 1824), warthog -*Phacochoerus africanus* (Gmelin, 1788), topi -*Damaliscus lunatus* (Burchell, 1823) and eland -*Taurotragus oryx* (Pallas, 1766).

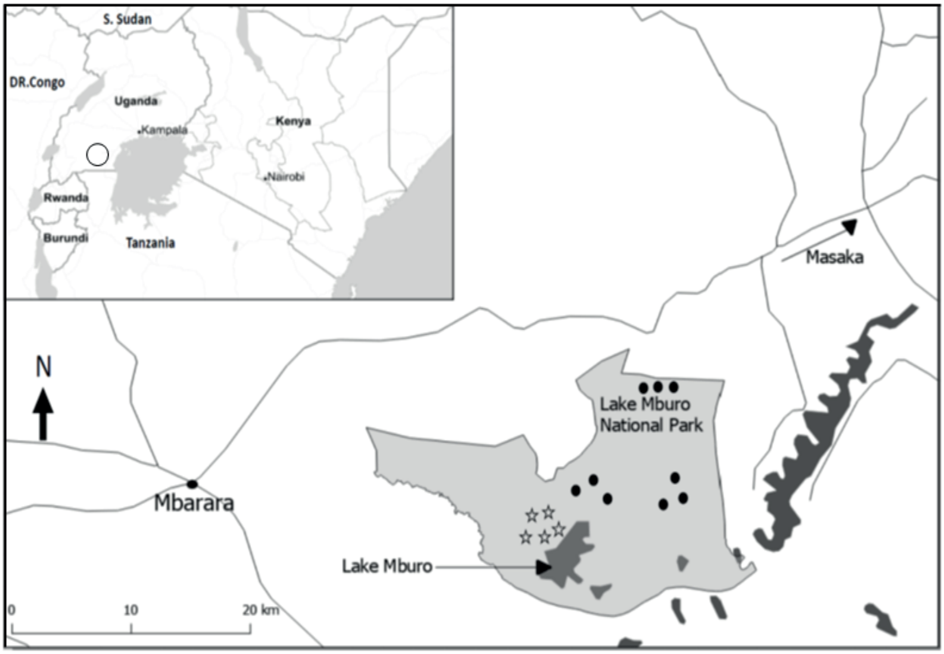

Figure 2. The location of Lake Mburo National Park in Uganda. All experiments for the study of the interactive effects of termites and ungulates on woody plant communities, seed removal and wood decomposition were conducted within this 260 km^2 park. The filled circles show approximate locations of the nine replicate sites. Each site had four plots; two on-mound and two off-mound; one of each pair of mound and off-mound plots was subjected to a fence treatment. The nine replicate sites were used to conduct experiments for Paper I, II and part of Paper III. The open stars show approximate location for the five pairs of active and inactive mounds. The five active-inactive paired mounds were used to conduct the experiment for Paper IV.

Figure 3. Vegetated *Macrotermes* mounds in the flat valley bottoms of Lake Mburo National Park. Most mounds have open (without shrub canopy cover) and shaded (with shrub canopy cover) parts (Photo: Acanakwo, E. F)

2.2 Experimental setup for **Paper I & II**

The first two papers of this thesis were based on woody plant species identities and abundance assessed in nine experimental replicate sites within 10 years (2005 to 2015). Two mound and two off-mound plots were located within each of the nine sites. One of each pair of mound and off-mound plots within each site was assigned to fencing treatment using a 5 cm galvanized chain link mesh, supported by 2 m high steel angle bars firmly fitted in the ground. Thus, each site was comprised of four treatments plots; unfenced off-mound, fenced off-mound, which limited access to the plots by ungulates (> 5kg); unfenced mounds, and fenced mounds (Fig. 4). All four treatments plots within a site were the same size, but plot sizes within the nine sites varied from 90 to 260 m^2 (Okullo & Moe 2012). Because plot sizes were different at the sites, woody plant abundances per plot were converted to densities, i.e., number per hectare (10000 m^2). All mounds were occupied by fungus-growing *Macrotermes* (active) when the experiment was originally established (Okullo and Moe 2012) but were all found to be without the *Macrotermes* (inactive) 10 years later (in 2015). *Macrotermes* mounds are stable and persistent features of the savanna landscape, with long life spans measured in centuries and millennia, and mounds are continuously recolonized and abandoned (Pomeroy 2005, Erens et al. 2015). The soil properties of large mounds are maintained regardless of the presence or absence of *Macrotermes* (Erens et al. 2015).

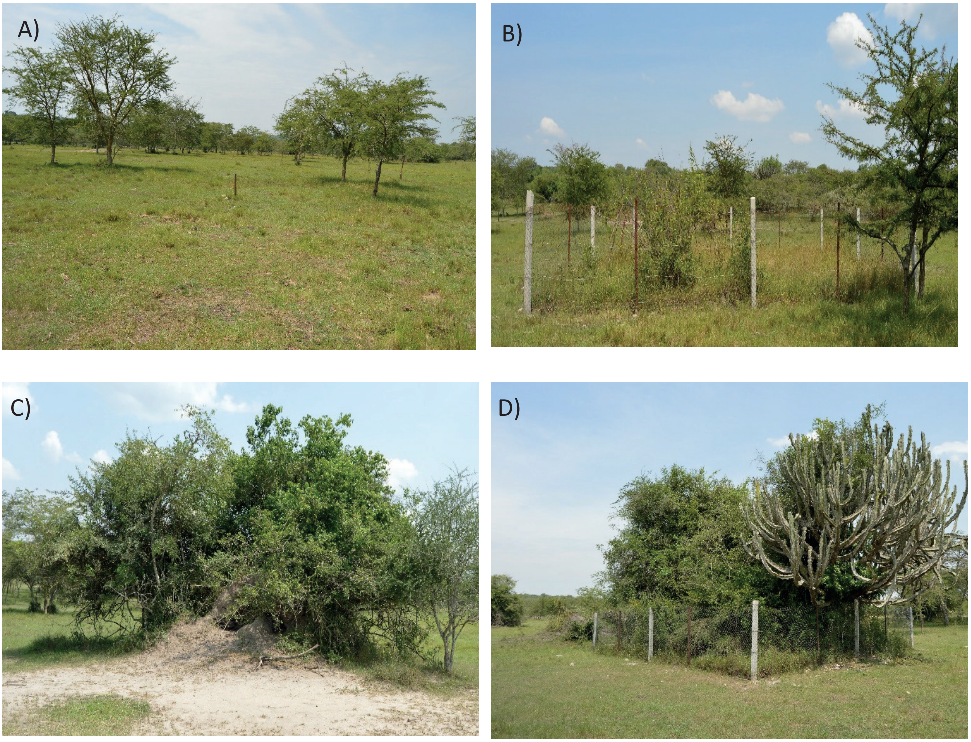

Figure 4: The four plots per experimental site (n = 9) used in this thesis for Papers I-III. A) Unfenced off-mound plots; B) Fenced off-mound plot; C) Unfenced on-mound plot; D) Fenced on-mound plot (Photos: Acanakwo E. F)

2.2.1 Dataset and explanatory variables for Paper I

Woody plant community survey

We recorded all woody plants taller than 30 cm, between April and August in 2006, 2008 and 2015 (that is, one, three and ten years after experimental setup). We identified woody plants in the field with reference to Katende et al. (1995) and local experts. For woody plants whose heights exceeded 130 cm from the ground, in 2008 and 2015, we measured diameter at breast height (dbh) 130 cm from the ground, using a diameter tape. In addition, we measured bark thickness for all individual trees recorded by extracting a wedge of bark from the stem at 20 cm from the ground using a sharp machete. When the woody material of the stem was visible, a calibrated ruler was inserted in the wedge and distance from the wood to the outer-most surface of the bark was recorded as bark thickness.

Woody plant traits

We examined four traits; fruit-type (whether fruits were fleshy or dry), whether leaves were evergreen or deciduous, spinescent (whether physically armed or unarmed with spines), and bark thickness. The traits were chosen to relate with plants´ regeneration strategy (we expected fleshy-fruited trees to be dispersed by animals), soil moisture stress strategies, anti-herbivore strategy, and fire tolerance.

2.2.2 Statistical analyses for Paper I

We constructed a generalized linear mixed effects model to test the effects of fencing (unfenced vs fenced), habitat type (on-mound vs off-mound) and year of survey as fixed variables, on stem density following negative binomial error distribution. We used plot identity as random variable. We used the same variables to test their effects on basal area measurements by constructing a generalized linear mixed effects model following Gaussian errors and log link function. To test the effect of treatment on tree composition, we used permutation analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity values. We used a generalized linear model following quasibinomial distribution to test the effects of fencing, habitat and year of survey on the proportion of stem density of fleshy fruited trees, evergreen and spinescent trees. Finally, we used a generalized linear mixed effects model following gamma distribution to model the effects bark thickness at 2 and 5 cm dbh.

2.2.3 Dataset and explanatory variables for Paper II

We calculated species richness (S), Shannon diversity index (H') and evenness (E) for each plot. Species richness is the sum of species present in each plot. We used species richness and relative species abundance to calculate Shannon index (H′) and evenness (E) using the following equations; $H' = -\sum_{i=1}^{S} PiInPi$ and $E = H'/In(S)$, where S was the number of species per plot and P_i the abundance of each species per plot divided by the total abundance of all species in the plot (Shannon 1948, Pielou 1969) (where a plot had one species, E was undefined).

2.2.4 Statistical analysis for Paper II

We constructed a generalized linear mixed effects model with Poisson errors using the "glmer" function within "lme4" R package to model species richness as a function of fencing (unfenced/fenced), habitat (off-mound/on-mound), and year of survey (2006, 2008 and 2015, i.e., one, three and 10 years after experimental setup). Since sampling was repeated within plots, plot identity was used as a random factor, while fencing, habitat and year were fixed factors. The most parsimonious model, determined through backward elimination of non-significant interactions and main terms ($P > 0.05$), was underdispersed, so we corrected for under-dispersion by running models using quasipoisson errors. We constructed a linear mixed effects model using "lmer" function within "lme4" R package to test the effects of fencing, habitat and year on Shannon diversity. We used a similar model for evenness but excluded habitat since we did not record sufficient species off-mound to calculate a meaningful measure of evenness. We first fitted a saturated model that included all terms and their interactions, then simplified the model by sequentially eliminating non-significant ($P > 0.05$) interactions and subsequently main terms (Crawley 2013; Zuur et al. 2013).

We assessed within treatment beta-diversity as dissimilarity in community composition, obtained as measures of distance of each treatment from the group centroids in multivariate dispersion space (Anderson et al. 2006). We tested for differences in beta-diversity within-treatment using the permutation multivariate analysis of variance (PERMANOVA) implemented using the “adonis” function in “vegan” package (Oksanen et al. 2017). When we detected a significant effect of treatment on beta-diversity, we ran pairwise comparisons between treatments using Tukey´s HSD test. We computed the distance of treatment to the group centroid using the “betadisper” function in the “vegan” R package (Oksanen et al. 2017).

To compare tree species compositional similarity between paired-treatment groups within each year of vegetation survey, we calculated Morisita-Horn indices using abundance data (Magurran and McGill 2011). We estimated 95% confidence intervals from 200 bootstrap replications using the function *similarityMult* in *SpadeR* package in R (Chao A et al. 2016).

2.3 Experimental setup for Paper III

We used the same nine replicate experimental sites as in Paper I and II (Fig 4, Fig 5A). Within fenced (excluding large herbivores > 5kg) and unfenced termite mound and adjacent off-mound plots, we placed seeds of nine native tree species and three agricultural crop seeds within small open “cages,” accessed by all animals, roofed cages that only allowed access to small vertebrates and invertebrates, and closed cages that permitted access by smaller invertebrates only (5 mm wire mesh) (Fig. 5B). Since all mounds in the previous experimental setup had become inactive, we checked whether mound status had an effect on seed removal by locating five active mounds where we laid cages in the same manner as in the nine replicate sites.

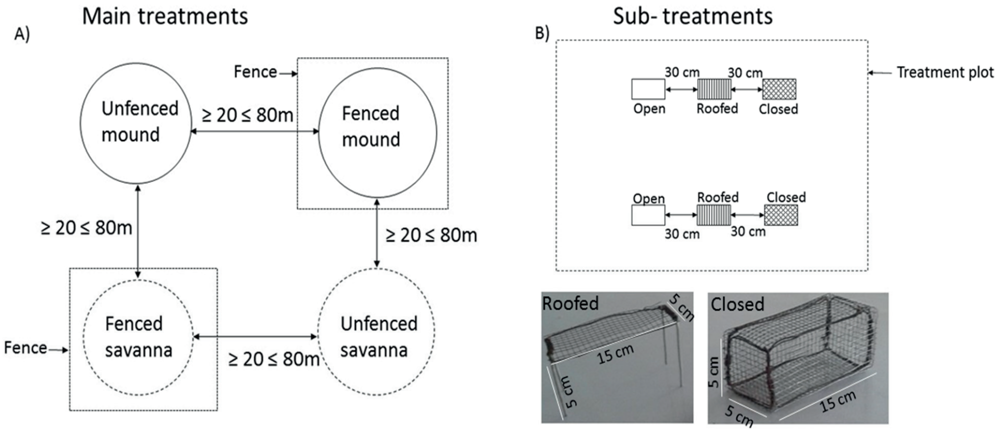

Figure 5. Schematic layout for field experimental setup in each site (n = 9) for Papers I and II (A), and sub-treatments (B) within the main setup for Paper III. Each site of the main treatments (n = 9) consisted of four plots (treatments) unfenced off-mound plot (savanna), fenced off-mound (savanna), fenced and unfenced on-mound plots.

2.3.1 Dataset and explanatory variables for paper III

Seed cages were revisited 10 times within six weeks between May and June 2015, at the end of the rainy season. At each visit, each cage was assessed for seeds that were removed or damaged. A seed was recorded as removed if it was not seen in the seed cage, and damaged if seed fragments were seen in the cage or if gnaw marks were seen on the seed within the seed cage. Removed and damaged seeds were replaced at each visit.

2.3.2 Statistical analysis for Paper III

Seed removal rates were analyzed as proportions of individual native tree seed species removed every three days, out of the maximum possible outcome of seed removal (i.e., 20 seeds of each species in each cage per treatment plot). Since data were repeatedly collected from the treatment plots within the sites, all analyses followed a generalized linear mixed model (GLMM) assuming a binomial distribution of error with a logit link function. We used the function “glmer” of the “lme4” package (Bates et al. 2015) in R to run the analysis (R Core Team 2015). We modelled seed removal rates as a function of cage type (open, roofed, or closed), habitat type (off-mound savanna or mound habitat), presence or absence of large herbivores (unfenced or fenced treatment plots), and native tree seed species as fixed factors. Site was modelled as a random factor. To test whether tree seed removal rates were higher on active mounds than inactive mounds, we modelled removal rates as a function of mound status (active or inactive), cage type and native tree seed species, all considered as fixed factors, while site was considered as a random factor.

2.4 Experimental setup for Paper IV

We used *Macrotermes* termite mounds in their active and inactive states, contrasted against the adjacent off-mound areas. We located five active mounds, each of which was paired with an inactive mound 20-80 m away (Fig. 6). We distinguished active from inactive *Macrotermes*-mounds, by checking for new constructions on mounds evidenced by moist soil deposits (Fig. 7). When no new constructions were observed, we punctured the mound with a sharp iron rod to a depth of c. 50 cm and checked if they were repaired five days later. A mound was active if it bore new constructions or if the puncture hole was repaired, otherwise, it was considered inactive.

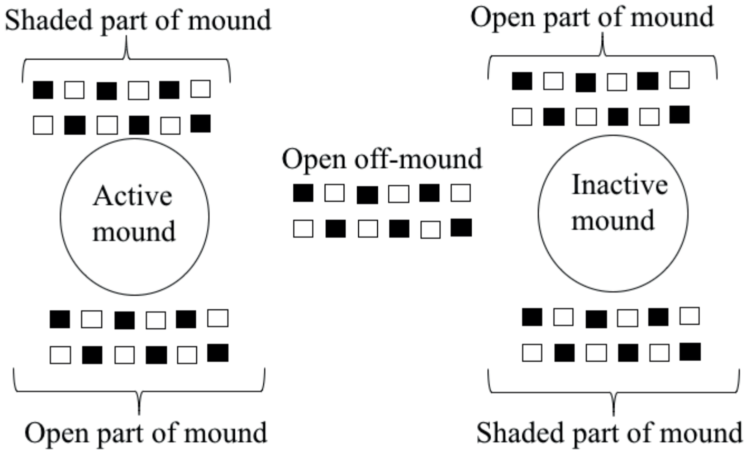

Figure 6. Schematic layout for field experimental setup for Paper IV (n = 5). Each of the mound pairs (active and inactive) had two experimental locations for the wood sample sets; the open (without canopy cover) and shaded (with canopy cover). An open off-mound experimental location was set up at the mid-point between the active-inactive mound pairs. Each sample set was comprised of a single piece of wood from each of the eight species. We used 12 wood sample sets for each location. Access by large macrodetritivores (> 1mm) to the wood samples was limited for half of the sample sets per location (filled squares) by wrapping them in a 1 mm mesh (protected), otherwise sample sets were (unprotected) (unfilled squares).

We established two wood decomposition "stations" at each mound (active and inactive). One station was located 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 was located at 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 established (all these areas bore open vegetation cover). All "stations" were set on bare ground with loose litter removed.

Figure 7: A) A fresh wet deposition of soil on a *Macrotermes* mound and B) *Macrotermes* soldier termites appearing to defend the colony after damage of part of the nest. We considered the fresh deposit of moist soil on mound and the presence of large soldier termites as evidence for an active mound.(Photos: Acanakwo, E. F. (Fig 7A), Sheil, D. (Fig 7B)

Wood samples

We assessed wood decomposition of eight common woody plant species within the landscape. We selected *Rhus natalensis* Bernh. ex C.Krauss, *Grewia similis* K.Schum., *Teclea nobilis* Del., and *Allophylus africanus* P. Beauv., as species that are common on-mounds, and *Acacia gerrardii* Benth., *A. sieberiana* DC., *A. hockii* De Willd. and *Dichrostachsys cinerea* (L.) Wight & Arn as species that are common off-mounds. For each species, we cut, debarked and sun-dried stems. The stems were later sized into pieces measuring 10 x 2 x 2 cm. The wood pieces were numbered, oven-dried and weighed to obtain initial dry mass. A set of wood pieces comprising one from each of the eight species were tied together using a twisted wire maintaining about 0.5 cm between samples. Half of the samples were wrapped in 1mm fibre-glass mesh to limit access by macrodetritivores. The wrapped sample sets are referred to as “protected”, otherwise, the wood sample-sets are “unprotected”.

We placed six unprotected and six protected wood sample-sets at each of the 25 stations (Fig. 6). After one, three and twelve 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 and weighed to obtain final dry mass. The difference between the initial and final dry mass provided our measure of wood mass loss.

2.4.1 Dataset and explanatory variables for Paper IV

We used the difference between initial dry and final dry wood mass as the measure of wood mass loss per species per treatment per sampling time period. For each piece of wood retrieved from the experimental station, we computed the percentage mass loss by dividing the difference between initial and final dry mass, by the initial dry mass for each period of exposure to decomposer groups. We used the mean percentage mass loss values in the analyses.

2.4.2 Statistical analysis for paper IV

To assess wood decomposition rates on-mound, we tested the effects of tree species, mound status (active versus inactive), mound microhabitat (open versus shaded), duration of exposure and access to wood samples by large macro-detritivores (unprotected versus protected). 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). The mean percentage mass loss was arcsine square-root transformed prior to analysis to approach normal distributions (McDonald 2014). We used decomposition station identity as a random factor in all our analyses (Crawley 2013).

To assess wood decomposition rates on- and off-mound, we tested the effects of tree species, mound status (considering only open mound parts on active mounds, inactive mounds and off-mound sites), duration of exposure and access to wood samples by large macro-detritivores. We constructed linear mixed effects models (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 the two models, the most parsimonious models were obtained through subsequent backward elimination of non-significant ($P > 0.05$) interaction 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 Development Core Team 2017).

3.0 Result and Discussion

3.1 Thesis overview

The results from this thesis show that the interactive effects of termites and large herbivores on tree communities and ecosystem services are context dependent. Termite mounds bore a different woody plant community composition relative to the off-mound areas (**Paper I**) and these compositions were not altered much by ungulate browsing. Although species richness and diversity measures were higher on- than off-mound, ungulates amplified these differences by reducing richness off-mound (**Paper II**). Our results also show higher seed removal rates on- than off-mound. However, in the absence of ungulates, seed removal significantly reduced on-mound, but did not show discernible changes off-mound (**Paper III**). In **Paper IV**, our results show that wood decomposition proceeds more rapidly on active mounds, relative to inactive or off-mound areas. Nonetheless, mound vegetation cover, wood species and whether woods are exposed to macrodetritivores also influence wood decomposition rates. These results highlight the ecological roles that *Macrotermes* termites play within the savannas in creating patches which maintain distinct woody vegetation composition relative to off-mound woody vegetation. Differences enhance ecological processes of seed removal and wood decomposition, both of which can impact on woody plant regeneration, secondary dispersal, composition and ultimately population dynamics.

3.2 Ungulates, termites and tree communities in a heterogeneous landscape (Paper I & II)

In the African savannas receiving more than 650 mm (MAP), canopy closure is prevented by disturbances such as herbivory and fires, but the difference in soil nutrient levels create variation to the amount of canopy closure (Sankaran at al. 2005, Sankaran et al. 2008). In **Paper I**, our results show that stem density and basal area are higher on-mound relative to off-mound sites. This result is attributable to termite induced resource and micro-topographic heterogeneity. During mound-building, *Macrotermes* termites move soil mineral particles vertically and horizontally in the process mixing mineral resources from lower soil layers with those at the top. Through foraging, *Macrotermes* termites concentrate minerals resulting from the breakdown of plant material within their nests (Boutton et al 1983). These mechanisms ultimately result in high resource levels on mound patches within the savanna landscape (Konaté et al. 1999, Traoré et al. 2008a). Our results are similar to findings from studies across the African savannas that have shown that *Macrotermes* mounds bear higher densities of seedlings than adjacent areas (Traoré et al. 2008b, Støen et al. 2013).

The elevation of *Macrotermes* termite mounds coupled with the high density of woody plants form a buffering against total suppression of trees by fire and floods. The canopy cover of established woody plants on mounds suppress herbaceous plant growth, thus reducing herbaceous plant biomass (Sileshi et al. 2010, Jouquet et al. 2011, Joseph et al. 2013). The tall woody plants on mounds are also likely to escape low fire intensity damage as fire skirts around the edge of the tree clumps due to elevation above grass fires (Bloesch 2008, Loveridge and Moe 2004). Therefore, the protection against fire damage and high nutrient levels on mounds are likely important factors that maintain a high woody plant density and basal area on mounds relative to the adjacent off-mound areas.

The influence of termite caused heterogeneity in soil resources is also reflected in woody plant species composition which varies with whether tree communities are located on- or off-mound **(Paper I)**. This result is consistent with findings from other savanna areas where *Macrotermes* mounds form refuges for plants that are more adapted to higher moisture levels and low fire incidences (Joseph et al. 2013, van der Plas et al. 2013, Seymour et al. 2016). Considering the influence of ungulates, our results in Paper I show that ungulates do not affect species composition either on-or off-mound. This result is surprising because in productive areas, light is a limiting resource that selects for faster growing woody plants. We expected that ungulate browsing would reduce light competition through selective browsing allowing for regeneration and establishment of other woody species (Borer et al. 2014). Lake Mburo National Park has a high diversity and density ungulates estimated at 87 kg ha^{-1} within and around the Park (Rannestad et al. 2006). Ungulates in the African savanna impact on seedling recruitment differently (Moe et al. 2014). While grazers increase seedling regeneration (Riginos and Young 2007), browsers reduce regeneration (Prins and van der Jeugd 1993, Moe et al. 2009b). Since the vegetation on mounds at our site are intensely browsed (Mobæk et al. 2005), we expected this vegetation to be impacted strongly by browsers. Nonetheless, high resource levels on mounds likely facilitate high rates of seedling regeneration and regrowth of browsed and injured plants (Chase et al. 2000). Because woody plants on mounds form thickets, it is possible that woody plants that are browse-vulnerable are protected from browsing by associating with well defended species within the thickets.

In Paper II, our results show that woody plant species richness and diversity measures are higher on- than off-mound. Ungulates did not cause discernible influence on species richness and diversity measures on-mound, but off-mound, richness and diversity were reduced in the presence of ungulates. This result only partially supports studies and ecological theories that predict that herbivory should result in higher plant diversity in more productive sites low diversity in low productive sites (Olff and Ritchie 1998, Lezama et al. 2014). Although these theories were largely developed mainly from the analyses of grasses and short-lived plants (e.g., Proulx and Mazumder 1998, Lezama et al. 2014), our results point to a possible difference in life strategies between woody plants and grasses which is exhibited differently in their diversity measures in relation to productivity and herbivory.

That species composition differed between on- and off-mound habitats (Paper I) and diversity was higher on mound than off-mound (Paper II) suggests that these habitats have a filtering effect for the species that establish. Compared to off-mound sites, mounds are higher in plant available moisture, minerals and nutrient levels (Konaté et al. 1999, Jouquet et al. 2011). Indeed, results in Paper I show that the proportion of evergreen woody plants is higher on mound that off-mound. The fact that species richness increases in the absence of ungulates both on- and off mounds suggests that these species come from a “species pool” from which plant propagules are able to disperse and establish elsewhere, in places with suitable conditions similar to their native habitats. The woody plants that commonly grow on mounds have traits similar to those growing in high moisture habitats. Indeed, our study sites were dominated by forest vegetation before anthropogenic related factors decimated the forest cover afew centuries ago transforming the vegetation to the present large open savanna landscape (Hamilton 1984, Howard 1991).

3.3 The influence of termites and ungulates on seed removal patterns in a heterogeneous landscape (Paper III)

The high density and diversity of woody plants on mounds relative to off-mound areas (Paper I and II) is a likely mechanism by which other ecological processes within the landscape are determined (Paper III and IV). In Paper III, we show that seed removal rates are higher on- than off-mounds. The vegetation on mounds support other taxa of vertebrates such as rodents (Fleming and Loveridge 2003, Okullo et al. 2013), birds (Moe et al. 2017) and invertebrates (Pringle et al. 2010) which can be potential seed removal agents in the landscape. The vegetated mounds enhance seed removal by providing cover for seed removing invertebrates and vertebrates from predators. In the absence of large mammalian ungulates, small mammal abundance increases in the savannas (Goheen et al. 2004, Okullo et al. 2013). We expected therefore, that in the absence of ungulates, seed removal would increase, because of increased vegetation cover. On the contrary, in the absence of ungulates, seed removal rates reduced on mounds, but showed weak increment off-mound. This reflects different requirements and abilities of fauna using the fenced mound habits, for example it is likely that fenced mound sites facilitate an increase in abundance of small mammals that are not predominantly granivorous. That seeds remain intact on mound sites in the absence of ungulates might point to mounds being sites suitable for seedling establishment ("safe sites"(Harper et al. 1961)).

Studies and theories of seed removal predict that seed removal rates should be higher for larger seeds and lower for small seeds (Moles et al. 2003). Our results in Paper III showed the contrary; removal rates were higher for smaller seeds (< 5 mm in width) than larger seeds in our study system. This may be attributed to both invertebrate and vertebrate seed removal agents being able to remove small seeds, hence the high removal rates, whereas, large seeds are only well handled by vertebrate seed removal agents.

Our results in Paper III also highlight the variation in seed removal rates arising from the difference in mound status. Seed removal rates were higher on active than inactive mounds. We know that termites are not seed consumers (Erpenbach and Wittig 2016), but whether the presence of *Macrotermes* in mounds attracts other organisms that are generalist feeders on these mounds requires further assessment.

3.4 Wood decomposition in a heterogeneous savanna landscape (Paper IV)

Termites are the most important decomposer organisms in arid and semi-arid landscapes, but their influence in the landscapes is variable (Schuurman 2005, Cornwell et al. 2009). Our results (Paper IV) show greater wood decomposition rates on-than off-mound. The efficiency in wood decomposition by *Macrotermes* mounds is attributable to *Macrotermes* symbiotic relation with *Termitomyces* fungus which breaks down lignin in the plant material (Schuurman 2005). Furthermore, our results in Paper IV show higher decomposition rates on active than inactive mounds. We observed that wood decomposition rates proceed faster in the shaded than open of the mound, but these differences are more pronounced on inactive mounds (Paper IV). The tree cover on mounds create cool microclimatic conditions which can sustain high humidity and formation of dew (Joseph et al. 2016). Moisture is an important requirement for fungal decomposition of wood (Gliksman et al. 2017). Moreover, fungal decomposition of wood can release chemical cues used by termites to locate food sources (Judd 2018). It is likely therefore, that even when mounds are abandoned, the wide foraging *Macrotermes* termites may still forage on these mounds, contributing to wood decomposition on inactive mounds.

Previous studies suggest that wood decomposition is reduced as density increases. Indeed, our results in Paper IV show that wood decomposition reduces with density, but this is more pronounced for wood exposed to both macro and micro-detritivores in the open parts of the mounds. Although wood decomposition can reduce with density, some studies argue that the influence of chemical defenses in different wood species in deterring wood decomposition is greater than density effects, for example Cowling and Merrill (1966).

3.5 Concluding remarks and implications for landscape management

The importance of *Macrotermes* mounds in determining woody vegetation patterns (Traoré et al. 2008b, Moe et al. 2009a, Davies et al. 2016) and ecosystem processes of the savanna landscape in the African savannas is recognized (Schuurman 2005, Cornwell et al. 2009, Jouquet et al. 2011, Acanakwo et al. 2017, Veldhuis et al. 2017). However, large mammalian herbivores also influence woody plant communities affecting their structural and composition patterns in the savanna landscape (Prins and van der Jeugd 1993, Moe et al. 2009b, Daskin et al. 2016). This thesis provides evidence_that the ecological effects of *Macrotermes* mounds and *Macrotermes* termites themselves, interact with large mammalian herbivores to create context dependent effects on woody plant communities and ecosystem processes in the savanna landscape.

The findings from this thesis highlight important theoretical implications for understanding savanna systems. For example, we found that woody plant stem density increased faster on- than off-mound both in the presence and absence of ungulates. The higher stem density on mounds would be expected to suppress grass biomass more on- than off-mound. The spatial variation in grass biomass across the landscape is likely therefore, to influence fire regimes, intensities and patterns. In addition, the termite mound associated variation in woody plant stem densities on- and off-mound is likely to affect the tree-grass balance, ultimately affecting grazers and other organisms which favour more open landscapes.

Our findings also highlight the issue of woody plant diversity measures that are important for understanding the ongoing debate on the levels of assessment of diversity (Cardinale et al. 2018). The current debate stems from the previous body of knowledge that showed that species extinctions were increasing globally (Cardinale et al. 2012, Ceballos et al. 2015), yet recent studies now indicate that species richness is in fact not declining at local spatial scales across the globe (Vellend et al. 2013, Dornelas et al. 2014, Hillebrand et al. 2018). Our results (Paper II) show that plot-level species richness and diversity are greater on- than off-mound plots. However, the mounds in our study area occupy only about 5% of the entire landscape of Lake Mburo National Park (Moe et al. 2009). Therefore, we cannot be certain that these increases necessarily imply corresponding increment in landscape or regional level diversity. The question as to whether landscape level diversity may be deduced from small-scale diversity assessments remains unanswered. Further studies in the relationship between small and large-scale diversity assessments would offer guidance on whether management efforts should be focused at small or large-scale levels.

Our results also highlight important practical implications for savanna landscape management. We found that diversity of woody plants was higher on- than off-mound, but the diversity on-mound was not affected by ungulates (Paper II). In addition, result show that wood decomposition rates are higher on- than off-mound (Paper IV). This suggests that the establishment of woody plants on mounds have a positive feedback effect. The high resource levels on mounds continuously facilitate tree regeneration and recruitment. The increase in atmospheric CO_2, high moisture levels (> 650 mm) and fertility are key drivers of increased tree cover within the African savannas (Wiegand et al. 2005, Conradi 2018). Lake Mburo National Park receives 865 mm of rainfall and *Macrotermes* mounds are nutrient-rich spots. It is possible therefore, that mounds can act as triggers of the unprecedented increase tree cover within the landscape. To develop management strategies for this potential increase in tree cover therefore, there is need for knowledge on how termites may facilitate tree cover, and development of strategies of how this can be mitigated.

Finally, we observed that the removal rates for seeds of selected woody species was reduced on mounds in the absence of ungulates. This implies that in the absence of ungulates, mounds may be sites suitable for seedling establishment (Harper et al. 1961) for seedling establishment. The absence of ungulates poses the risk of possible establishment of invasive plants. A previous study in Lake Mburo National Park, showed lower survival of native tree species, compared to exotic species on mounds in the absence of ungulates (Moe et al. 2016). With the ongoing global decline in large herbivore populations (Collen et al. 2009, Dirzo et al. 2014), concerted effort in managing sustainable populations of diverse large herbivore populations is crucial to ensure normal functioning of the ecosystem.

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Paper I

Termites confer resistance to changes in tree composition following reduced browsing in an African savanna

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Abstract

Questions: Ungulate herbivory affects plant community structure and composition. Plant response to these effects are variable. Wild large herbivore populations are declining globally, but how tree communities respond to this change is not clear. Here, we experimentally examined how tree community responses to changes in ungulate abundance vary in spatially heterogeneous habitats in a savanna landscape.

Location: Lake Mburo National Park, Uganda

Methods: We recorded tree species in nine replicate sites each with four treatment plots; fenced off-mound (excluding ungulates), unfenced off-mound, fenced and unfenced on-mound. Each species was assessed for fruit-type, leafing strategy, spinescence and bark thickness. We compared tree communities on- and off-mound, with and without large herbivores using PERMANOVA and the effects of habitat, fencing and time on traits using GLMM.

Results: Stem density increased by 88% off-mound and 138% on-mound ($P = 0.005$) in the absence of ungulates between 2006 and 2015. Whether tree communities occurred on or off-mound determined species composition, but fencing had little effect. Tree traits were not markedly altered by fencing on-mound. Off-mound, fencing was associated with 38% increase in proportion of fleshy-fruited tree stems ($P < 0.001$), 18% decline in armed trees ($P = 0.035$) and a reduction in mean bark thickness.

Conclusion: This study highlights the important role mounds play in maintaining tree community composition with declining ungulate abundance. Ungulates had weak effects on tree composition and traits of mound-borne trees. Thus, *Macrotermes* mounds support distinct tree communities within the landscape that are robust to reduced ungulate herbivory.

Key words: African savanna, browsers, landscape heterogeneity, species composition, *Macrotermes* mounds, tree traits, ungulates, fencing, Lake Mburo National Park, Uganda, East Africa.

INTRODUCTION

Vegetation cover is changing worldwide with implications for biodiversity, atmospheric carbon, albedo, hydrology and many other environmental outcomes (Foley et al. 2005; Hansen et al. 2013; Zhu et al. 2016). These changes are thought to be driven by a range of factors that include human induced climate change, CO_2-fertilization, N-deposition, fires and agricultural practices (Zhu et al. 2016). Nonetheless, the nature of these changes, their relative importance and long-term implications remain contested (e.g., Bond 2008; Veenendaal et al. 2018). While abiotic factors such as climate, fire and edaphic conditions appear to determine large scale vegetation patterns (Bond, Woodward, & Midgley 2005), biotic factors including large herbivores and invertebrates play an important role at smaller spatial scales (Prins & van der Jeugd, 1993; Dangerfield, McCarthy & Ellery 1998; Sileshi, Arshad, Konaté &Nkunika 2010).

Wild large herbivore populations are declining globally with broad potential implications for tree community structure and composition (Collen et al. 2009; Dirzo et al. 2014). For example, in the open woodlands and grasslands of the tropical savannas the balance in tree-grass cover is generally dependent not only on climate, fire frequency and edaphic environment, but also on the large herbivore community. Studies suggest that in tropical African regions with precipitation above 650 mm per year, closed forest canopies can form in the absence of fires and ungulates (Sankaran et al. 2005; Sankaran, Ratnam & Hanan 2008). What is less clear is how declining ungulate populations impact on tree community structure and composition within the savanna landscape. It is important to understand the context under which herbivory affects plant community properties, because plant responses to herbivory are variable in magnitude and direction (Augustine & McNaughton 1998; Vesk & Westoby 2001). With respect to tree recruitment, the loss of large herbivores has shown both negative (Goheen, Keesing, Allan, Ogada & Ostfeld 2004) and positive effects (Prins & van der Jeugd 1993; Moe, Rutina, Hytteborn & du Toit 2009b) within African savannas. However, the ultimate effects of ungulate selective herbivory on tree community structure, composition and traits are likely mediated by abiotic gradients (Augustine & McNaughton 1998; Proulx & Mazumder 1998; Pringle, Prior, Palmer, Young & Goheen 2016).

In this study, we examined ten-year effects of ungulate exclusion on a spatially heterogeneous African savanna. Large-epigeal *Macrotermes* mounds (hereafter referred to as mounds) built by termites of the Macrotermitinae sub-family (Termitidea family) are widespread and create habitat patches of high nutrient and moisture levels relative to adjacent off-mound areas (Konaté, Roux, Tessier & Lepage 1999; Sileshi et al. 2010; Okullo & Moe 2012). These mounds are also protected from fires due to elevation, and support much of the local tree cover in these savannas (Sileshi et al. 2010; Okullo & Moe 2012; Erpenbach & Wittig 2016). We therefore separate our evaluations into the effects of ungulate exclusion on and off these mounds.

We conducted this study in Lake Mburo National Park in Uganda, which supports a high abundance (c. 87 kg ha^{-1}) and diversity of ungulates (Rannestad, Danielsen, Moe & Stokke 2006). Relative to the off-mound habitats, the mounds support higher densities of tree seedlings and large trees (Moe, Mobæk & Narmo 2009a; Støen, Okullo, Eid & Moe 2013). In recent years, as in many savanna habitats elsewhere (Stevens, Lehman, Murphy & Durigan 2017), tree cover in the park has been increasing and park authorities are concerned. The increase in tree cover has been ascribed to loss of elephants and other large herbivores: as the Uganda Wildlife Authority states “Once covered by open savanna, Lake Mburo National Park now contains much woodland as there are no elephants to tame the vegetation” (www.ugandawildlife.org). Several approaches to check the spread of woody cover are being trialled, for example, burning, manual tree cutting and introduction of Giraffes (*Giraffa camelopardalis*) (Personal observations).

Here, we experimentally examined how tree community responses to changes in ungulate abundance relate to on-mound and off-mound sites. Few previous studies have assessed the effects of mounds and large herbivores on tree communities (e.g. Støen et al. 2013; Joseph et al. 2015; Seymour et al. 2016). Nonetheless, we know no previous experimental study that has examined the effects of ungulates on tree community structure, species composition and traits on- and off-mound.

Our study aimed to assess the effects of ungulates and mounds on tree community structure, species composition and traits in an African savanna. To examine the effects of mounds and ungulates together and separately on tree communities, we used an on-going experiment composed of four main treatment plots; 1) unfenced off-mound; 2) fenced off-mound, where herbivores (> 5kg) were excluded; 3) unfenced on-mounds and 4) fenced on-mound plot.

We hypothesized that mounds and ungulates affect tree community structure, composition and traits in this landscape, but the extent of these effects and the direction they take may be determined by presence or absence of ungulates on- or off-mound. We predicted that fencing would increase differences in stem density and basal area between on- and off-mound habitats, because i) in the absence of ungulates, accumulated grass cover would suppress seedling establishment and increase fuel-load in the grass dominated off-mound habitats (Okullo & Moe 2012; Keesing & Young 2014) and ii) reduced browsing on-mounds coupled with low fire incidences would facilitate tree establishment (Joseph, Seymour, Cumming, Mahlangu & Cumming 2013; Støen et al. 2013). We also predicted that, excluding ungulates would result in greater effects on tree species composition on-mound than off-mound, because, i) the effect of herbivory on species richness can increase with resource availability (Chase, Leibold, Downing & Shurin 2000); ii) competitive dominance occurs sooner in more productive sites (Hautier, Niklaus & Hector 2009). Finally, we predicted that in fenced treatments; i) the per-plot proportion of fleshy-fruited tree species would increase because the majority of these trees are dispersed by birds, and in the absence of ungulates the abundance and diversity of birds increases (Ogada, Gadd, Ostfeld &Young 2008; Moe et al. 2017); ii) the per-plot proportion of armed (i.e. spine or thorn bearing) trees would decline because the benefits are removed; iii) the proportion of evergreen trees would increase due to release from dry season browsing and trampling (Moe et al. 2009b); iv) mean bark thickness would be greater off-mound than on-mound and increase after ungulate exclusion, because of differences in fuel load and the resulting fires.

METHODS

Study area

The experiment was carried out within the savanna landscape in the flat valleys of the eastern and western parts of the approximately 260 km^2 Lake Mburo National Park. Located in southwestern Uganda (00º32'-00º37'S and 30º47'-31º04'E) at elevations between 1200 and 1300 m above sea level, the park has an average annual temperature and rainfall of 20.7 ºC and 865 mm, respectively (www.climate-data.org). The park is primarily a grass-dominated savanna, with scattered trees and steep hills surrounding a perennial lake fringed by forest patches (Bloesch 2008).

Large epigeal mounds (mean height: 1.7 m and radius: 3.7m), constructed by *Macrotermes subhyalinus* Rambur occur in much of the park´s flatter terrain (Moe et al. 2009a). Tree species common on mounds include *Capparis erythrocarpos* Isert*, Scutia myrtina* (Burm.f.) Kurz and *Grewia similis* K. Schum, while *Acacia gerrardii* Benth., *A. sieberiana* DC. and *A. hockii* De Willd. dominate off-mound (Moe et al. 2017). Common ungulates include impala

(*Aepyceros melampus* (Lichtenstein, 1812)), waterbuck (*Kobus ellipsiprymnus* (Ogilby, 1833)), bushbuck (*Tragelaphus scriptus* (Pallas, 1766)), zebra (*Equus q. burchelli* (Gray, 1824)), warthog (*Phacochoerus africanus* (Gmelin, 1788)), topi (*Damaliscus lunatus* Burchell, 1823)) and eland (*Taurotragus oryx* (Pallas, 1766)). The biomass density of ungulates within the park is estimated at about 87 kg ha^{-1} (Rannestad et al. 2006).

Experimental setup

We used a 10 year (2005 to 2015) experimental setup comprised of four treatments; unfenced savanna (off-mound), fenced savanna (off-mound), which limited access to the plots by ungulates; unfenced mounds, and fenced mounds. Two mound and two off-mound plots were located within nine sites. One of each pair of mound and off-mound plots within each site were randomly assigned to fencing treatment using a 5 cm galvanized chain link mesh, supported by 2 m high steel angle bars firmly fitted in the ground. All four treatments plots within a site were the same size, but plot sizes within the nine sites varied from 90 to 260 m^2 (Okullo & Moe 2012). All mounds were occupied by fungus-growing *Macrotermes* (active) when the experiment was originally established (Okullo & Moe 2012) but were all found to be without the *Macrotermes* (inactive) 10 years later (in 2015). *Macrotermes* mounds are stable and persistent features of the savanna landscape, with long life spans measured in centuries and millennia, and are continuously recolonized and abandoned (Erens et al. 2015). The soil properties of these mounds are maintained regardless of the presence or absence of *Macrotermes* (Erens et al. 2015).

Tree community survey

We recorded all woody plants taller than 30 cm, between April and August in 2006, 2008 and 2015 (that is, one, three and ten years after experimental setup). We identified trees in the field with reference to Katende, Birnie & Tengnas (1995) and local experts. We took vouchers to Makerere University herbarium in Kampala for verification. We verified the nomenclature of the identified trees using *The Plant List,* an online database (The Plant List, 2013). For woody plants whose heights exceeded 130 cm from the ground in 2008 and 2015, we also measured diameter at breast height (dbh), 130 cm from the ground, using a diameter tape. In addition, we measured bark thickness for all individual trees recorded by extracting a wedge of bark from the stem at 20 cm from the ground using a sharp machete. When the woody material of the stem was visible, a calibrated ruler was inserted in the wedge and distance from the wood to the outer-most surface of the bark was recorded as bark thickness. For small, weak stems (< 1 m height) we peeled a small part of the bark at 20 cm and measured bark thickness using a vernier caliper. Since our plot sizes differed among sites, the number of individuals per species were calculated as densities per hectare, i.e., number of stems per 10 000 m^2 for each plot.

Tree traits

We examined four traits, namely, fruit-type (whether fleshy or dry), whether leaves were evergreen or deciduous, spinenscence (armed or unarmed), and bark thickness. The traits were chosen to relate to plants´ regeneration strategy (we expected fleshy-fruited trees to be dispersed by both birds and mammals), soil moisture stress strategies, anti-herbivore strategy, and fire tolerance. We searched plant databases (e.g., tropical.theferns.info, www.prota4u.org, www.plants.jstor.org, and www.worldagroforestry.org) to obtain information on each species relating to its fruit type and whether a tree species was evergreen or deciduous. Based on field observations, we recorded a tree with thorns, hooks and spines as armed, otherwise it was unarmed (see species list in Appendix S1). Untransformed bark thickness values obtained from bark thickness measurements (see above for details) were plotted against dbh and reference bark thickness values derived for each species at dbh values of 2 and 5 cm using the function *approx* in R (R Development Core Team 2017).

Analysis

We used tree stem density and basal area to compare tree community structure in the fenced and unfenced on- and off-mound habitats.

To test the effect of fencing (unfenced vs fenced), habitat type (on-mound vs off-mound), and year of survey on stem density, we constructed a generalized linear mixed effects model (GLMM) with stem density as response variable within the “lme4” R package, with Poisson errors and log-link (Crawley 2013, Zuur, Hilbe & Elena 2013). Since we undertook repeated measurements within the plots, we used plot identity as a random factor and fencing, habitat type and year of survey as fixed factors. Initially, we fitted a full model which we reduced to obtain the most parsimonious model by eliminating non-significant interactions ($P > 0.05$) (Crawley 2013, Zuur et al. 2013). However, the simplified model was overdispersed, so we used negative-binomial error distribution to model stem densities. We visually investigated the assumptions of constant variance and normality of errors with residual plots with no apparent violations. For basal area, we constructed a generalized linear mixed model following Gaussian errors and log link functions to model the effects of fencing, habitat and year of survey, as fixed effects, and plot identity as random effects using the “glmmPQL” function within the “MASS” R package.

We tested the effects of fencing, habitat and their interaction on tree composition using permutation analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity values of species abundance with the function “adonis” in the “vegan” package in R (Oksanen and others 2017). We used the function “betadisper” of the “vegan” package in R to compare differences in species composition among treatments and tested pairwise differences between treatments using parametric Tukey’s HSD test. We assessed the 95% confidence intervals around treatment centroids to show differences in community composition (Oksanen et al. 2017). The functions “adonis” and “betadisper” are multivariate analogues of analysis of variance (ANOVA) and Levene's test for comparing group means and variances, respectively (Oksanen et al. 2017).

We examined the effects of fencing, habitat type and year of survey, on the per-plot proportion of stem density for tree species grouped into four species level tree traits (i.e., fleshy-fruited, evergreen, spinescent and bark thickness). Initially we constructed generalized linear mixed effects models following binomial distribution errors using the "glmer" function within the "lme4" R package to model the per-plot proportion of fleshy-fruited tree species, evergreen and armed-stem density. However, due to overdispersion we refitted the models using quasibinomial distribution. We used a generalized linear mixed model following Gamma distribution with "glmmPQL" function within "MASS" R package to model stem-weighted per-plot mean bark thickness at two reference diameters of 2 and 5 cm. For each model, we first fitted a saturated model, then simplified the model by sequentially eliminating non-significant interactions then non-significant main terms ($P > 0.05$) except the main terms that were also in significant interactions. All data were analysed using R statistical software (R Development Core Team 2017).

RESULTS

Tree stem density did not change significantly either on- or off-mound between 2006 and 2008 regardless of fencing treatment ($P = 0.76$, Fig. 1, Appendix S2). However, stem density appeared to increase between 2006 and 2015 in unfenced on-mound plots from 2431 ± 441 in 2006 to 3859 ± 536 stems ha^{-1} with a marginally significant effect of year ($P = 0.06$, Fig. 1, Appendix S2). Evaluation of the unfenced off-mound plots did not indicate any significant changes in stem densities (mean stem density per plot ± SE: 632± 205 stems ha^{-1} in 2006, 673 ± 268 stems ha^{-1} in 2008, and 533 ± 128 stems ha^{-1} in 2015). With fencing, mean stem density increased significantly over the years both off-mound (by 88% from 795 ± 243 stems

ha^{-1} in 2006 to 1492 ± 411 stems ha^{-1} in 2015) and on-mound (by 138% from 2640 ± 723 stems ha^{-1} in 2006 to 6287 ± 1242 stems ha^{-1}in 2015) (Fencing x Year interaction, $P = 0.005$) (Fig. 1, Appendix S2).

Overall, regardless of fencing treatment, basal area increased between 2008 and 2015 both off-mound by 224% (from 0.0058 ± 0.003 m^2 ha^{-1} in 2008 to 0.0188 ± 0.008 m^2 ha^{-1} in 2015) and on-mound by 123% (from 3.66 ± 0.66 m^2 ha^{-1} in 2008 to 8.17 ± 1.46 m^2 ha^{-1} in 2015) ($P < 0.001$) (Appendix S3, S4). We found no significant change in mean basal area with fencing (Appendix S3, S4). Mean basal area was substantially lower off-mound (0.012 ± 0.004 m^2 ha^{-1}) than on-mound (5.92 ± 0.88 m^2 ha^{-1}), irrespective of fencing treatment and year ($P < 0.001$) (Appendix S3, S4).

Overall, whether the vegetation occurred off- or on-mound determined species composition ($P = 0.001$, Appendix S5), but fencing did not result in significant differences in either habitat ($P = 0.607$, Appendix S5). Although we did not detect an overall significant effect of fencing on species composition, stem density of some common species responded to fencing in off-mound habitats. For example, the stem density of *Acacia gerrardii* declined ($P = 0.02$), while *Dichrostachys cinerea* increased ($P = 0.01$, Appendix S6, S7). No differences in stem density were detected among common species on-mound (Appendix S6, S8).

There was a lower mean stem density of fleshy-fruited tree species off-mound (proportion: 0.24 ± 0.03 and a stem density of 273.7 ± 71.2 out of 859.6 ± 66.7 stems ha^{-1}) relative to on-mound (proportion: 0.92 ± 0.01 and a stem density of 3227.9 ± 3443.8 out of 3443.8 ± 195.8 stems ha^{-1}) ($P < 0.001$, Table 1, Fig. 2). Fencing was associated with a 36% increase in stem density of fleshy-fruited trees off-mound (from a mean of 120 ± 37 out of a stem density of 597 ± 66 stems ha^{-1} in unfenced off-mound plots to 427 ± 132 out of a mean total of 1123 ± 191 stems ha^{-1} in fenced off-mound plots) (Fencing x Habitat interaction, $P = 0.036$, Table 1, Fig. 2, Appendix S9). No discernible effect of fencing on fruit type was detected on-mound.

Stem density of evergreen trees was lower off-mound (proportion of 0.12 ± 0.03, with a stem density of 125 ± 40 out of 860 ± 116 stem ha^{-1}) than on-mound (proportion of 0.46 ± 0.02, with a stem density of 1678 ± 215 out of 3444 ± 341 stems ha^{-1}) ($P < 0.001$, Table 1, Fig. 2). Fencing was associated with a reduction in the proportion of evergreen trees on-mound but not off-mound (Fig. 2), although the interaction between habitat and fencing was only marginally significant ($P = 0.059$) and thus not included in the most parsimonious model (Table 1). Armed trees had a greater proportion of stems ha^{-1} off-mound (0.76 ± 0.04, with a stem density of 645 ± 81 out of 860 ± 116 stems ha^{-1}) than on-mound (0.38 ± 0.02, with a stem density of 1289 ± 148 out of 3444 ± 341 stems ha^{-1}) ($P < 0.001$, Table 1). Fencing was associated with 18% reduction in proportion of armed-stem density in off-mound (from a stem density of 505 ± 110 out of 597 ± 116 stems ha^{-1} in the unfenced off-mound plots to 785 ± 116 out of 1123 ± 191 stems ha^{-1} in the fenced off-mound plots) (Habitat x Fencing interaction, $P = 0.035$, Table 1, Fig. 2).

We detected no significant effects of fencing, habitat type, year of survey on mean bark thickness for small trees (dbh = 2cm) (Table 1, Fig. 2). Among large trees (dbh = 5 cm), mean bark thickness was higher off-mound regardless of fencing (5.50 ± 0.36 mm per-plot) than on-mound (3.90 ± 0.1 mm per-plot) ($P < 0.001$, Table 1, Fig. 2, Appendix S9). Fencing was associated with reduced mean bark thickness (44% reduction in bark thickness off-mound, from 7.03 ± 0.43 mm per plot in unfenced off-mound plots to 3.94 ± 0.38 mm per plot in the fenced off-mound plots) ($P = 0.001$), while mean bark thickness did not change significantly with fencing on-mound.

DISCUSSION

Overall, our results highlight the important roles of mounds and ungulates in the savanna landscape. Tree species composition was influenced by habitat type (off- or on-mound), but not ungulates. Nonetheless, the exclusion of ungulates markedly altered tree traits off-mound, but not on-mound.

The exclusion of ungulates resulted in a significant increase of stem density, but not basal area, both on- and off-mound. Thus, our prediction that stem density and basal area would be greater on- than off-mound in the absence of large herbivores was only partly supported. These results may reflect limitations in our method. While we surveyed all trees taller than 30 cm to obtain stem density, basal area was derived from diameters measured at a minimum height of 130 cm from the ground. Thus, within the ten-year study period we observed a substantial increase in tree saplings in the fenced plots, but these changes were not yet reflected in the basal area of larger stems. Furthermore, the variation in basal area between plots is large, particularly in off-mound plots so the power of our tests with nine replicates is low. Off-mound plots are prone to fires and the variation in cover is probably related to irregular fire patterns influencing the abundance and size distributions of stems in the plots. Seedlings establishing in fenced off-mound plots may suffer greater fire related mortality as the accumulation of flammable grass in these plots can increase fire intensity (Hoffman et al. 2012).

Woody species composition depended markedly on whether the location was on- or off-mound while ungulate exclusion had little influence. The limited effect of ungulate exclusion was surprising, because Lake Mburo National Park has a high herbivore density, at about 87 kg ha^{-1} (Rannestad et al. 2006) and many of these species are selective browsers (Mobæk et al. 2005). We know that in the African savannas, ungulate herbivory can have contrasting impacts on seedling recruitment (Moe, Rutina, Hytteborn, du Toit 2014); grazers may increase seedling recruitment by reducing grass cover and fire frequency (Riginos & Young 2007; Goheen, Palmer, Keesing, Riginos, Young 2010) while browsers generally reduce the regeneration of trees by predating seedlings and saplings (e.g., Prins & van der Jeugd 1993;

Moe et al. 2009b). Since the vegetation on mounds at our sites are more intensely browsed by ungulates relative to surrounding off-mound vegetation (Mobæk et al. 2005), we had expected that exclusion of ungulates would impact tree species composition on-mound to a greater extent than on off-mound habitats.

The relative consistency of tree composition on mounds, with or without ungulates may be due to localised thickets which are relatively impenetrable to ungulates and thus may protect plant species within from browsers (Bloesch 2008; Moe et al. 2009a). Scogings, Dziba & Gordon (2004) in South Africa, grouped woody plants into two major categories of shoot morphology; those that produce new leaves on new long shoots (shoot-dominated species) and those that produce their leaves in clusters on short shoots at the nodes of old unbrowsable branches (shoot-limited species). In Zimbabwe, Sebata & Ndlovu (2012) found that goats avoided shoot-dominated species (e.g., *Grewia tenex*, *Grewia monticola* and *Colophospermum mopane*) which were associated with high neutral detergent fibre, acid detergent fibre and condensed tannins. In this study, we found shoot-dominated species of *Grewia similis* and *Grewia trichocarpa*, to be abundant on-mound both in the presence and absence of large herbivores. This suggests that within the mound thickets, shoot-dominated species may protect other more palatable species. In addition, the higher moisture and nutrient levels on mounds may facilitate compensatory regrowth thus enabling plants to survive in the presence of herbivores (Hawkes& Sullivan 2001).

Although the overall effect of fencing on species composition appeared minor, some common species off-mound appeared to respond. *Dichrostachys cinerea*, had three times more stems in the fenced relative to unfenced off-mound plots in 2006 (Appendix S7), only one year after fencing. *D. cinerea* spreads vegetatively (Munkert 2009) permitting dense regeneration following the removal of browsers. On the other hand, the stem density of *Acacia gerrardii* reduced off-mound with fencing (*P* = 0.02, Appendix S6). *A. gerrardii* is physically armed against herbivory. Browsing of undefended woody species reduces competition for the limited resources in off-mound habitats, and this is expected to facilitate growth and survival of this armed species in the presence of large herbivores (Milewski, Young & Madden 1991). In the absence of ungulates, the competitive advantage of being armed is lost leading to a reduction in abundance of these species.

We found that overall, the proportion of fleshy-fruited species was higher on- than off-mound. In the absence of ungulates, the proportion of fleshy-fruited stem density increased off-mound (the stem density of other species also increased but at a slower rate). This suggests that smaller seed moving agents or birds, that were able to access the exclosures, transported seeds into the fenced plots. Ogada et al. (2008) working in a Kenyan savanna found that bird diversity and abundance increased in the savanna when ungulates were absent, which suggests that increased dispersal by birds is a possible explanation for our results. We know that birds use mound plots much more than off-mound plots and that bird abundance increase on fenced mounds (Moe et al. 2017), but we do not know how important seed dispersal by birds is in the two habitats. It is possible that small mammals and invertebrates move and scatter-hoard seeds into off-mound exclosures (Acanakwo , Sheil & Moe 2017). In addition, the increase in herbaceous cover in the fenced off-mound plots (Okullo & Moe 2012), may have made seeds less apparent to predators, thus providing “safe sites” for seed regeneration (Harper 1994).

The proportion of evergreen tree species was higher on- than off-mound. Similar observations were made in southern Africa (Van der Plas, Howison, Reinders, Fokkema & Olff 2013; Joseph, Seymour, Cumming & Cumming 2014). Nonetheless, our results showed little change in the proportion of evergreen trees in the absence of large mammalian herbivores, but the proportion of evergreen trees appeared to be reduced by excluding browsers on-mound, although the relationship was only marginally significant (i.e. habitat x fencing interaction, *P*

= 0.059). This implies that herbivory is not an important determinant of leafing strategy. The difference in abundance of evergreen trees in the two habitat types likely reflects differences in adaptation to soil moisture stress. Compared to soils off-mound, mound soils have higher moisture content which facilitates growth of evergreen plants even during dry periods (Konaté et al. 1999), while off-mound, where available moisture is reliable lower, trees shed their leaves to reduce water loss (Ernst 1975).

Armed trees were dominant among off-mound tree communities, but not on-mound communities. This is attributable to the requirement for physical defence to reduce tissue loss among the slow-growing tree species in the lower-resource off-mound habitats, in contrast to trees growing on the higher-moisture mound habitats that facilitate fast-tree growth and support compensatory regrowth after browsing (Endara & Coley 2011). The per-plot proportion of armed-tree stem density reduced off-mound in the absence of ungulates. This trend is as we expected given that the competitive advantage of being armed is lost when ungulate herbivores are excluded.

Mean bark thickness of large trees (dbh = 5 cm) was higher off-mound than on-mound suggesting greater benefits from protection against fires. Off-mound plots are more prone to fires than are the elevated on-mound plots (Joseph et al 2013). We expected ungulate exclusion in off-mound plots to result in increased bark thickness because of increased fuel load due to accumulation of grass. Instead, our results indicated reduced bark thickness in fenced plots. However, this result should be treated with some caution since trees in fenced off-mound plots already head thinner bark in 2006, only one year after the fences were established. Potentially there may have been a pre-existing difference in bark thickness between unfenced and fenced off-mound plots.

Our study has shown that Lake Mburo National Park’s *Macrotermes* mounds maintain a robust community of trees, on which stem density and biomass have been increasing over the last ten years. The increase in tree cover has implications for evaporation and the local climate (Ellison et al. 2017; Joseph et al. 2018). In addition, increased tree cover is associated with greater biomass and enhanced sequestration of atmospheric carbon. While woody vegetation supports many organisms within the landscape (Moe et al. 2017), increasing tree cover may impact negatively on grass, grazers and other animals which favour more open landscapes (Riginos, Grace, Augustine &Young 2009; Smit & Prins 2013). With global increase in atmospheric CO2 levels and changing fire regimes through much of the savannas (Bond & Midgley 2000, Bond 2008), we anticipate a continued increase in tree cover through the savanna landscape of Lake Mburo National Park. Although our results suggest that ungulates do not prevent the increase in cover, we do note that it is faster in their absence. While fire, herbivory and human activities will continue to be important in determining the future vegetation in the region, our study shows that *Macrotermes* mounds play a critical role in sustaining the diversity and composition of the tree community.

Conclusion

Our study findings reinforce the importance of mounds within the savanna landscape. We have shown that over ten years, the exclusion of ungulates increased stem density both on- and off-mound but had little effect on basal area. Much of the local variation in tree species composition was determined by habitat (on-mound versus off-mound) rather than ungulates, although some of the common tree species off-mound may be responding to ungulate exclusion. Ungulate exclusion did not have a marked effect on tree traits on-mound but off-mound, the proportion of armed trees reduced, while the proportion of fleshy-fruited tree species increased. We conclude that mounds support a distinct suite of woody plants whose species composition and traits appear robust to reduced herbivore density.

Acknowledgements We thank the Uganda Wildlife Authority (UWA) who granted permission and allowed access to Lake Mburo National park for fieldwork. Lawrence Kabito, Fred Matovu, Antonia Nyamukuru helped with fieldwork. The study received support from the Norwegian State Education Loan Fund for which we are thankful.

Author contributions

S.R.M. conceived and designed the original experiment; E.F.A. and P.O. collected and analyzed data with guidance from S.R.M. and D.S.; E.F.A. led in writing the manuscript with guidance and input from P.O., D.S. and S.R.M.

Data accessibility

Primary data prepared as part of this study are to be stored in an online archive at Dryad Digital Repository.

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Appendix S9. Mean stem density for tree species traits considered in the study

Table 1. The most parsimonious models for the effects of fencing (Fenced vs Unfenced), habitat type (off-mound vs on-mound), year (2006, 2008 and 2015) and their interactions on tree traits (animal-dispersal mode, leaf strategy, spinescence and bark thickness) by relative stem density. For all treatments n = 9.

	Estimate	SE	t-value	P-value
Fleshy-fruited trees				
(Intercept)	2.86	0.30	9.63	< 0.001
Fenced (vs Unfenced)	-0.37	0.36	-1.03	0.304
Off-mound (vs On-mound)	-4.17	0.47	-8.84	<0.001
Fenced : Off-mound	1.18	0.55	2.13	0.036
Evergreen trees				
(Intercept)	-0.04	0.08	-0.50	0.620
Off-mound (vs On-mound)	-1.69	0.24	-7.02	< 0.001
Armed trees				
(Intercept)	-0.31	0.16	-1.96	0.052
Fenced (vs Unfenced)	-0.08	0.15	0.53	0.595
Off-mound (vs On-mound)	2.25	0.36	6.24	< 0.001
2008 (vs 2006)	-0.24	0.18	-1.35	0.180
2015 (vs 2006)	-0.41	0.16	-2.5	0.013
Fenced : Off-mound	-0.88	0.41	-2.14	0.035
Bark thickness (dbh = 2 cm)				
(Intercept)	1.17	0.09	12.5	< 0.001
Bark thickness (dbh = 5 cm)				
(Intercept)	1.57	0.07	21	< 0.001
Fenced (vs Unfenced)	0.03	0.11	0.3	0.743
Off-mound (vs On-mound)	0.51	0.10	5.2	<0.001
Fenced : Off-mound	-0.51	0.14	-3.5	0.001

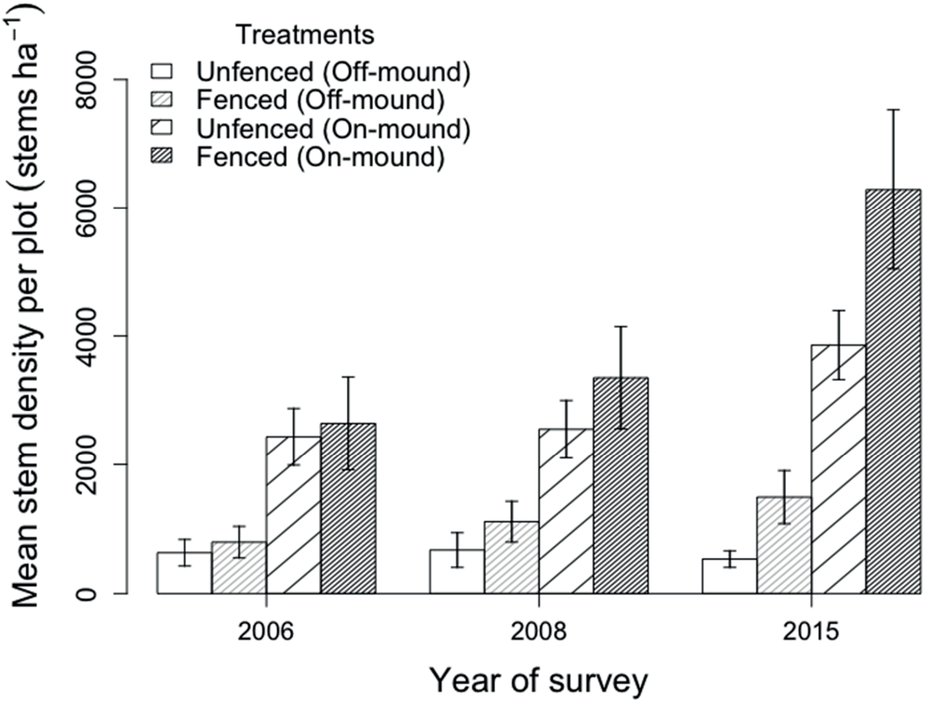


Figure 1. Mean (per plot ± SE) stems ha^{-1}, off- and on-mound in the presence (unfenced) and absence (fenced) of ungulates in 2006, 2008 and 2015 (i.e., 1, 3 and 10 y, respectively, after the onset of the exclosure experiment).

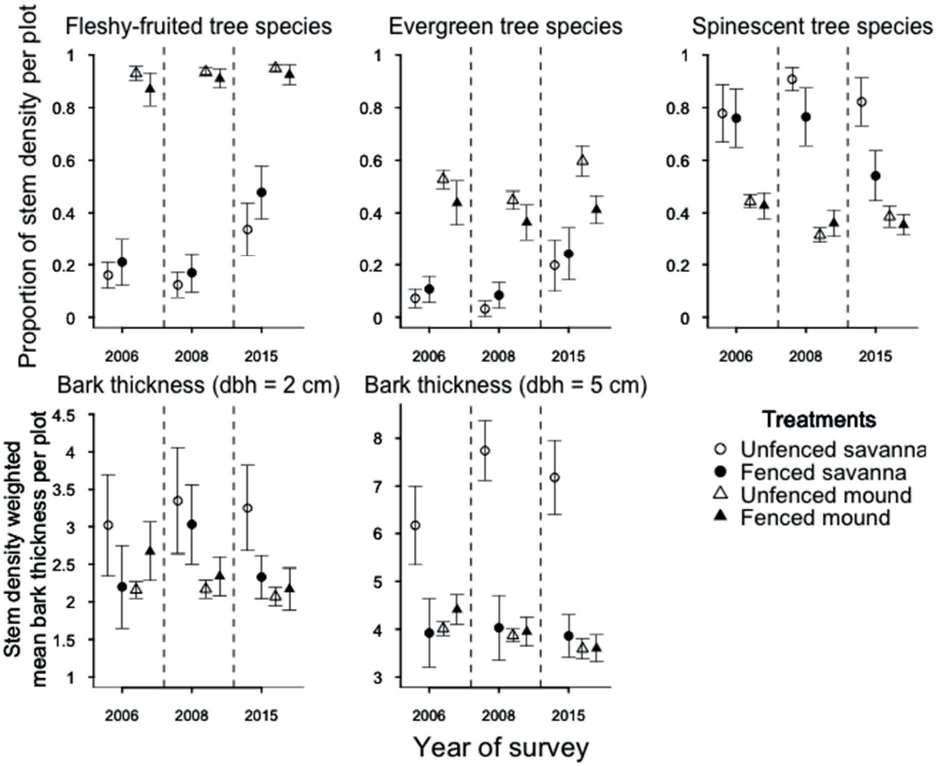


Figure 2. Mean (per plot ± SE) proportion of stem density for trees that are animal dispersed, evergreen, armed, and stem density-weighted (per plot ± SE) mean bark thickness at reference DBH sizes of 2 and 5 cm, off- and on-mound in the presence and absence of large mammalian herbivores

Appendix

Supporting Information to the paper Acanakwo, E. F., Okullo, P., Sheil, D. & S. R. Moe. Termites confer resistance to changes in tree composition following reduced browsing in an African savanna. *Journal of Vegetation Science*

Appendix S1. List of species recorded in all treatment plots showing mode of seed dispersal, leaf phenology, and armed status

Family	Species	Leaf	Primary seed dispersal agent	Armed
Anacardiaceae	Searsia natalensis (Bernh. ex C. Krauss) F.A.Barkley Synonym: Rhus natalensis Bernh. ex C. Krauss	Evergreen	Bird	No
Apocynaceae	Carissa edulis (Forssk.) Vahl	Evergreen	Bird	Yes
Capparaceae	Boscia angustifolia A.Rich	Evergreen	Bird	No
	Cadaba farinosa Forssk.	Evergreen	Mammal	No
	Capparis erythrocarpos Isert	Evergreen	Mammal	Yes
	Capparis fascicularis DC.	Evergreen	Mammal	Yes
	Capparis tomentosa Lam.	Evergreen	Mammal	Yes
	Maerua angolensis DC.	Deciduous	Other	No
	Maerua sessiliflora Gilg	Deciduous	Other	No
	Maerua triphylla A. Rich.	Deciduous	Other	No

Celastraceae	Gymnosporia heterophylla (Eckl. & Zehy.) Loes. Synonym: Maytenus heterophylla Eckl. & Zehy.	Deciduous	Other	Yes
	Maytenus undata (Thunb.) Blackelock	Evergreen	Bird	No
	Mystroxylon aethiopicum (Thunb.) Loes.	Evergreen	Bird	No
Ebenaceae	Euclea racemosa L.	Evergreen	Bird	No
Euphorbiacea	Erythrococca bongensis Pax	Evergreen	Other	No
	Erythrococca trichogyne (Mull.Arg.) Prain	Evergreen	Other	No
	Euphorbia candelabrum Kotschy	-	Other	Yes
Malvaceae	Grewia similis K. Schum	Deciduous	Bird	No
	Grewia trichocarpa Hochst. ex A.Rich	Deciduous	Bird	No
Mimosaceae	Cassia obtusifolia L.	Deciduous	Other	No
	Dichrostchys cinerea (L.) Wight & Arn.	Deciduous	Other	Yes

	Vachellia gerrardii (Benth.) P.J.H Hurter Synonym: Acacia gerrardii Benth.	Deciduous	Other	Yes
	Vachellia hockii (De Willd.) Siegler & Ebinger Synonym: Acacia hockii De Willd.	Deciduous	Other	Yes
	Senegalia polyacantha (Willd.) Siegler & Ebinger Synonym: Acacia polyacantha Willd.	Deciduous	Other	Yes
	Vachellia sieberiana (DC.) Kyal. & Boatwr Synonym: Acacia sieberiana (DC.) Kyal. & Boatwr	Deciduous	Other	Yes
Ochnaceae	Ochna inermis (Forssk.) Schweinf.ex Penz.	Deciduous	Bird	No
Olacaceae	Ximenia americana L.	Deciduous	Mammal	Yes
Oleaceae	Olea europea cuspidata (Wall. & G.Don) Cif.	Evergreen	Bird	No

Phyllanthaceae	Flueggea virosa (Roxb. ex Willd.) Royle	Deciduous	Bird	No
	Phyllanthus ovalifolius Forssk.	Deciduous	Bird	No
Polygalaceae	Securidaca longipedunculata Fresen.	Deciduous	Other	No
Rhamnaceae	Scutia myrtina (Burm.f.) Kurz	Evergreen	Bird	Yes
Rubiaceae	Psydrax schimperiana (A.Rich.) Bridson	Evergreen	Mammal	No
	Psydrax parviflora (Afzel.) Bridson	Evergreen	Mammal	No
	Rytigynia bagshawei (S.Moore) Robyns	Evergreen	Bird	No
	Tarenna graveolens (S.Moore) Bremek	Evergreen	Mammal	No
Rutaceae	Clausena anisata (Willd.) Hook.f. Ex Benth.	Deciduous	Bird	No
	Vepris nobilis (Delile) Mziray Synonym: Teclea noibilis Del.	Evergreen	Bird	No
Saliaceae	Dovyalis macrocalyx (Oliv.) Warn	Evergreen	Mammal	Yes
Sapindaceae	Allophylus africanus P.Beauv.	Evergreen	Bird	No

Haplocoelum foliolosum (Hiern.) Bullock	Deciduous	Other	No
Pappea capensis Eckl. & Zehy.	Evergreen	Bird	No

Appendix S2. The most parsimonious model results of the effects of fencing (fenced and unfenced), habitat type (off-mound and on-mound) and year (2006, 2008, 2015) on stem density, in the presence and absence of ungulates. The reference categories are Unfenced, on-mound and 2006. The model was arrived at by sequentially eliminating non-significant interactions and main terms (P > 0.05) from the saturated model.

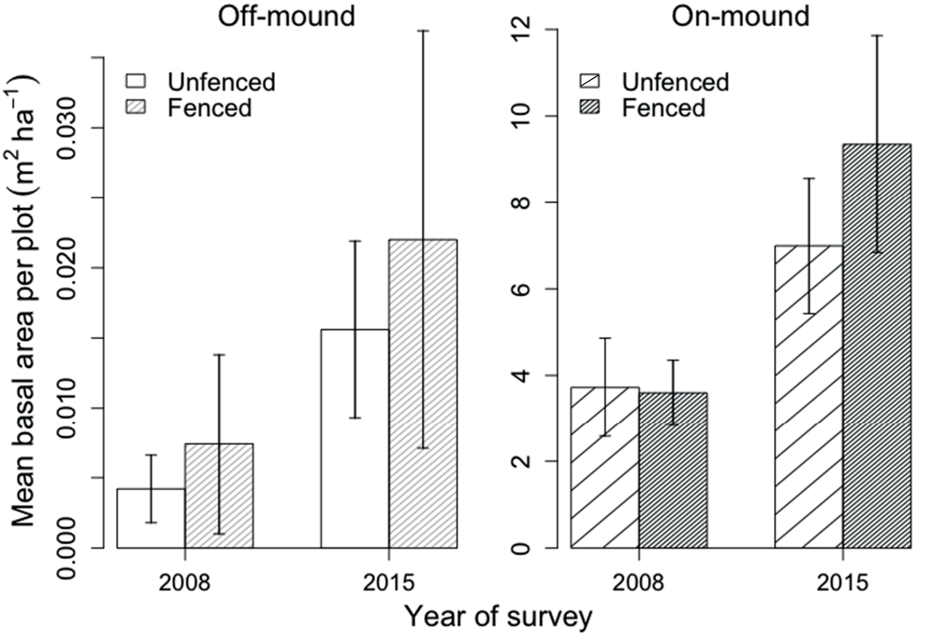
	Estimate	SE	Z	P
(Intercept)	7.70	0.29	26.25	< 0.001
Fenced (vs Unfenced)	-0.02	0.35	-0.05	0.96
Off-mound (vs On- mound)	-1.74	0.32	-5.42	< 0.001
2008 (vs 2006)	0.05	0.16	0.30	0.76
2015 (vs 2006)	0.31	0.17	1.87	0.06
Fenced : 2008	0.25	0.23	1.10	0.27
Fenced : 2015	0.66	0.23	2.82	0.005

Appendix S3. The most parsimonious model results of the effect of fencing, habitat type, and year on tree basal area in the presence and absence of large herbivores. The model is a generalized linear mixed effect model that followed a Gaussian distribution with a log link. The reference categories were Unfenced, On-mound and 2008. The model was arrived at by sequentially eliminating non-significant interactions and main terms (P > 0.05) from the saturated model.

	Estimate	SE	t	P
(Intercept)	1.33	0.14	9.2	< 0.001
Off-mound (vs On-mound)	-1.96	0.36	-5.5	< 0.001
2015 (vs 2008)	0.82	0.10	8.51	< 0.001

Notes: We measured DBH at 1.30 m, for two survey years (2008 and 2015; 3 and 10 years after the onset of the exclosure experimental)

Appendix S4. Mean (per plot ± SE) basal area ($m^2 ha^{-1}$) for trees off- and on-mound, in the presence (unfenced) and absence (fenced) of ungulates. Note the narrow y-axis scale for mean basal area against year of survey for off-mound habitat relative to the mound habitat that arose from few trees encountered having low dbh values.



Appendix S5. Permutation tests for homogeneity of multivariate dispersions on Bray-Curtis distance of tree communities for the effect of treatment (unfenced off-mound, fenced off-mound, unfenced on-mound, fenced on-mound). (Tukey´s multiple comparisons of mean with 95% family-wise confidence level was used to assess differences in treatment)

Sources of variation	df	SS	MS	F	P
Fenced	1	0.002	0.002	0.277	0.607
Residuals	101	0.752	0.007		
Habitat	1	0.582	0.582	70.27	0.001
Residuals	101	0.837	0.008		
Treatment	3	0.36	0.12	9.69	0.001
Residuals	99	1.231	0.012		

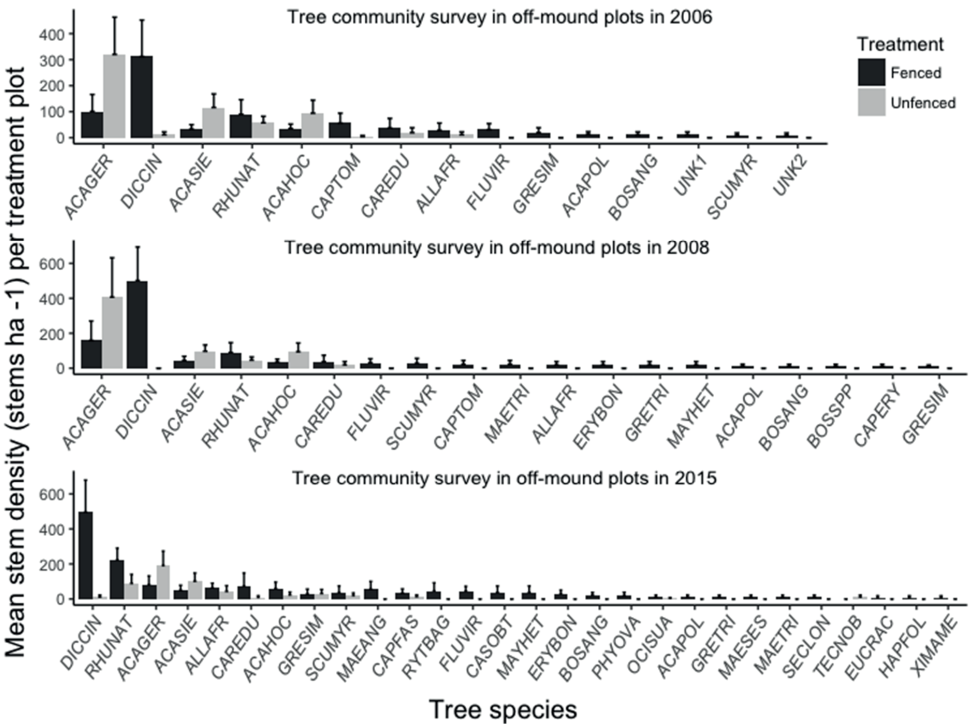
Treatment comparisons	Difference	Lower	Upper	P-adjusted
Unfenced on-mound – Fenced on-mound	-0.06	-0.14	0.02	0.24
Unfenced off-mound – Fenced off-mound	0.04	-0.04	0.13	0.52
Fenced off-mound – Fenced on-mound	0.06	-0.03	0.14	0.28
Unfenced off-mound – Fenced on-mound	0.10	0.02	0.18	0.01
Fenced off-mound – Unfenced mound	0.11	0.03	0.20	0.002
Unfenced off-mound – Unfenced on-mound	0.16	0.08	0.24	<0.001

Appendix S6. Changes in tree abundance of six most common tree species off- and on-mound habitat after 10 years of large mammalian herbivore exclusion experimental setup. The numbers in parentheses are proportional values of the total number of stems per habitat type. The underlined values highlight decline in number of stems per plot with fencing. Significance testing was done with Mann-Whitney test with V as the test statistic. *P* values were adjusted by the *Benjamini-Hochberg (fdr)*-procedure. We considered species that were identified in five or more plots to be common.

Species	Number of plots in which present (N = 18)	Total number of stems per habitat type	Mean number of stems per plot (Stems ha^{-1}) in unfenced plots	Mean number of stems per plot (Stems ha^{-1}) in fenced plots	v	*P-Adjusted*
Common trees growing off-mound						
Acacia gerrardii	9	2461	191 ± 82 (0.70)	82 ± 48 (0.30)	0.00	0.027
Acacia hockii	5	744	23 ± 16 (0.28)	59 ± 37 (0.72)	8.00	0.172
Acacia sieberiana	7	1349	101 ± 47 (0.67)	48 ± 29 (0.33)	4.50	0.249

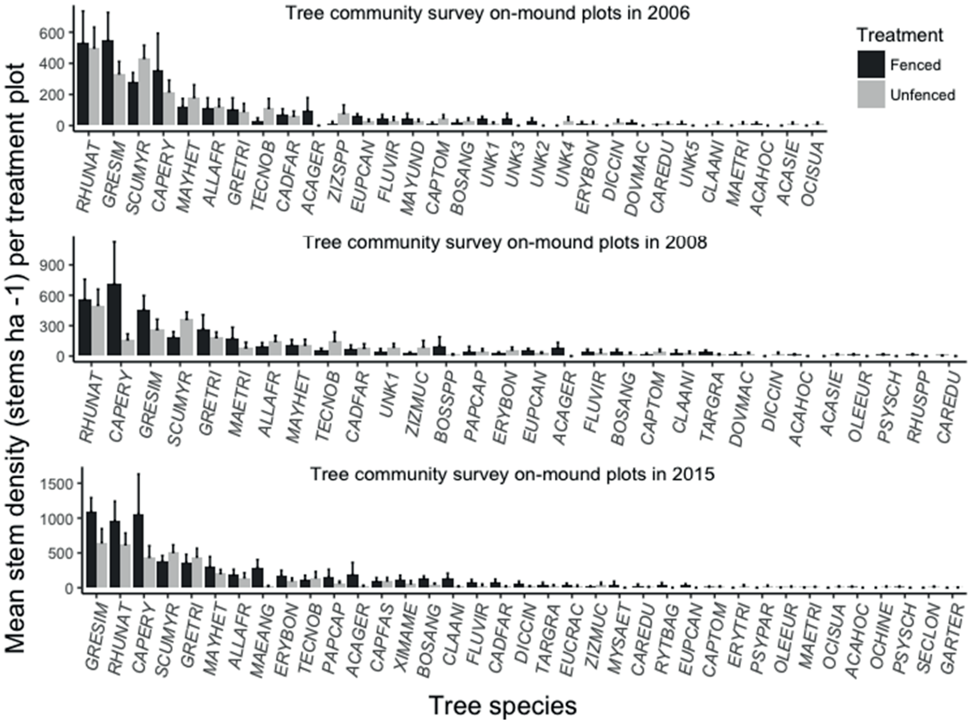
Allophylus africanus	6	950	43 ± 33 (0.40)	63 ± 27 (0.60)	10.0	0.294
Dichrostachys cinerea	7	4567	11 ± 11 (0.02)	496 ± 186 (0.98)	21.0	0.018
Rhus natalensis	10	2809	88 ± 51(0.28)	223 ± 67 (0.72)	24.0	0.053
Common trees growing on-mound						
Capparis erythrocarpos	15	13521	438 ± 165 (0.29)	1064 ± 575 (0.71)	23.5	0.242
Erythrococca bongensis	12	2543	101 ± 38 (0.36)	181 ± 69 (0.64)	14.5	0.231
Grewia similis	18	15675	648 ± 199 (0.37)	1093 ± 200 (0.63)	34.0	0.096
Grewia trichocarpa	16	7291	442 ± 123 (0.55)	368 ±112 (0.45)	19.0	0.361
Maytenus heterophylla	13	4536	204 ±5 7 (0.40)	300 ±147 (0.60)	28.0	0.276
Rhus natalensis	18	14241	618 ± 167 (0.39)	965 ± 276 (0.61)	29.0	0.071

Appendix S7. Mean (per plot ± SE) species abundance distribution from off-mound plots in the presence and absence of ungulates for tree community surveys in 2006, 2008, and 2015, (1, 3 and 10 y after the establishment of the experimental exclosures).



Species abbreviations are first three letters of the genus name and first three letters of the species name: *Acacia gerrardii* (ACAGER), *Acacia hockii* (ACAHOC), *Acacia sieberiana* (ACASIE), *Acacia polyacantha* (ACAPOL), *Allophylus africanus* (ALLAFR), *Boscia angustifolia* (BOSANG), *Boscia species* (BOSSPP), *Capparis erythrocarpos* (CAPERY), *Capparis fascicularis* (CAPFAS), *Capparis tomentosa* (CAPTOM), *Carissa edulis* (CAREDU), *Cassia obtusifolia* (CASOBT), *Dichrostachys cinerea* (DICCIN), *Erythrococca bongensis* (ERYBON), *Euclea racemose* (EUCRAC), *Flueggea virosa* (FLUVIR), *Grewia similis* (GRESIM), *Grewia trichocarpa* (GRETRI), *Haplocoelum foliolosum* (HAPFOL), *Maerua sessilifolia* (MAESES), *Maerua triphylla* (MAETRI), *Maytenus heterophylla* (MAYHET), *Ocimum suave* (OCISUA), *Phyllanthus ovalifolius* (PHYOVA), *Rhus natalensis* (RHUNAT), *Rytigynia bagshawei* (RYTBAG), *Scutia myrtina* (SCUMYR), *Securidaca longipedunclata* (SECLON), unknown 1 (UNK 1), unknown 2 (UNK 2), *Teclea nobilis* (TECNOB), *Ximenia americana* (XIMAME).

Appendix S8. Mean (per plot ±SE) species abundance distribution from mound plots in the presence and absence of ungulates for tree surveys in 2006, 2008, and 2015, (1, 3 and 10 y after the establishment of the experimental exclosures).



Species abbreviations are first three letters of the genus and first three letters of the species name: *Acacia gerrardii* (ACAGER), *Acacia hockii* (ACAHOC), *Acacia sieberiana* (ACASIE), *Allophylus africanus* (ALLAFR), *Boscia angustifolia* (BOSANG), *Boscia* species (BOSSPP), *Cadaba farinosa* (CADFAR), *Capparis erythrocarpos* (CAPERY), *Capparis fascicularis* (CAPFAS), *Capparis tomentosa* (CAPTOM), *Capparis tomentosa* (CAPTOM), *Carissa edulis* (CAREDU), *Clausena anisata* (CLAANI), *Dichrostachys cinerea* (DICCIN), *Dovyalis macrocalyx* (DOVMAC), *Erythrococca bongensis* (ERYBON), *Euclea racemose* (EUCRAC), *Euphorbia candelabrum* (EUPCAN), *Flueggea virosa* (FLUVIR), *Gardenia terniflora* (GARTER), *Grewia similis* (GRESIM), *Grewia trichocarpa* (GRETRI), *Maerua triphylla* (MAETRI), *Maytenus heterophyla* (MAYHET), *Mystroxylon aethiopicum* (MYSAET), *Ochna inermis* (OCHINE), *Ocimum suave* (OCISUA), *Olea* *europea* (OLEEUR), *Pappea capensis* (PAPCAP), *Phyllanthus ovalifolius* (PHYOVA), *Psydrax parviflora* (PSYPAR), *Psydrax schimperiana* (PSYSCH), *Rhus natalensis* (RHUNAT), *Rhus spp* (RHUSPP), *Rytigynia bagshawei* (RYTBAG), *Scutia myrtina* (SCUMYR), *Securidaca longipedunclata* (SECLON), *Tarenna graveolens* (TARGRA), *Teclea nobilis* (TECNOB), unknown 1 (UNK 1), unknown 2 (UNK 2), unknown 3 (UNK 3), unknown 4 (UNK 4), unknown 5 (UNK 5), *Ximenia americana* (XIMAME), *Ziziphus mucronata* (ZIZMUC), *Ziziphus species* (ZIZSPP).

Appendix S9. Mean (per plot ± SE) stem density (stems ha^{-1}) for traits considered in our study, that is, fruit type, leaf phenology (evergreen or deciduous), spinescent (spined or unspined). The values in parentheses are stem density-weighted per plot mean bark thickness at for dbh at 2 and 5 cm

Treatment	Year	Mean Total stem density per treatment plot (stems ha^{-1})	Mean stem density for fleshy-fruited trees per plot (stems ha^{-1})	Mean stem density for Evergreen trees per plot (stems ha^{-1})	Mean stem density for Spined trees per plot (stems ha^{-1})	Stem density-weighted per plot mean BT at dbh = 2cm (mm)	Stem-density weighted per plot mean BT at dbh = 5cm (mm)
SUF	2006	632 ± 205	91 ± 28	34 ± 20	563 ± 199	(3.0 ± 0.8)	(6.17 ± 0.8)
SF	2006	775 ± 233	281± 162	141 ± 79	596 ± 158	(2.2 ± 0.6)	(3.9 ± 0.8)
MUF	2006	2383 ± 446	2298 ± 442	1279 ± 285	1052 ± 183	(2.1 ± 0.1)	(4.0 ± 0.1)
MF	2006	2506 ± 671	2325 ± 685	1131 ± 361	1010 ± 291	(2.7 ± 0.4)	(4.4 ± 0.3)
SUF	2008	626 ± 267	64 ± 21	19 ± 19	580 ± 259	(3.4 ± 0.9)	(7.7 ± 0.6)
SF	2008	1101 ± 317	329 ± 195	176 ± 121	870 ± 219	(3.0 ± 0.7)	(4.0 ± 0.7)
MUF	2008	2451 ± 428	2326 ± 418	1134 ± 224	763 ± 146	(2.2 ± 0.1)	(3.9 ± 0.13)
MF	2008	3176 ± 724	3000 ± 736	1225 ± 378	1190 ± 401	(2.3 ± 0.2)	(4.0 ± 0.3)
SUF	2015	533 ± 128	205 ± 103	86 ± 45	370 ± 83	(3.3 ± 0.6)	(7.2 ± 0.7)
SF	2015	1492 ± 411	671 ± 308	294 ± 186	890 ± 225	(2.3 ± 0.2)	(3.8 ± 0.4)
MUF	2015	3858 ± 537	3674 ± 527	2321 ± 470	1412 ± 175	(2.1 ± 0.1)	(3.6 ± 0.2)
MF	2015	6287 ± 1243	5743 ± 1180	2978 ± 918	2303 ± 594	(2.2 ± 0.3)	(3.6 ± 0.2)

SUF-Unfenced savanna plots (Off-mound), SF- Fenced savanna plots (Off-mound), MUF-Unfenced mound plots, MF-Fenced mound plots. BT -Bark thickness

Paper II

Exclusion of large herbivores increases woody plant diversity in a low nutrient savanna landscape, but not on nutrient rich termite mounds

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Author Contributions: SRM conceived and designed the original experiment. EFA and PO collected field data. EFA analyzed the data. EFA led in writing the manuscript in collaboration with DS, PO and SRM.

Abstract

Grazing generally reduces grass species richness in resource-poor ecosystems and increases it in more resource-rich systems. While many studies have explored the influence of ungulates and nutrients on herbs and grasses, fewer have focused on woody plants. Here we report a 10-year experiment in an open savanna to assess how excluding large herbivores influence the diversity patterns of woody plants on resource-rich *Macrotermes* termite mounds, and on relatively resource-poor areas (i.e. off-mound). We recorded all woody plants in nine replicate sites each with four treatments comprising two resource-poor plots; unfenced and fenced off-mound (excluding large herbivores), and two resource-rich plots; unfenced and fenced on-mound plots. We found that species richness and plot-level Shannon diversity were markedly higher on the resource-rich mounds than off-mound ($P < 0.001$ for both richness and diversity). Fencing resource-poor off-mound plots resulted in 75% mean increment in species richness ($P = 0.04$), but richness in resource-rich on-mound plots were not affected by fencing. Similarly, we found no marked effect of fencing on plot-level diversity on-mound, but off-mound diversity increased in 2015, from 0.68 ± 0.22 in unfenced off-mound plots to 1.28 ± 0.25 in fenced plots ($P < 0.001$). Rarefaction indicates that these differences do not simply reflect changes in stem densities. Within-treatment beta-diversity was substantially higher off- than on-mound but ungulate exclusion was associated with little discernible changes on either habitat. We conclude that ungulates reduce woody species diversity in resource-poor savanna areas but have little influence in resource-rich areas.

Keywords: Browsers ● *Macrotermes* ●Plant-herbivore interactions ● Uganda ● Ungulates

Introduction

The presence of large herbivores has consequences for vegetation composition, diversity and dynamics (e.g. Goheen et al. 2010; Bakker et al. 2016; Pringle et al. 2016). The ongoing global decline in large herbivore populations may have broad implications for the vegetation properties (Collen et al. 2009; Dirzo et al. 2014; Ceballos et al. 2017). Previous studies have shown contrasting responses to changes in large herbivore populations. For example, absence of large herbivores has been associated with increases, decreases and mixed outcomes for vegetation richness (Collins et al. 1998; Kohyani et al. 2008; Scogings 2012). The disparities in vegetation responses to large mammalian herbivory have been attributed to variation in habitat productivity (Proulx and Mazumder 1998; Anderson et al. 2007; Borer et al. 2014; Lazema et al. 2014). Several studies suggest that herbivores increase grass species diversity in high-productivity conditions and decrease it at low productivity (Olff and Ritchie 1998; Borer et al 2014; Fraser et al. 2015). A meta-study comprising terrestrial, lake, stream and marine grazing ecosystems documented that grazers invariably reduced plant species richness in nutrient-poor systems, with responses more variable, but generally positive or neutral in nutrient-rich systems (Proulx and Mazumder 1998). Despite the many studies of effects of large herbivores on grass species richness in systems with contrasting productivity, we are not familiar with any such studies on woody plants. We expect that many of the same mechanisms found in grazing ecosystems would also be applicable to the woody species.

In African savannas, large herbivores and termites influence the local availability of resources (Augustine et al. 2003; van der Waal 2011; Erpenbach and Wittig 2016). The interactions between these two biotic factors can be competitive or complementary in causing vegetation heterogeneity (Sileshi et al. 2010). Large mounds built by termites of the genus *Macrotermes* are conspicuous features of the African savannas (Davies et al. 2016a). Through large-mound construction and foraging activities, these *Macrotermes* form and maintain comparatively resource-rich spots within the landscape in the form of higher plant nutrient content and soil moisture relative to adjacent off-mound areas (Jouquet et al. 2011; Seymour et al. 2014; Erpenbach and Wittig 2016). In addition to possessing richer soils than the surrounding areas, *Macrotermes* mounds are better protected from flood and fire damage due to their raised structure and often denser vegetation cover (Konaté et al. 1999; Jouquet et al. 2011; Okullo and Moe 2012a; Joseph et al. 2013; Seymour et al. 2014). Embedded within a relatively resource-poor off-mound matrix, these mound-habitats support woody species adapted to eutrophic, clay-rich substrates (Fleming and Loveridge 2003; van der Plas et al. 2013). This landscape is therefore, well suited for examining how herbivores affect vegetation diversity patterns in contrasting resource environments. The combined plots and treatments account for confounding effects from variations in ungulate assemblages and climate, commonly seen in other studies.

In a 10-year experiment we assessed the effects of large savanna herbivores on woody species diversity patterns. Using the same experiment as Okullo and Moe (2012b), we examined diversity patterns for woody species over 10-year on resource-rich patches (i.e. *Macrotermes* mounds) and on relatively resource poor areas (i.e. the savanna matrix). The results of that previous study only partly fitted the patterns seen in other grazer-grass diversity studies with herbivore exclusion leading to reduced diversity on-mounds, though little difference could be detected in off-mound plots (Okullo and Moe 2012b). Over that study, beta-diversity of herbaceous species remained high on mounds, but was unaffected by herbivore exclusion, but excluding herbivores from off-mound plots increased beta diversity towards mound site levels (Okullo and Moe 2012b). Based on these previous observations and noting that woody species have to establish in the same contexts as the herbaceous species, we hypothesized that the effect of excluding large herbivores on woody plant diversity would be similar with regard to both productivity and exclusion. In line with Okullo and Moe (2012b) we therefore predicted that: 1) ungulate exclusion would reduce woody species richness, evenness and plot-level diversity in the resource-rich plots (i.e., termite mounds) while exclusion would not affect these diversity measures on resource-poor plots (i.e. termite mounds) 2) exclusion would increase within-treatment beta-diversity on the off-mound areas, but have little influence across the on-mound plots and finally; 3) exclusion would have little impact on the compositional similarity of woody plants between fenced and unfenced plots (Okullo and Moe 2012a).

Materials and methods

Study area

We collected data on woody species identities and abundance from an experiment within the savanna of the approximately 260 km^2 Lake Mburo National Park. Located in southwestern Uganda (00°32’-00°37’S and 30°47’-31°04’E) between elevations of 1200 and 1300 m a.s.l., the park receives an annual rainfall of about 865 mm and has an annual mean temperature of 20.7 °C (www.climate-data.org). The park has two wet seasons; from October to December and February to May. The vegetation in the park is primarily grass-dominated savanna, with scattered woody plants and steep hills surrounding a perennial lake fringed by forest patches (Bloesch 2008; Moe et al. 2009).

The park has about 4 - 8 large termite mounds ha^{-1} (Pomeroy 1977). Most of these mounds are constructed by *Macrotermes subhyalinus* Rambur of the Macrotermitinae subfamily (Termitidae family) and have mean height of 1.7 m and radius of 3.7 m (Moe et al. 2009). Within the flat valley bottoms of the eastern and western parts of the park, the mounds typically support denser woody cover than the surrounding grasslands. Woody species common on mounds include *Scutia myrtina* (Burm.f.), *Capparis erythrocarpos* Isert and *Grewia similis* K. Schum, while *Dichrostachys cinerea*, *Acacia gerrardii* Benth., *A. sieberiana* DC. and *A. hockii* De Willd. are common in the adjacent savanna matrix (Acanakwo et al. submitted; Moe et al. 2017).

The park supports numerous large herbivores including impala - *Aepyceros melampus* (Lichtenstein, 1812), waterbuck - *Kobus ellipsiprymnus defassa* (Ogilby, 1833), bushbuck - *Tragelaphus scriptus* (Pallas, 1766), zebra - *Equus q. burchelli* (Gray, 1824), warthog - *Phacochoerus africanus* (Gmelin, 1788), topi - *Damaliscus lunatus* (Burchell, 1823) and eland - *Taurotragus oryx* (Pallas, 1766).

Experimental setup

Our experiment was established in 2005 and comprised nine sites. Each site included four treatment plots, two on- and two off-mound. One of each pair of mound and off-mound plots was fenced using a 5 cm galvanized chain link mesh, supported by 2 m high steel angle bars that were firmly fitted in the ground. The fences limited access to the plots by large herbivores (> 5kg). Our previous study from these sites indicated that woody plants that grow on termite mounds likely have access to various other nutrients like Ca and Mg that are known to be enriched in these soils (Okullo and Moe 2012a). Large herbivores fed more on vegetated mounds than off-mound (Mobæk et al. 2005). All termite mounds were active when the experiment was originally established (Okullo and Moe 2012a), many were abandoned and re-colonized during the study period, but all were inactive enduring our assessment in 2015.

Woody species community survey

Within each plot, we recorded all woody plants taller than 30 cm between April and August in 2006, 2008 and 2015 (that is, one, three and 10 years after the fences had been established). All these plants were identified with reference to Katende et al. (1995) and local experts. We took vouchers to Makerere University Herbarium for verification. Nomenclature follows Katende et al. (1995)

Statistical analyses

We calculated species richness (S), Shannon diversity index (H') and evenness (E) for each plot. Species richness is the sum of species present in each plot. We used species richness and relative species abundance to calculate Shannon index (H′) and evenness (E) using the following equations; $H' = -\sum_{i=1}^{S} PiInPi$ and $E = H'/In(S)$, where S was the number of species per plot and P_i the abundance of each species per plot divided by the total abundance of all species in the plot (Shannon 1948; Pielou 1969). Plots with one or no woody species would give undefined values of evenness. Since some of our off-mound sites had one or no woody plant species, we excluded all savanna plots from our assessment of evenness.

We constructed a generalized linear mixed effects model with Poisson errors using the "glmer" function within "lme4" R package to model species richness as a function of fencing (unfenced/fenced), habitat (off-mound/on-mound), and year of survey (2006, 2008 and 2015, i.e., one, three and 10 years after experimental setup). Since sampling was repeated within plots, plot identity was a random factor, while fencing, habitat and year were fixed factors. The most parsimonious model was determined through backward stepwise elimination of non-significant variables ($P > 0.05$). The most parsimonious model was underdispersed, so we corrected for under-dispersion by running models using quasipoisson errors. To test the effects of fencing, habitat and year on Shannon diversity, we constructed a linear mixed effects model using “lmer” function within “lme4” R package. We used a similar model for evenness but excluded habitat since we recorded low stem numbers per plot (0 – 5 individuals) in 41% of all off-mound plots and gave less meaningful measures of evenness. We first fitted a saturated model that included all terms and their interactions, then simplified the model sequentially through backward stepwise elimination of non-significant ($P > 0.05$) interactions and subsequently main terms (Crawley 2013; Zuur et al. 2013).

We assessed within treatment beta-diversity as dissimilarity in community composition, obtained as measures of distance of each treatment from the group centroids in multivariate dispersion space (Anderson et al. 2006). We obtained beta-distance of each treatment group from the group centroid using Whittaker’s index. We tested for differences in within-treatment beta-diversity using the permutation multivariate analysis of variance (PERMANOVA) implemented using the “adonis” function in “vegan” package (Oksanen et al. 2017). When we detected a significant effect of treatment on beta-diversity, we ran pairwise comparisons between treatments using Tukey´s HSD test. We used the “betadisper” function in the “vegan” R package (Oksanen et al. 2017) to compute values of the distance to the group centriods.

To compare woody species compositional similarity between paired-treatment groups we calculated Morisita-Horn indices using abundance data (Magurran and McGill 2011). We estimated 95% confidence intervals from 200 bootstrap replications using the function *similarityMult* in *SpadeR* package in R (Chao et al. 2016).

Results

We recorded a total of 52 woody species within 18 families through the ten-year study period. When we look at our two landscape categories of plots (unfenced -with ungulates present; and fenced -without ungulates) we see that most woody species occur on- rather than off- mounds in both cases (see numbers in Fig. 1) and comprising over two thirds of all our recorded total species in 2015 (69 %). There was an increase in total species richness from 2006 to 2015 in the unfenced plots, with the count rising from 27 to 32, and also in the fenced plots rising from 29 to 36.

The number of species shared between off- and on-mound plots varied considerably over periods and fencing treatments (from just 2 for unfenced plots in 2008 to 19 for fenced plots in 2015) but appears to rise overall over the ten years: from 19% (5 of 27) to 25% (8 of 32) in the unfenced and 34% (10 of 29) to 53% (19 of 36) in the fenced plots (Fig 1).

While, per plot woody species richness was lower off-mound (3.3 ± 0.39 species per plot) than on-mound (10.9 ± 0.58) ($P< 0.001$, Fig. 2a, Table 1), fencing increased species richness in off-mound plots ($P = 0.04$, Fig. 2a, Table 1), but not on-mound. Combined and rarefied species richness (N = 50 individuals) increased with time in fenced on- and off-mound plots (Appendix S1: Table. 1, Appendix S1: Figures S1-S3).

Plot-level Shannon diversity was higher on-mound (55% higher), than off-mound (mean Shannon diversity index: 1.97 ± 0.05 and 0.78 ± 0.09 on- and off-mound, respectively) ($P< 0.001$, Figure 2b, Table 1). Fencing was associated with increased (88% increase) plot level diversity off-mound in 2015 (from 0.68 ± 0.22 in unfenced off-mound plots to 1.28 ± 0.25 in the fenced off-mound plots) ($P < 0.001$, Fig. 2b, Table 1). Fencing did not significantly change plot-level Shannon diversity on-mound.

Although species evenness of woody species communities in fenced mounds was slightly lower (0.82 ± 0.03) than in unfenced mounds (0.89 ± 0.02) in 2008, we did not detect significant differences (Fig. 2c, Table 1).

Within treatment beta-diversity differed significantly among the four study treatments (PERMANOVA: F = 16.98, $R^2 = 0.34$, P = 0.001, Fig. 2d, Table 2). Fencing was not associated with significant changes in within-treatment beta-diversity either on- or off-mound ($P = 0.710$, $P = 0.40$, respectively, Fig. 2d, Table 2).

Across treatments, regardless of the year of survey, species composition was most similar between unfenced and fenced on-mound plots (mean Morisita-Horn index = 0.94, Fig. 3), and least similar between unfenced off-mound and unfenced on-mound paired treatments (mean Morisita-Horn index = 0.16). Similarity values were consistently higher for all paired-treatment comparisons in the 2015 survey and lowest in the 2008 survey, while similarity values in 2006 were intermediate.

Discussion

Our predictions did not match our observations. Firstly, our prediction that herbivore exclusion would reduce richness, evenness and plot-level diversity of woody species on mounds and have little influence in off-mounds locations was incorrect. In fact the only clear effect of exclusion was that richness and plot-level diversity increased in off-mound plots (with evenness on-mound showing no clear change). Secondly, our prediction that exclusion would increase within-treatment beta-diversity off-mounds but have little impact on within-treatment beta-diversity on-mounds were also only correct for the latter case: within-treatment beta-diversity changed little in both locations. Finally, our prediction that exclusion would have little influence on the compositional similarity among treatments was also inaccurate. In fact we observed some divergence in the composition of the woody vegetation in off-mound plots following fencing. Our predictions follow previous observations of herbaceous vegetation in the same site and experimental context (Okullo and Moe 2012b). We conclude that, at least on the timescale of our study, the processes and mechanisms that determine plot level patterns of diversity for woody and for herbaceous vegetation are distinct.

There may be systematic changes in our study area. Specifically, the increase in woody species richness observed in the unfenced off-mound plots is only slightly less than observed in the treatments (Figure 1 and Figure 2a). These increases likely result in some part from an increase in woody cover across the region as well as in the plots (Acanakwo et al. submitted) but rarefaction (see S1-S3) suggests that this is not a complete explanation. In all periods, most species occurred on Macrotermes mounds, and that even many of the species found off-mounds were also recorded in mound plots. As woody vegetation on the on-mound plots grows denser we observe that it spreads out into neighboring areas—possibly indicating edge related facilitation. In any case, regardless of the mechanisms, it is not surprising that mound-centered plots share many species with off-mound plots as these plots contain a woody fringe of off-mound vegetation, and this increases as stem densities increase. This same density increase effect is particularly marked when herbivores are excluded explaining how the number of shared species between off and on mound plots grows to 53% in fenced treatments. The density effects have wider implications, for example the high beta-diversity in off-mound sites reflects the lower stem counts in these locations: as the mean slope of the species number (s) versus individual plants (n) curve declines. As n increases a greater increase in diversity across plots occurs when each plot has few stems and species (see, e.g., Hurlbert 1971). The high species richness on mounds (in all periods and treatments) is striking given that these comprise such a small area of the landscape. Until a few centuries ago the Lake Mburo landscape was likely dominated by forest (Hamilton 1984; Howard 1991). The lake and wet hillsides still include residual forest and forest species. The high richness of woody species observed on the termite mounds may thus reflect their ability to sustain forest species that disperse in from the wider landscape.

The mismatch between previous observations for herbaceous plants, and our observations indicate differences in the determinants of woody versus herbaceous diversity. This difference is unexpected: both herbaceous and woody species have to establish in the same conditions in these locations. We know that competition from grass can influence the establishment of woody species (Riginos 2009). For example, reduced competition from grass was recently highlighted as critical for the establishment of *Acacia robusta* and *A. tortilis* in the Serengeti (Morrison et al. 2018). When grassland productivity is high, grazing can maintain and increase diversity among grass species by reducing competition and preventing exclusion (e.g., Borer et al. 2014). This would explain why other studies indicate that exclusion of herbivores can bolster grass species diversity in low productivity contexts and decrease it in high-productivity conditions (Olff and Ritchie 1998; Borer et al 2014; Fraser et al. 2015). We would thus expect this reduced competition to benefit woody species too this is not what we see. So what is the explanation? Perhaps some other consequence of dense grass-cover is important: for example, fire. Though we lack the records needed to examine this directly we suspect that changed fuel loads impact the frequency and intensity of fires (n.b., even if we had such data, our study does not replicate this “landscape level” outcome of herbivore loss as fire occurrence and behavior depend primarily on the external matrix). In any case, whereas grasses and many herbaceous species can benefit from recurrent fires, many seedlings are vulnerable (especially to hot or frequent burns) though some individuals may reach the larger, thicker barked, sizes where they are less vulnerable (Hoffman et al. 2012; Pausas 2015). Such intermittent impacts might also explain both the fluctuating values seen in some of our measures as well as why earlier observations detected no effects from herbivore exclusion (Støen et al. 2013). These influences may be greater off-mounds rather than on them as fire seldom burns the woody cover on mounds (Joseph et al. 2013, van der Plas 2013). There are other possible explanations too. It has long been recognized that herbivory can have a range of effects on vegetation properties. Harper (1969), for example, identified four ways in which herbivores can affect plant diversity: 1) removal of intense herbivory can allow the development of increased species diversity, but this may be transient as succession progresses; 2) generalist herbivory will generally increase diversity if the dominant species are preferred over the rarer species; 3) generalist herbivory is likely to reduce diversity if the dominant species are unpalatable and avoided; 4) that herbivory will act to maintain higher diversity if predation (per individual) increases with density. Observations in tropical grasslands indicate that selective browsing tends to favor unpalatable woody plants (Augustine and McNaughton 1998). This effect may be strongest on nutrient-poor sites as plants are more vulnerable to damage in less-productive environments (Chase et al. 2000). Such relationships are further complicated by recognizing that animals choose not only what to eat but where to feed (Muvengwi, et al. 2013; Davies et al. 2016b). While many browsers favour time on and near termite mounds (Brody et al. 2010, Loveridge and Moe 2004, Mobæk et al. 2005), they seek out the nutrient rich foliage of leguminous tree species which comprise a greater component of the off-mound tree cover (Van der Plas et al. 2013). As noted for grazing behaviours in Zimbabwe (Muvengwi et al. 2018) such selective behaviors may be contingent on nutrient availability and thus may differ in other geological settings.

In any case, we would expect that if herbivores are excluded, more palatable species would be able to establish. In fact, we observed that herbivore exclusion had little influence on the richness of on-mound woody vegetation. We see at least four plausible explanations.

Species that grow on mounds may be relatively less sensitive to browsing given the better growing conditions and improved compensatory regrowth. The thicket like woody vegetation on some mounds may be difficult for larger herbivores to access and thus provide localized “safe sites” for browse vulnerable woody species even without fencing – thus fencing does not offer opportunities for additional species. Alternatively, given the high abundance of large herbivores in the surrounding landscape, there may be few if any browsing intolerant species in the wider region, so while such species might establish on mounds if their seeds arrived, this remains hypothetical if no such seeds occur. Furthermore, we note that where richness off-mounds increase these rises may be transient as succession progresses (Harper 1969; Sheil 1999).

Many other factors may play a role in the different results for woody versus herbaceous diversity patterns. For example, when compared to herbaceous plants woody species are typically longer lived, have larger seeds, rely on different dispersal mechanisms, are subject to different seed predators (see e.g., Acanakwo et al. 2017, for some evaluation for woody species), and are usually less vulnerable to competition, fire, and other threats in mature life-stages. The extent and specializations of the local species pools for the different life-forms may also be distinct. A recent study of vegetation and soils on and off mounds in Zimbabwe concluded that termite mound soils were richer in a range of nutrients and soil properties (clay content, drainage, bases) and supported distinct vegetation. This mound vegetation comprised fewer grasses and forbs than the surrounding matrix but, as in our study, was richer in woody species (Muvengwi et al. 2016). The facilitation role of tree cover also requires further examination. These aspects remain to be explored.

We found that the diversity of woody and herbaceous vegetation responds differently to the exclusion of large herbivores in our study system. In contrast to previous observations of how herbaceous species respond to herbivore exclusion (Okullo and Moe 2012b), our findings, showed that fencing out large herbivores had little discernible effect on the species richness and plot-level diversity of woody species on nutrient rich mounds but increases richness and diversity on the relatively nutrient poor off-mound sites. Our findings only partially agreed with the general grazer-grass diversity theory which suggests that increased herbivory should increase diversity on resource-rich sites and decrease diversity on resource poor sites. We conclude that the influences of large herbivores on local as well as landscape scale diversity patterns are clearly life-form and context dependent.

Acknowledgements We thank the Uganda Wildlife Authority (UWA) who granted permission and allowed access to Lake Mburo National park for fieldwork. Lawrence Kabito, Fred Matovu, Antonia Nyamukuru helped with fieldwork. The study received support from the Norwegian State Education Loan Fund for which we are thankful.

Conflict of Interest The authors declare that they have no conflict of interest

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Tables

Table 1. Model results of the effects of fencing (fenced or unfenced), habitat (on- or off-mound habitat) and time (2006, 2008, 2015, i.e., 1, 3, and 10 years since the experiment setup) on tree species richness, diversity and evenness in Lake Mburo National Park, Uganda. The reference factors are Unfenced plots, on-mound habitat and year of survey 2006.

Fixed effects	Estimate	SE	t	*P*
Species richness				
Intercept	2.207	0.107	20.50	< 0.001
Fenced (vs. unfenced)	0.067	0.108	0.628	0.532
Off-mound (vs. on-mound)	-1.46	0.18	-8.16	< 0.001
2008 (vs. 2006)	0.107	0.121	1.882	0.380
2015 (vs. 2006)	0.315	0.116	2.72	0.008
Fenced : Off-mound	0.478	0.230	2.08	0.04
Diversity				
Intercept	1.95	0.180	10.0	< 0.001
Fenced (vs. Unfenced)	-0.201	0.255	-0.780	0.436
Off-mound (vs. On-mound)	-1.261	0.255	-4.93	<0.001
2008 (vs. 2006)	0.109	0.099	1.10	0.275

2015 (vs. 2006)	0.142	0.099	1.434	0.156
Fenced : Off-mound	0.299	0.361	0.829	0.412
Off-mound : 2008	-0.328	0.140	-2.334	0.02
Off-mound : 2015	-0.158	0.140	-1.125	0.264
Fenced : On-mound : 2008	0.011	0.140	0.081	0.935
Fenced : Off-mound : 2008	0.179	0.140	1.277	0.206
Fenced : On-mound : 2015	0.187	0.140	1.329	0.189
Fenced : Off-mound : 2015	0.05	0.140	3.55	<0.001
Evenness				
Intercept	0.882	0.021	41.432	< 0.001
Beta-diversity				
(Intercept)	0.284	0.034	8.189	< 0.001
Off-mound (vs On-mound)	0.167	0.037	4.554	< 0.001

Table 2. Difference in within- treatment beta-diversity detected using permutation tests for homogeneity of multivariate dispersions on Whittaker´s distance for tree communities in four experimental treatments -unfenced off-mound, fenced off-mound (excluding ungulates), unfenced on-mound and fenced on-mound treatment plots. Tukey´s multiple comparisons of mean with 95% family-wise confidence level.

	df	SS	MS	F model	R2	P value
Treatment	3	10.281	3.43	16.98	0.3353	0.001
Residuals	101	20.38	0.201		0.664	
Totals	104	30.661			1	
Treatment comparisons			Difference	Lower	Upper	P-adjusted
On-MUF – On-MF			-0.037	-0.125	0.052	0.705
Off-MF – On-MF			0.142	0.052	0.233	<0.001
Off-MUF – On-MF			0.088	-0.002	0.177	0.058
Off-MF – On-MUF			0.179	0.088	0.270	<0.001
Off-MUF – On-MUF			0.124	0.034	0.214	0.002
Off-MUF – Off-MF			-0.055	-0.146	0.036	0.405

Figure legends

Fig. 1 Venn diagrams of total tree species richness on landscapes comprised of on-mound and off-mound habitats with and without ungulates for the three tree community surveys in 2006, 2008 and 2015 divided into the number of species on-mound plots only, off-mound plots only and the number of species shared by both habitats.

Fig. 2 Effect (mean ± SE) of treatment (i.e. fenced and unfenced off- and on-mound plots) on tree community richness (a), diversity (b), evenness (c) and beta diversity (i.e. Whitakker´s mean distance to group centroids) (d) in three years of tree community survey in 2006, 2008 and 2015 (that is 1, 3 and 10 years after experimental setup). Evenness values from off-mound plots were not included in the analysis because of low species richness and abundance values that resulted in consistently high evenness values.

Fig. 3 Morisita-Horn similarity indexes for paired-treatment comparisons of tree community surveys undertaken in 2006, 2008 and 2015. The Morisita-Horn paired similarity comparisons are between the four experimental treatments of; unfenced off-mound plot (Off.MUF), fenced off-mound plot (Off.MF), unfenced on-mound plot (On.MUF) and fenced on-mound (On-MF)

Figures

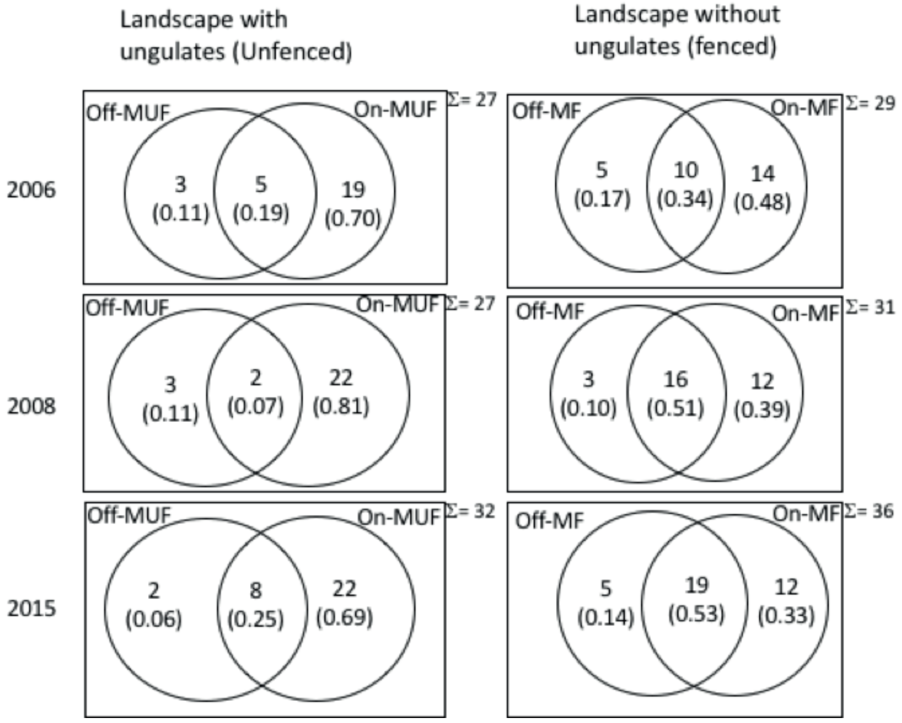

Fig. 1

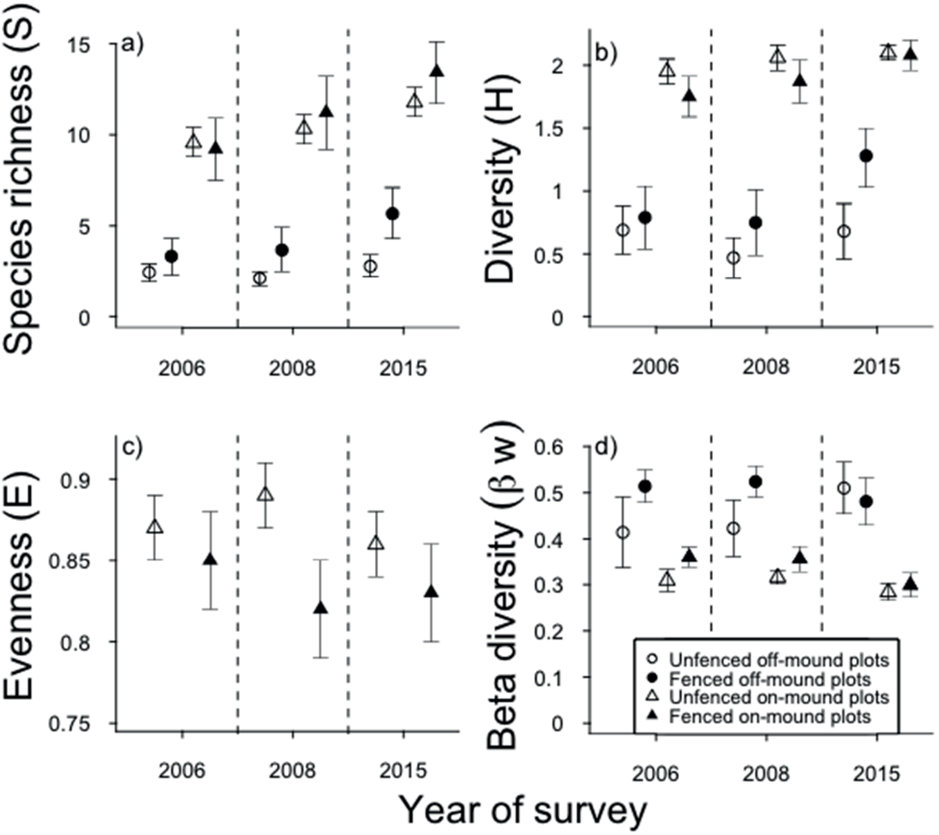
a)
Species richness (S)
15
10
5
0
2006
2008
2015
b)
Diversity (H)
2
1.5
1
0.5
0
c)
Evenness (E)
0.9
0.85
0.8
0.75
d)
Beta diversity (β w)
0.6
0.5
0.4
0.3
0.2
0.1
○ Unfenced off-mound plots
● Fenced off-mound plots
△ Unfenced on-mound plots
▲ Fenced on-mound plots
Year of survey

Fig. 2

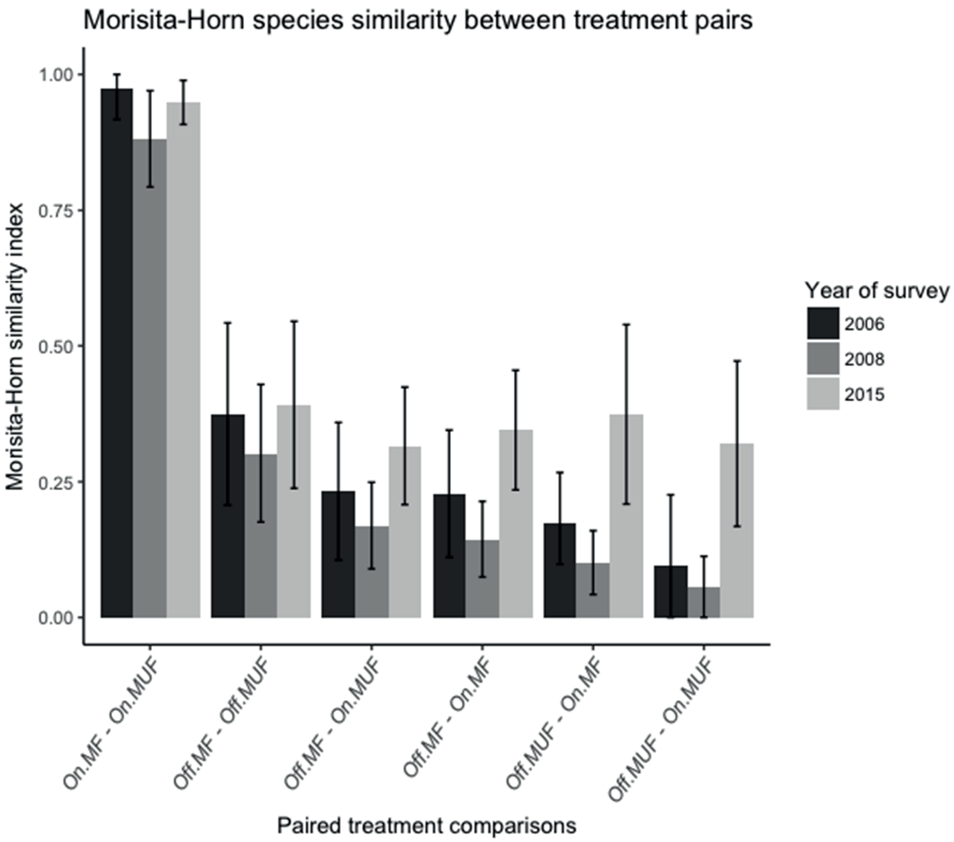
Morisita-Horn species similarity between treatment pairs
Morisita-Horn similarity index
1.00
0.75
0.50
0.25
0.00
On.MF - On.MUF
Off.MF - Off.MUF
Off.MF - On.MUF
Off.MF - On.MF
Off.MUF - On.MF
Off.MUF - On.MUF
Paired treatment comparisons
Year of survey
2006
2008
2015

Fig.3

Appendix

APPENDIX S1

Table 1 Observed and rarefied species richness in the four experimental treatments (i.e., unfenced off-mound, fenced off-mound, unfenced on-mound, fenced on-mound) from three tree community surveys in 2006, 2008 and 2015 in Lake Mburo National Park, Uganda.

Treatment	Year	Observed species richness (S)	Rarefied species richness at N = 50 individuals in unfenced off-mound treatment
Unfenced Off-mound	2006	8	7.5
Fenced Off-mound	2006	15	12.9
Unfenced On-mound	2006	24	14.9
Fenced On-mound	2006	24	14.9
Unfenced Off-mound	2008	5	5.0
Fenced Off-mound	2008	19	13.8
Unfenced On-mound	2008	24	16.5
Fenced On-mound	2008	28	16.6
Unfenced Off-mound	2015	10	10.0
Fenced Off-mound	2015	24	16.7
Unfenced On-mound	2015	30	15.0
Fenced On-mound	2015	31	16.9

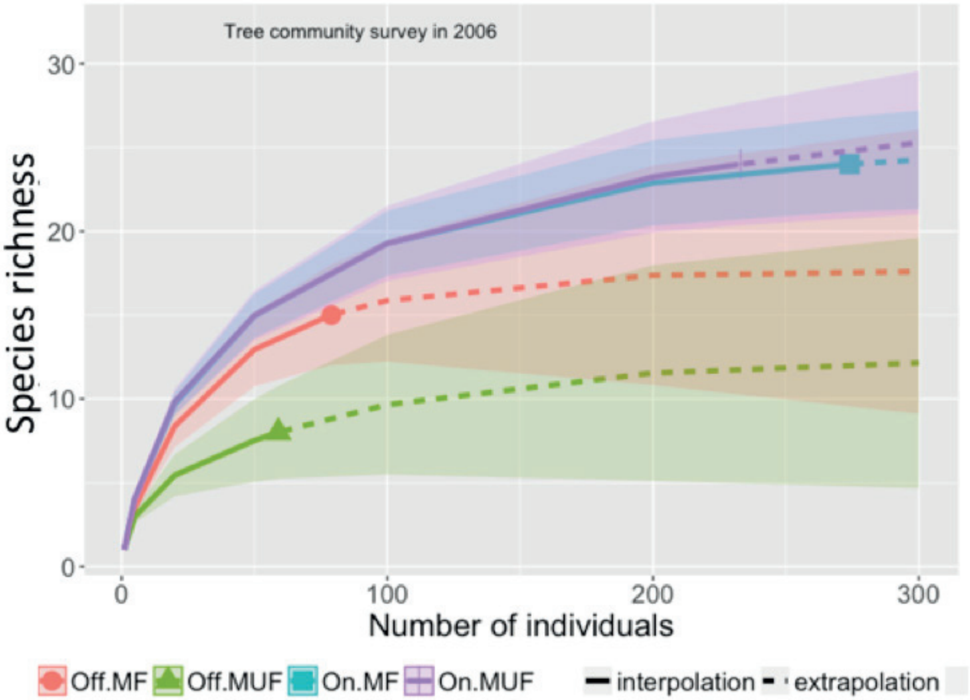

Figure S1. Individual-based species accumulation curves for the different treatments (SUF-unfenced savanna (off-mound), SF-Fenced savanna (off-mound), MUF-Unfenced mound (on-mound) and MF-fenced mound (on-mound) for the tree community survey undertaken in 2006.

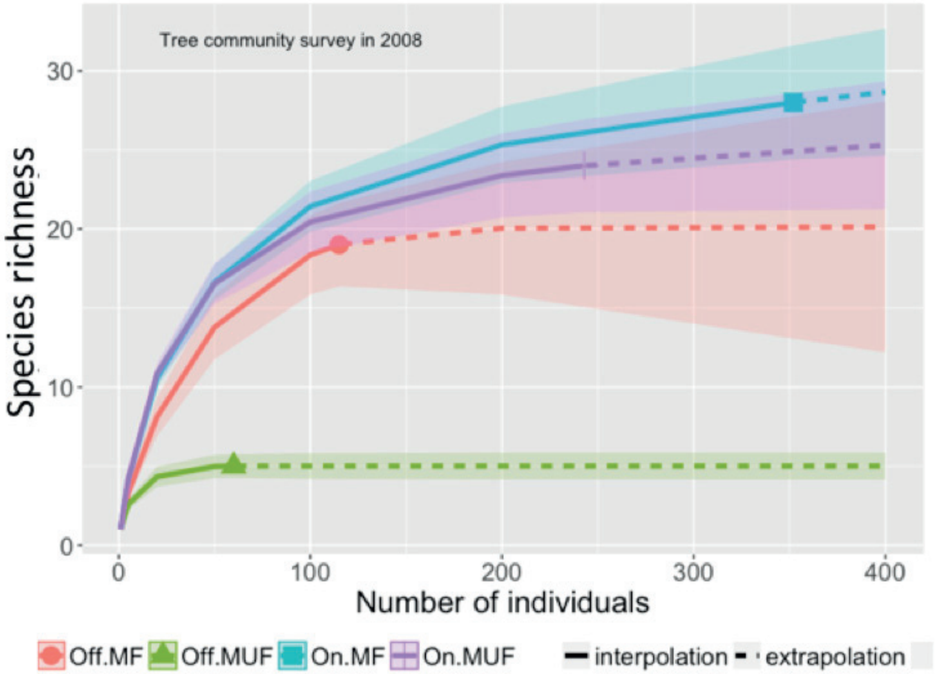

Figure S2. Individual-based species accumulation curves for the different treatments (SUF-unfenced savanna (off-mound), SF-Fenced savanna (off-mound), MUF-Unfenced mound (on-mound) and MF-fenced mound (on-mound) for the tree community survey undertaken in 2008.

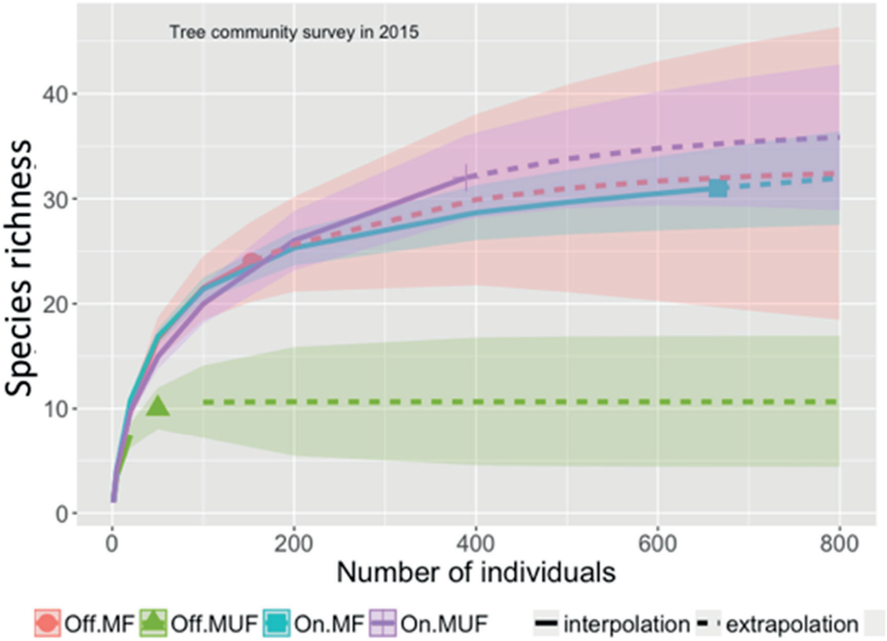

Figure S3. Individual-based species accumulation curves for the different treatments (SUF-unfenced savanna (off-mound), SF-Fenced savanna (off-mound), MUF-Unfenced mound (on-mound) and MF-fenced mound (on-mound) for the tree community survey undertaken in 2015.

Paper III

Ecology, 98(12), 2017, pp. 3165–3174

Termites and large herbivores influence seed removal rates in an African savanna

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Abstract. Seed removal can influence plant community dynamics, composition, and resulting vegetation characteristics. In the African savanna, termites and large herbivores influence vegetation in various ways, likely including indirect effects on seed predators and secondary dispersers. However, the intensity and variation of seed removal rates in African savannas has seldom been studied. We experimentally investigated whether termites and large herbivores were important factors in the mechanisms contributing to observed patterns in tree species composition on and off mounds, in Lake Mburo National Park, Uganda. Within fenced (excluding large herbivores) and unfenced termite mound and adjacent savanna plots, we placed seeds of nine native tree species within small open "cages," accessed by all animals, roofed cages that only allowed access to small vertebrates and invertebrates, and closed cages that permitted access by smaller invertebrates only (5 mm wire mesh). We found that mean seed removal rate was high (up to 87.3% per 3 d). Mound habitats experienced significantly higher removal rates than off-mound habitats. The mean removal rate of native seeds from closed cages was 11.1% per 3 d compared with 19.4% and 23.3% removed per 3 d in the roofed and open cages, respectively. Smaller seeds experienced higher removal rates than larger seeds. Large herbivore exclusion on mounds reduced native seed removal rates by a mean of 8.8% in the open cages, but increased removal rates by 1.7% in the open cages when off-mound habitats were fenced. While removal rates from open cages were higher on active mounds (30.9%) than on inactive mounds (26.7%), the removal rates from closed cages were lower on active vs. inactive mounds (6.1% vs. 11.6%, respectively). Thus, we conclude that large herbivores and *Macrotermes* mounds influence seed removal rates, though these effects appear indirect.

Key words: African savanna; herbivores; invertebrates; Macrotermes *mounds; seed cages; seed removal; Uganda; vertebrates.*

INTRODUCTION

Seed removal by animals has important consequences (Zhang et al. 1997). It influences plant colonization, regeneration, distribution, and reproductive success and can thus influence the composition, structure, and associated properties of vegetation (Hulme 1998, Bell and Clark 2016). Seed removal may result in seed predation or translocation to other microsites that may favor seedling establishment (Vander Wall et al. 2005). Seed removal rates typically vary with factors such as habitat type, seed species, seed density, seed size, and removal agents (Hulme and Borelli 1999).

Tropical savannas maintain abundant and diverse termite faunas (Bignell et al. 2011). At approximately 10 million km^2 (Riggio et al. 2013), African savannas are the world's largest savannas; characterized by a continuous grass layer, most of which possess tree cover and termite mounds (Frost et al. 1986, Sileshi et al. 2010). Termites of the Macrotermitinae sub-family (*Macrotermes*), build large epigeal mounds (Sileshi et al. 2010). These *Macrotermes* mound soils have enhanced water and nutrient availability for plants relative to off-mound soils and support increased growth of vegetation (Sileshi et al. 2010, Okullo and Moe 2012*b*).

Established *Macrotermes* mounds typically have higher densities and diversities of woody plants and forbs than the surrounding savanna (Traoré et al. 2008, Moe et al. 2009, Sileshi et al. 2010, Okullo and Moe 2012*a*). This vegetation has implications for local fauna. The abundance and diversity of small mammals is high on vegetated mounds relative to the surrounding savanna (Fleming and Loveridge 2003, Okullo et al. 2013). The mound vegetation is also preferentially fed on by large herbivores (Loveridge and Moe 2004, Mobæk et al. 2005).

The vegetation on mounds, mainly recruited from seeds, creates local shaded habitats that reduce stress from heat and desiccation (Traoré et al. 2008, Støen et al. 2013, Bonachela et al. 2015, Joseph et al. 2016). These habitats enable the persistence of species that would otherwise be vulnerable to climate extremes (Joseph et al. 2016).

African savannas support abundant and diverse vertebrate herbivore populations (Du Toit and Cumming

Manuscript received 27 February 2017; revised 20 July 2017; accepted 11 September 2017. Corresponding Editor: Todd M. Palmer.

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1999). Those African savannas receiving a mean annual rainfall below 650 mm have their maximum woody cover constrained by rainfall, but in areas receiving higher rainfall, closed forest develops in the absence of fire and herbivory (Sankaran et al. 2005).

The extent of seed predation by ants, birds and rodents was assessed in the savanna in Zimbabwe (Linzey and Washok 2000). However, the study did not consider the biotic effects of termites and large mammalian herbivores (see Pringle et al. 2010, Okullo and Moe 2012*a*).

Previous studies show that exclusion of large mammals increases woody vegetation cover that sustains small mammal and arthropod communities (Ogada et al. 2008, Okullo et al. 2013, Keesing and Young 2014), some of which are important seed and seedling predators. The interaction between large herbivores and granivorous animals in the savanna landscape will likely influence seed removal rates. Nonetheless, such interactions have not been assessed in African savannas (Maclean et al. 2011).

In the savanna of South Africa, up to 25% of the annual seed crop of *Acacia* species is reported to be consumed by rodents, suggesting that these animals have the potential to influence plant communities (Miller 1994). Seed removal may provide an explanation for the difference in species composition on and off mounds in the wetter savannas, resulting from indirect effects of termite and large herbivores (Okullo and Moe 2012*a*, Okullo et al. 2013).

Although *Macrotermes* themselves do not move seeds or store them in their nests (Erpenbach and Wittig 2016), they, together with large mammalian herbivores, modify vegetation through herbivory and nutrient redistribution (Moe et al. 2009). These activities consequently alter the distribution and composition of plants and animal communities (Traoré et al. 2008, Pringle et al. 2010). In the presence of large herbivores, diversity, abundance, and biomass of insects and small mammals decreases with distance from mounds (Fleming and Loveridge 2003, Pringle et al. 2010).

While there has been some examination of how termites and large herbivores influence African savanna vegetation (Okullo and Moe 2012*a*, *b*, Støen et al. 2013, Joseph et al. 2015, Seymour et al. 2016), we know little concerning their influence on seed removal. Understanding how seed removal rates are determined offers insights into mechanisms that potentially drive observed patterns in tree species composition on and off mounds.

This study aimed to assess seed removal rates on and off *Macrotermes* mounds with and without large mammalian herbivores. We postulated that *Macrotermes* mounds would influence seed removal rates indirectly through "bottom-up" effects on soil properties, thereby altering the habitat for seed removal agents. Large mammalian herbivores similarly, modify habitats through "top-down" effects of grazing and browsing, which reduces vegetation cover, resulting in variation in behavior, abundance and distribution of removal agents (Ogada et al. 2008, Keesing and Young 2014).

To study the influence of *Macrotermes* mounds and large mammalian herbivores on seed removal, we used an ongoing experiment with four main treatments: (1) unfenced savanna (off-mounds), (2) fenced savanna (off-mounds), where large herbivores (>5 kg) were excluded by fencing, (3) unfenced *Macrotermes* mounds, and (4) fenced *Macrotermes* mounds. Within each main treatment, there were sub-treatments ("seed cages") that regulated animal access to seeds: (1) closed seed cages that permitted access by only small invertebrates (mesh < 5 mm), (2) roofed seed cages that permitted access by small mammals and invertebrates, and (3) open seed cages that permitted access by all animals.

Our main focus was the study of removal rates of native tree seeds. Experiments were conducted using nine native tree species and three species of agricultural seeds known to be attractive to seed removal agents. Agricultural seeds were used to evaluate the potential rates of seed removal in the landscape.

We predicted that (1) seed removal rates would be higher on *Macrotermes* mound habitat than in savanna matrix habitat since the abundance of small mammals is higher on mounds than adjacent savanna (Fleming and Loveridge 2003, Okullo et al. 2013); (2) the exclusion of large herbivores would lead to higher seed removal rates both on mound and savanna habitats, due to increased vegetation cover that would reduce small mammal and arthropod predation risk (Keesing 1998); (3) removal rates of seeds of tree species typically growing off-mound would be higher on than off-mound habitats, because small mammals and arthropods on vegetated mounds might preferentially remove non-mound tree species seeds contributing to the observed distinct tree species composition on mounds (Fleming and Loveridge 2003, Pringle et al. 2010).

METHODS

Study area

Lake Mburo National Park, extending over an area of about 260 km^2, in southwestern Uganda (00°30′-00°42′ S and 30°47′-31°04′ E) has an average annual temperature and rainfall of 20.7°C and 865 mm, respectively (data *available online*).[2] It has two rainy seasons; from October to December and February to May. The vegetation of the park is primarily open grass-dominated savanna, with scattered trees dominated by *Vachellia hockii* (De Wild.) Seigler & Ebinger formerly *Acacia hockii* De Wild. (Bloesch 2008, Kyalangalilwa et al. 2013).

Macrotermes mounds with a mean height of 1.7 m and mean radius of 3.7 m are distinct features of the park landscape, with higher density and diversity of plants relative to the adjacent savanna matrix (Moe et al. 2009).

[2] www.climate-data.org

The mounds are typically covered with thicket vegetation consisting of trees, dense clusters of multi-stemmed, much branched, often armed woody plants, with intertwining climbers, in addition to succulent plants. The mounds have a sparse herbaceous layer (Bloesch 2008). The most common woody species on *Macrotermes* mounds are *Grewia* spp., *Gymnosporia heterophylla* (Eckl. & Zeyh.) Loes; synonym *Maytenus heterophylla* (Eckl. & Zeyh.) N.Robson (data *available online*),[3] and *Searsia natalensis* (Bernh. ex C.Krauss) F.A.Barkley; synonym *Rhus natalensis* Bernh. ex C.Krauss (see footnote 3), whereas *Dichrostachys cinerea* (L.), *Vachellia sieberiana*, and *Vachellia gerrardii* are common off mound (Moe et al. 2009). One recent estimate of large herbivore biomass (>5 kg) in the park was of about 89 kg/ha. The common large herbivores include impala (*Aepyceros melampus*), bushbuck (*Tragelaphus scriptus*), zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus defassa*), African buffalo (*Syncherus caffer*) and warthog (*Phacochoerus africanus*) (Rannestad et al. 2006).

Experimental seed species

Seeds from three agricultural and nine native tree species were used. Based on a previous study at the same sites (Moe et al. 2009), we chose *Allophylus africanus* P.Beauv, *Grewia* spp., *Searsia natalensis* (Bernh. ex C.Krauss), *Scutia myrtina* (Burm.f.) Kurz and *Vepris nobilis* (Delile) Mziray; synonym *Teclea nobilis* Delile (see footnote 3) (species that typically grow on mounds) and *Vachellia gerrardii* (Benth.), *Vachellia hockii* (De Wild.), *Vachellia sieberiana* (DC.), and *Dichrostachys cinerea* (L.) Wight & Arn. (species that typically grow off-mounds) (Moe et al. 2009). The three agricultural seeds were: maize (*Zea mays* L.), rice (*Oryza sativa* L.), and groundnut (*Arachis hypogeae* L.), which have high caloric values, easily metabolized carbohydrates and are attractive to seed predators (Wiens and Johnston 1977). All native tree seeds were locally abundant at the time of the experiment and encompassed a range of mean sizes from 18 to 298 mg (Appendix S1: Table S1). Only intact seeds were used. Structures that are usually lost during seed dispersal (such as pods and fleshy parts of the fleshy-fruited species) were removed from the seeds before they were air-dried on newspapers for three days and stored in dry airtight containers.

Seed removal experimental design

We used an experimental setup established in 2005, 10 yr before this study. The experiment was composed of nine replicate sites, each site having four treatment plots (Appendix S1: Fig. S1). The treatment plots consisted of two *Macrotermes* mound plots, one unfenced mound and a fenced mound where large herbivores (>5 kg) were excluded, and two adjacent savanna plots, with one unfenced savanna and the other a fenced savanna. Further details of the experimental setup are described by Okullo and Moe (2012*a*). In each treatment plot, two clusters of three seed cage types were placed. The clusters of seed cages were each placed at opposite sides of the treatment plots, 30 cm from plot boundary. Each cage type within a cluster was located 30 cm away from the other. The closed cage was covered by a 5 mm wire mesh on all sides of a 5 cm wide × 5 cm high × 15 cm long wire frame, that allowed access by only small invertebrates, but kept out animals >5 mm in size (presumably all vertebrates as well as some larger invertebrates). A wire and nails were used to strap and secure the closed cages to the ground. The roofed seed cage was covered only at the top by a 5 mm wire mesh located 5 cm above the ground, and allowed access to invertebrates and small mammals. The third "cage type" was left completely open to allow free access to seeds by all seed removal agents. All cages had the same dimensions of length and width.

The seed cages were placed on a flat surface where grass had been removed to expose the bare ground. Grass was removed to enable a clear view of the seed conditions during the subsequent visits. A seed from each agricultural and native tree species was placed in the center of each seed cage and revisited three days later. The seed cages were revisited 10 times within six weeks between May and June 2015, at the end of the rainy season. At each visit, each cage was assessed for seeds that were removed or damaged. A seed was recorded as removed if it was not seen in the seed cage, and damaged if seed fragments were seen in the cage or if gnaw marks were seen on the seed within the seed cage. A seed that was identified outside the cage area was considered to be removed. Removed and damaged seeds were replaced at each visit. In the first two weeks of the study, 16 closed and 10 roofed cages were damaged by animals. Data were not collected from locations with damaged cages on these occasions, but the cages were replaced and observations repeated until all sites had equal coverage with undamaged cages (10 observation periods). We did not assess how seed availability and density of removal agents might vary with seasons, since the study was undertaken within one season.

In 2005 when the large mammalian experimental exclosures were erected, all selected mounds (nine fenced and unfenced mounds) were occupied by *Macrotermes* (active mounds; Okullo and Moe 2012*b*). However, during our study in 2015, the mounds had been abandoned (inactive mounds). *Macrotermes* mounds are stable and persistent features of the savanna landscape, with long life spans measured in centuries and millennia, and are continuously recolonized and abandoned (Erens et al. 2015). To assess whether mound status had an impact on seed removal rates, we selected five additional vegetated active *Macrotermes* mounds. The mounds were confirmed active after holes drilled into them were repaired by termites. The arrangement of seed cages on the active mounds was the same as in the set up with inactive mounds.

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[3] http://www.theplantlist.org/

Data analysis

Data from the two clusters of seed cages per treatment plot were pooled for each cage type to avoid pseudoreplication. Seed removal rates were analyzed as proportions of individual native tree seed species removed every three days, out of the maximum possible outcome of seed removal (i.e., 20 seeds of each species in each cage per treatment plot). Since data were repeatedly collected from the treatment plots within the sites, all analyses followed a generalized linear mixed model (GLMM) assuming a binomial distribution of error with a logit link function. The binomial distribution of error was assumed, because the response variable (seed removal rate) was computed as a proportion. We used the function glmer of the lme4 package (Bates et al. 2015) in R to run the analysis (R Core Team 2015). We used $\mathrm{AIC_c}$ and Akaike weights to compare possible GLMM models obtained from the dredge function of the MuMIn package in R. Using the subset function, we calculated model averaged parameter estimates for each model with delta AIC < 4. Each model's contribution to parameter estimate was proportional to its Akaike weight (Barton 2016). The model with lowest AIC and highest Akaike weight was considered the most parsimonious model. We used analysis of deviance (a maximum likelihood equivalent of ANOVA) to examine the amount of total variation explained by each of the fixed terms and their interactions. We tested the effect of cage, habitat type, tree species, and fencing by modelling seed removal rate as a function of cage type (open, roofed, or closed), habitat type (off-mound savanna or mound habitat), presence or absence of large herbivores (unfenced or fenced treatment plots), and native tree seed species as fixed factors, while site was modelled as a random factor. To test whether tree seed removal rates were higher on active mounds than inactive mounds, removal rates were modelled as a function of mound status (active or inactive), cage type and native tree seed species, all considered as fixed factors, while site was considered as a random factor. To test whether seeds of tree species typically growing off-mound had higher removal rates, we modelled tree seed removal rates as a function of seed source (tree species typically growing off or on mounds), cage type, habitat type, and fencing, all considered as fixed factors, while site was considered a random factor.

Removal rates for agricultural seeds followed similar patterns as native seeds and were comparable through the treatments. Since our major focus was on removal rates of native seeds, we do not report details of agricultural seed removal rates in our results and discussion.

RESULTS

Overall, 3,530 (47.8%) agricultural seeds and 3972 (17.9%) native tree seeds were removed from savanna and mound habitats. Seed removal occurred in all cage types in all treatments. Mean seed removal rates for agricultural seeds were consistently higher than removal rates for tree seeds in all seed cages and habitats (Table 1). As expected, seed removal rates for both agricultural and native tree seeds were highest in open "cages" (62.6% ± 4.7%, 23.3% ± 1.0%, for agricultural and native tree seeds per 3 d, respectively) and lowest in closed cages (25.7% ± 7.1%, 11.1% ± 0.7%, for agricultural and tree seeds, respectively). Removal rates from the roofed cages were only marginally lower than rates from open cages (Figs. 1 and 2, Appendix S1: Fig. S2). Mean seed removal

TABLE 1. Native tree and agricultural seeds that remained intact, were removed, and remaining seeds damaged from open, roofed, and closed cages in unfenced savanna, fenced savanna, inactive unfenced mound, inactive fenced mound, and active unfenced mounds.

			Native tree seeds (%)			Agricultural seeds (%)		
Mound	Fenced	Cage	Left intact	Removed	Remaining seeds damaged	Left intact	Removed	Remaining seeds damaged
No	no	open	73.5 ± 2.0	21.3 ± 1.6	7.3 ± 1.4	37.0 ± 5.8	54.3 ± 6.0	18.5 ± 3.9
No	no	roofed	74.3 ± 2.3	17.2 ± 1.6	11.4 ± 1.9	44.4 ± 5.7	45.4 ± 6.4	18.5 ± 4.2
No	no	closed	82.0 ± 2.1	11.5 ± 1.4	8.1 ± 1.8	67.6 ± 5.8	22.6 ± 5.7	17.7 ± 4.2
No	yes	open	69.1 ± 2.9	23.0 ± 2.4	11.8 ± 2.3	38.1 ± 5.3	54.3 ± 6	13.8 ± 2.8
No	yes	roofed	69.6 ± 2.7	20.7 ± 2.1	13.7 ± 2.3	36.1 ± 5.6	53.3 ± 6.3	23.7 ± 3.8
No	yes	closed	78.1 ± 2.8	13.6 ± 2.0	10.7 ± 2.3	65.0 ± 5.8	26.9 ± 5.3	14.0 ± 3.4
Yes	no	open	66.7 ± 2.3	26.7 ± 2.0	10.6 ± 1.6	29.4 ± 4.9	64.8 ± 5.1	16.2 ± 4.9
Yes	no	roofed	71.7 ± 2.5	22.2 ± 1.9	10.4 ± 2.1	33.1 ± 5.4	62.0 ± 5.8	13.4 ± 4.3
Yes	no	closed	82.8 ± 1.9	11.6 ± 1.3	6.4 ± 1.5	61.3 ± 6.2	29.4 ± 6.8	12.8 ± 2.7
Yes	yes	open	75.0 ± 2.4	17.9 ± 1.8	10.7 ± 2.1	38.7 ± 5.5	52.2 ± 6.1	18.9 ± 3.6
Yes	yes	roofed	76.1 ± 2.5	16.7 ± 1.7	10.9 ± 2.1	39.4 ± 5.6	53.5 ± 6.0	14.4 ± 3.8
Yes	yes	closed	82.6 ± 2.1	10.3 ± 1.3	8.7 ± 1.8	66.3 ± 5.9	25.0 ± 6.3	12.1 ± 2.4
Yes (active)	no	open	65.7 ± 3.7	30.9 ± 3.4	7.3 ± 2.1	8.7 ± 2.5	87.3 ± 2.8	22.2 ± 9.2
Yes (active)	no	roofed	75.8 ± 3.2	21.2 ± 2.7	6.3 ± 2.2	10.7 ± 1.8	86.0 ± 2.0	19.0 ± 7.2
Yes (active)	no	closed	87.9 ± 2.1	6.1 ± 1.0	6.5 ± 2.0	69.0 ± 7.8	24.3 ± 8.0	9.2 ± 2.4

Note: Values are mean ± SE.

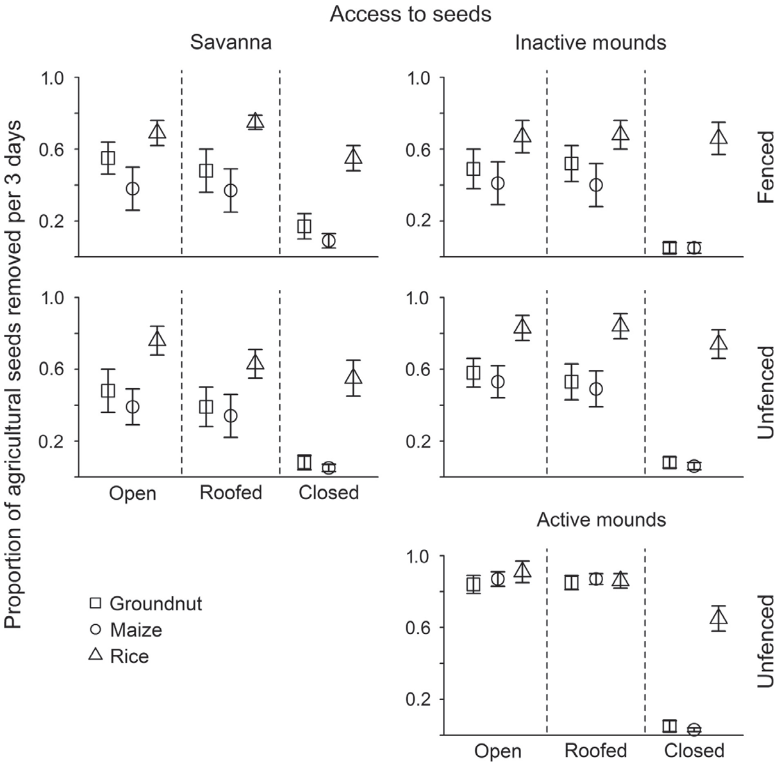

FIG. 1. Proportions (mean ± SE) of agricultural seeds removed from nine replicate sites, each with four treatments (i.e., unfenced savanna, fenced savanna, unfenced mounds, and fenced mounds) and three sub-treatments (i.e., open, roofed, and closed seed cages). Sub-treatments (three cages) were replicated for each treatment at each site (i.e., in four treatments at nine sites) with inactive mounds and on the five additional active unfenced mounds. The agricultural seeds used were groundnut, *Arachis hypogaea*; maize, *Zae mays*; and rice, *Oryza sativa*.

rates from the closed cages were about one-half (11.1% ± 0.7%) the rates of removal from the open (23.3% ± 1.0%) and roofed cages (19.4% ± 0.9%) per 3 d. The highest mean removal rates of agricultural seeds (87.3% ± 2.8%,) and native tree seeds (30.9% ± 3.4%) per 3 d were in the open cages of active mounds (Table 1). Damage rates of seeds that were not removed were higher for agricultural seeds, ranging from 13.8% ± 2.8% to 22.2% ± 9.2% in the open "cages" compared to 7.3% ± 1.4% to 11.8% ± 2.3% for native tree seeds.

With a mean seed removal rate of 26.7% ± 2.0% in the open "cages" on mound habitats compared to 21.3% ± 1.6% in the open "cages" off-mound in the adjacent savanna matrix habitat, seed removal rates were significantly higher on mound than on adjacent savanna habitats (GLMM, estimate ± SE = 0.18 ± 0.05, $z = 3.5$, $P < 0.001$, Appendix S1: Table S2). However, while large herbivore exclusion resulted in a non-significant increase in mean removal rates of all tree seeds in the non-mound savanna matrix habitat by 1.7% in the open seed cage, mean removal rates were significantly reduced on mound habitats by 8.8% when large herbivores were excluded (GLMM, estimate ± SE = −0.42 ± 0.07, $z = -5.6$, $P < 0.001$, Fig. 3, Appendix S1: Table S2).

The species of the tree seeds accounted for 62.4% of the total variation in removal rates (agricultural seeds excluded). In the open cages, the smallest native seeds *Scutia myrtina* had the highest mean seed removal rate per 3 d period (47.9% ± 3%) followed by *Dichrostachys cinerea* (28.2% ± 3%), *Searsia natalensis* (27.7% ± 2.4%) and *Vachellia hockii* (26.1% ± 3.2%; Fig. 4, Appendix S1: Tables S1 and S2). The mean removal rates of the larger seeds of *Vachellia sieberiana*, *Allophylus africanus*, *Vachellia gerrardii*, and *Vepris nobilis* from the open cages ranged between 12.1% and 23.6%, while *Grewia* spp. had the lowest mean removal rate of 9.9% ± 1.5%.

Scutia myrtina had the highest mean damage rate (42.5% ± 4.2%) for tree seeds not removed from open cages, followed by *Allophylus africanus* (10.2% ± 2%), *Vepris nobilis* (9.2% ± 2%) and *Grewia* spp. (7.8% ± 1.4%), while all the other species had damage rates of <5%.

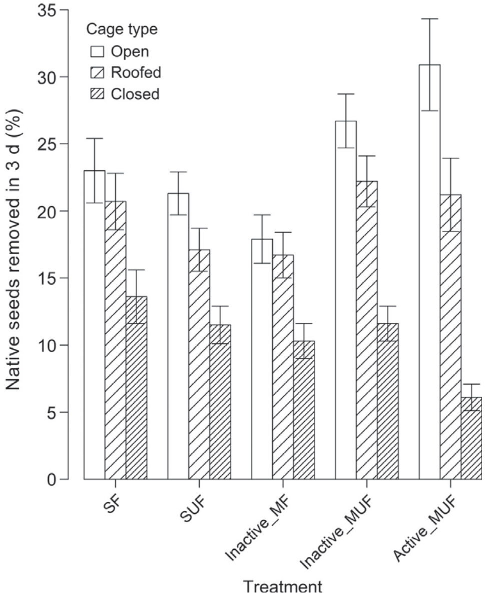

FIG. 2. Overall percentage (mean ± SE) of native tree seed removal rates from each of the three seed cage types (open, roofed, and closed) under four treatments (fenced savanna [SF], unfenced savanna [SUF], fenced mound [Inactive_MF], unfenced mound [Inactive_MUF]) replicated in nine sites ($n = 9$), and active unfenced mounds (Active_MUF) replicated five times ($n = 5$).

Seed removal rates of native tree seeds correlated positively with seed damage rates across treatments (Kendall's tau = 0.12, $P = 0.018$, $n = 135$, Appendix S1: Fig. S3).

Mean seed removal rate for tree seeds was higher in open cages on active mounds (30.9% ± 3.4%) than on inactive mounds (26.7% ± 2%; Table 1, Fig. 2), but lower in the closed cages on active mounds (6.1% ± 1%) than on inactive mounds (11.6% ± 1.3%). However, removal rates were significantly higher on active mounds when native tree seeds were accessible by all seed removal agents compared to removal by invertebrates alone on inactive mounds (GLMM, estimate ± SE = −0.73 ± 0.18, $z = 3.97$, $P < 0.02$; Fig. 2, Appendix S1: Table S3).

With a mean seed removal rate of 23.1% ± 1.3% from open cages for tree species typically growing on-mound, compared to 23.5% ± 1.4% for tree species typically growing off-mound, there was no significant difference in mean removal rates of tree seed species typically growing on and off mounds (GLMM, estimate ± SE = −0.11 ± 0.07, $z = -1.56$, $P = 0.11$; Appendix S1: Table S4).

DISCUSSION

Our results show high seed removal rates, reaching 87.3% in three days, and that rates vary considerably among habitats. These differences may translate into even larger ecological differences due to the compounding nature of these rates over time. Seed removal rates were higher on *Macrotermes* mounds than in the adjacent off-mound savanna matrix. Contrary to our expectation, seed removal rates decreased when large herbivores were excluded from *Macrotermes* mounds even though they increased off-mound. Removal rates of seeds, when accessible to all removal agents, were greater on active than inactive mounds, but this pattern was reversed when removal by small invertebrates alone (closed cages) was considered, indicating that differences in both vertebrates and invertebrates removal agents are involved. In general, smaller seeds experienced higher rates of removal than larger seeds.

Removal rates of agricultural seeds surpassed those of native tree seeds in all cases, showing that seed removal agents are selective. The agricultural seeds are likely more conspicuous and more palatable than native tree seeds (Wiens and Johnston 1977).

Cover vegetation differs among locations throughout the savanna landscape. Compared to the non-mound savanna matrix, *Macrotermes* mounds tend to possess denser and more diverse woody and forb plant communities that provide cover to granivores (Fleming and Loveridge 2003, Bloesch 2008, Traoré et al. 2008, Moe et al. 2009, Okullo and Moe 2012*b*, Okullo et al. 2013). Coupled with reduced predation risk, the lower temperatures on vegetated *Macrotermes* mounds compared to the adjacent savanna matrix may sustain granivorous animal communities (Joseph et al. 2016). Similar to our finding, a study in the savanna of South Africa found greater tree seed removal rates in dense tall-grass habitat than grazing lawn and open sub-canopy habitats (Walters et al. 2005). Since small mammal and arthropod densities typically correlate with cover, seed removal rates are also expected to increase with cover. The increase in seed removal rates with exclusion of large herbivores in the savanna habitat is thus attributable to increased cover leading to increased density of granivores (Ogada et al. 2008, Keesing and Young 2014).

Our finding that seed removal rates from mound habitats were reduced when large herbivores are excluded was unexpected and indicates different requirements or abilities of the fauna using this habitat. A previous study at the same locations, found that in the fenced mound plots, the rodents *Aethomys kaiseri* and *Mus minutoides* were the most captured small mammals (Okullo et al. 2013). *Aethomys kaiseri* eats mainly grass (Kingdon 2003) and a study in Nigeria found that leaves and grass comprised 85.1% of the gut contents of *Mus minutoides* (Iwuala et al. 1980). Therefore, small mammals that are not predominantly granivorous appear to dominate fenced mound plots. On the other hand, five out of the twelve small mammals species captured in the unfenced mound plots (Okullo et al. 2013) had mainly granivorous and insectivorous diets (Rowe-Rowe 1986).

Aside from small mammals and invertebrates, birds and primates may also have removed seeds. A study in Zimbabwe showed that mounds provided nesting sites for

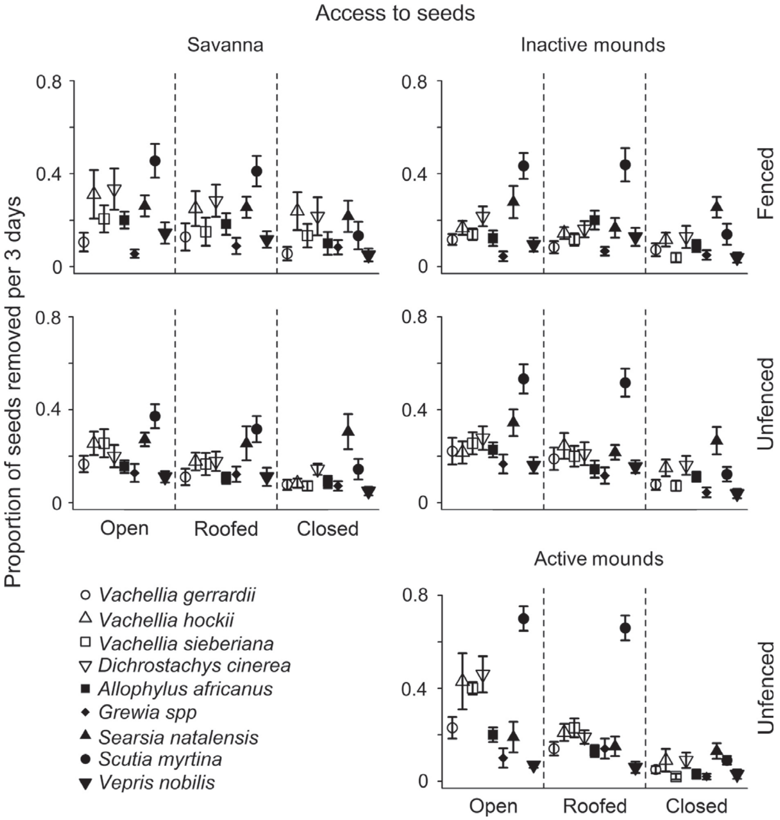

FIG. 3. Proportions (mean ± SE) of native tree seeds removed from nine replicate sites each with four treatments (i.e., unfenced savanna, fenced savanna, unfenced mounds, and fenced mounds). Each treatment plot in the nine replicate sites with inactive mounds and five additional unfenced active mounds had three sub-treatments (i.e., open, roofed, and closed cages). All open symbols are tree species typically growing off-mound in the savanna matrix, while filled symbols are tree species typically growing on-mound.

21 species of cavity using birds, 62% of which were frugivorous (Joseph et al. 2011). Similarly, observations in our study area indicate that birds spend more time on mounds than in off-mound habitats and that insectivorous birds are more common on fenced than on unfenced mounds (*unpublished data*). We do not know how birds influence seed removal rates in our study area, but it is likely that birds deposit seeds from fruit producing trees on mounds more frequently than in the surrounding savanna, since they tend to nest and roost on trees growing mounds. Primates were likely responsible for damaging the seed cages on several occasions, however, as with birds we remain uncertain whether these animals are significant seed removal agents and how they influence other such agents. Incorporation of camera traps in future investigations would provide more details on the identities of animals involved in seed removal.

The design of our study, with its clustering of native tree seeds, the inclusion of agricultural seeds and perhaps the seed cages, may attract or repel some seed removal agents thus influencing local removal rates. Such influences are comparable among the treatments as our set-up was consistent across all locations, though differences in visibility could cause some biases (but would also influence removal in a natural context). Comparison of seed removal rates as a function of proximity to other seeds, and visibility requires further evaluation.

Plant recruitment depends on both seed availability and suitable sites for seedling establishment (Duncan et al. 2009). An earlier study at the same sites showed that the density of common tree seedling species was higher on fenced than unfenced mound plots (Støen et al. 2013). The lower seed removal rates on these fenced mounds (this study) suggests that fenced mounds may be “safe sites”: ideal places for seed germination and recruitment (Harper 1994).

Contrary to the often-predicted higher seed removal rates for large seeds (Moles et al. 2003), smaller tree seeds in our study experienced higher removal rates than larger seeds. Although seed removal rates by small invertebrates

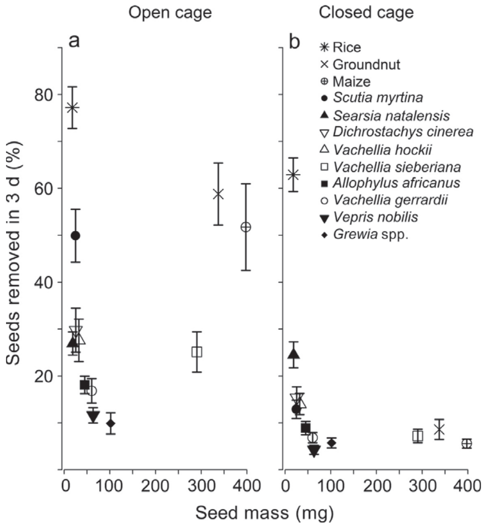

FIG. 4. Relationship between seed mass and seed removal rates (mean ± SE) for agricultural and native tree seeds taken from (a) open "seed cages" accessed by all vertebrate and invertebrate seed removal agents and (b) closed cages accessed by invertebrates only. Data used included seed removal from all treatment types.

(<5 mm) were about half of the removal rates for seeds accessible by all removal agents, *Searsia natalensis* and *Vachellia hockii* experienced higher removal rates compared to other species of native tree seeds. These seeds were smaller (<5 mm) than the mesh size, thus their removal reflects their ability to be removed without first breaking them. While more species of seed removal agents can process small-sized seeds, vertebrate seed removal agents can handle and process larger-sized seeds more efficiently. This suggests, that invertebrates may be specialized in processing small-sized seeds. In addition, as strength is proportional to muscle cross-sectional area, smaller seed predators should be able to exert greater forces relative to their body mass to break and consume small, tough seeds that appear mechanically better defended than larger seeds (Fricke and Wright 2016). Defensive compounds may also provide an explanation as protective tissue investments tend to be proportionally related to the seed reserve mass, potentially reducing removal rates of larger seeds (Moles et al. 2003). Our result of more frequent seed removal of smaller seeds than larger seeds is similar to a result from the savanna in South Africa where smaller seeds of *Vachellia karroo* (Hayne) Banfi & Galasso formerly *Acacia karroo* Hayne, (Kyalangalilwa et al. 2013) had higher removal rates than large seeds of *Vachellia nilotica* (L.) P.J.H. Hurter & Mabb formerly *Acacia nilotica* (L.) Willd. ex Del. (Walters et al. 2005, Kyalangalilwa et al. 2013).

Seed damage rates correlated with removal rates across all treatments in all sites (Appendix S1: Fig. S3). Overall then, similar patterns were observed when removal and damage were considered rather than removal alone, implying that these processes are dependent on the same animals.

The reduction in seed removal by small invertebrates on active mounds affirms observations that *Macrotermes* themselves are not major seed removers (Erpenbach and Wittig 2016). Overall, removal rates on active mounds are higher than inactive mounds. The reasons are unclear, though it may reflect the improved foraging opportunities for some granivores that can compensate for the reduced seed removal by small invertebrates on active mounds. It may also be that the termites, through their foraging and mound-building activities, attract seed removal agents. The nature of these interactions requires further investigations.

We had expected that the seeds of tree species that grow off-mound would be preferentially removed on the *Macrotermes* mounds and vise-versa. However, since the relative removal rates of seeds of tree species typically growing on and off-mound showed no such consistent differences in the two habitats, the removal agents appear to lack a distinct preference of tree seed by habitat. This may reflect the ranging behavior and generalist feeding habits of seed removal agents in the savanna landscape and suggests that differential seed removal is not the main determinant of the distinct composition of the trees though we acknowledge that further work is required to investigate seed germination and establishment safe sites within these habitats.

Seed removal rates do not indicate seed fate. We expect that predation is the dominant pathway, and this is also consistent with our seed damage observations. Various animals, including ants, rodents and birds, are known to move seeds to sites where germination might be possible (secondary dispersal; Vander Wall et al. 2005). It is likely that some seeds were moved to other microsites where germination may be favored.

CONCLUSION

Our results show high removal rates, although patterns are context dependent. Seed removal rates differed among species, but those with smaller seeds experienced higher rates. Seed removal rates were significantly higher on-mound relative to off-mound. However, while exclusion of large herbivores reduced seed removal rates on mounds, it increased removal rates in the savanna habitats. Seed removal rates by invertebrates were lower when *Macrotermes* were present in mounds. We conclude that termites and large herbivores influence seed removal rates through a range of indirect effects resulting from their influence on soil properties and plant structure, which alter habitat quality.

ACKNOWLEDGMENTS

We thank the Uganda Wildlife Authority (UWA) who granted permission to undertake the study in Lake Mburo

National Park. We appreciate Paul Okullo's assistance with arrangements for fieldwork. Lawrence Kabiito and Rose Kentalo helped with data collection in the field. Three anonymous referees provided valuable comments on earlier drafts.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2038/suppinfo

Paper IV

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 microdetritivores, 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 locations. In addition, for each mound pair, one additional sample location was located off-mound, in the open level area between the mounds. After one, three, and 12 months, protected (wrapped in 1-mm mesh fibre-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, and 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 ± 0.8%) than on active (25.9 ± 1.5%) or inactive mounds (19.7 ± 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

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, the biota, particularly the detritivores, can also play a major role, though many such determinants remain poorly characterized (Lavelle et al. 1993, Andrén 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 six-fold variation in decomposition rates that was attributed primarily to the local dominance of different termites (Shuurman 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). Despite our awareness that these organisms play a major role in determining decomposition rates, the factors that influence these rates and their local variation remain uncertain.

Within 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 local abundance of *Macrotermes* in the landscape cannot be simply inferred from the distribution 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 (Jouquet et al. 2011, Moe et al. 2009). *Macrotermes* mounds possess distinct clay rich soils that enhance plant available water and ensure high cation exchange capacity and a greater availability of plant nutrients than occur in the surrounding soils (Sileshi and Arshad 2012). 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). As elevated sites, *Macrotermes* mounds also protect plants from fires and floods (Jouquet et al. 2011, Joseph et al. 2013).

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 anticipate that the local turnover of woody debris reflects properties of the wood itself as well as the activity of decomposers.

In this study we experimentally assessed wood decomposition in Lake Mburo National Park, in Uganda, where *Macrotermes* mounds are locally abundant (typically 4-8 mounds ha^{-1}, Pomeroy 1977). We assessed wood decomposition for eight common tree species using five paired replicates of active and inactive mounds, each with open (without tree canopy cover) and shaded (with vegetation cover) microhabitats, and also in the open area between each pair of mounds. We assessed percentage mass loss as the measure of wood decomposition for the eight common 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-mounds. Six wood sample sets consisting of a piece of wood from each of the eight species, were placed in the open and shaded parts of active and inactive mounds, and in an off-mound location between the 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 microhabitats? We expected decomposition rates to be higher in the shaded microhabitat because of enhanced moisture availability (Gliksman et al. 2017) and 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 km^2 Lake Mburo National Park in south western 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-May and between September-November. June and July are the driest months. Average monthly temperatures range from 19.8 ºC to 20.9 ºC (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 (Acanakwo et al. submitted, Støen et al. 2013). 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 *Dichrostachsys cinereal* (L.) Wight & Arn dominate in off-mound areas (Acanakwo et al. submitted, Moe et al. 2009). Woody cover on vegetated mounds is typically clumped and uneven typically creating both shaded and exposed areas.

Experimental setup

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 20-80 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 c. 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 *Rhus natalensis* Bernh. ex C.Krauss, *Grewia similis* K.Schum., *Teclea nobilis* Del., and *Allophylus africanus* P. Beauv., as species that are common on-mounds, and *Acaia gerrardii* Benth., *A. sieberiana* DC., *A. hockii* De Willd. and *Dichrostachsys cinereal* (L.) Wight & Arn as species that are common off-mounds. 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 x 2 x 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 assume that all our samples are entirely sapwood. The wood pieces were numbered, and oven dried for 72 hours at 80 ^{o}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 a 1 mm fibre-glass mesh. 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 hours at 80 ºC 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 x 2 x 2 cm wood chips from roughly sized sun-dried wood samples. The wood chips were soaked in distilled water for 24 hours. 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; "green mass" = (Mass of chip and bag – mass of empty bag) / 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 values against explanatory variables i.e., 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 microhabitats (open and shaded), while off-mound sites were all open. Due to this we required separate models to examine the effect of; i) micro-habitats on mounds, and ii) on-mound versus 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 versus inactive), mound microhabitat (open versus shaded), duration of exposure and access to wood samples by large macro-detritivores (unprotected versus 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 open mound parts on active mounds, inactive mounds and off-mound sites), duration of exposure and access to wood samples by large macro-detritivores. We constructed linear mixed effects models (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 ± 1.0% in the first month, 36.0 ± 1.3% in the third month and 63.6 ± 1.6 % after 12 months (Fig.1). Wood mass loss was consistently higher, on average four times greater, for samples exposed to macrodetritivores than those that were protected.

After 12 months, mean (± SE) percentage mean mass loss was 63.6 ± 1.6% for unprotected wood samples and 14.4 ± 0.6% for protected wood samples across all tree species located on mound sites (when decomposition in shaded and open microhabitats was combined) (Fig.1, Fig. 2). In the adjacent off-mound sites, unprotected samples lost a mean percentage mass of 35.1 ± 2.1% while protected samples lost 8.10 ± 0.95% (Fig 1, Fig. 3).

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

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 with and without including these lost samples differed by less than 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 ± 2.0%) than on inactive mounds (59.1 ± 2.3%), whereas mean percentage wood mass loss for protected samples on active mounds was 14.8 ± 0.9% vs 14.0 ± 0.91% on inactive mounds (Fig 2, Appendix S1: Table S3). Overall mean percentage mass loss from unprotected samples was 1.1 times higher in the shaded than the open mound locations (67.8 ± 4.4% versus 59.3 ± 4.0%). However, this difference was most pronounced on inactive mounds (66.7 ± 4.9% shaded versus 52.0 ± 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 higher in the shade than in the open parts of mounds (15.29 ± 1.0% versus 13.47 ± 0.8%). On active mounds, mean percentage mass loss across species was marginally higher in the shaded parts of mounds (15.46 ± 1.4%) than in the open (14.08 ± 1.2%). Similarly, on inactive mounds, wood mass loss across species was marginally higher in the shaded (15.12 ± 1.5%) than open (12.84 ± 1.1%) mound locations.

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

The species by site wood decomposition rates for unprotected samples after 12 months spanned a 6.4-fold range (Fig.1, Appendix S1: Table S3). The highest mass losses occurred with *Rhus natalensis* (81.8 ± 3.5%), *Teclea nobilis* (82.8 ± 5.0%), *Grewia similis* (84.5 ± 5.4%) on the shaded parts of inactive mounds *Allophylus africanus* (80.4 ± 3.8%) and with *Acacia sieberiana* (82.0 ± 5.3%) on the shaded parts of active mounds. The lowest losses (less than 6.0%) were recorded in off-mound sites for *Acacia hockii* (6.1 ± 1.8%), Acacia *sieberiana* (6.6 ± 3.3%), *Teclea nobilis* (6.2 ± 2.9%) and *Rhus natalensis* (6.9 ± 1.6%) (Fig.1, Fig. 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 ± 3.7%) and *Rhus natalensis* (19.6 ± 2.7%) in the shade of active mounds, and *Grewia similis* and *Allophylus africanus* in the shade of inactive mounds (19.4 ± 4% and 19.5 ± 4.2%, respectively). The lowest 12 month losses were all experienced off-mound where *Acacia hockii, Acacia sieberiana, Teclea nobilis* and *Rhus natalensis* lost 6.1 ± 1.8%, 6.6 ± 3.3%, 6.1 ± 2.9% and 6.9 ±1.6%, respectively.

The relative wood decomposition rates in unprotected samples appeared greater for species with lower (versus higher) wood density, with the dense wooded *Dichrostachys cinerea* proving strikingly more durable than the other species. After 12 months percentage mass loss across species reduced with increasing wood density both in more open on-mound sites (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). These relationships were not detected for protected samples either in open (lm: Estimate = -2.25, t = 0.53, R^2= 0.045, $P = 0.61$) or shaded conditions (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 four times more rapidly when macrodetritivores had access to the wood samples versus when they did not. Macrodetritivores 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 versus open microhabitat. The results indicate that macrodetritivores are the main agents of decomposition and that mound status (active or inactive), shade 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 showed support for this prediction;

though mass losses only proceeded 1.2 times faster on active compared to inactive mounds for exposed samples for 12 months. This implies that the occupancy of mounds influences how decomposition rates vary across the 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 35m (Darlington 1982)—and we did not assess the status of all the other mounds within the study neighborhood. Veldhuis et al. (2017) used the earth tunnels left by the *Macrotermes* termites (a protection against predators) to differentiate the presence of *Macrotermes* termites from other Macrodetritivores organisms like millipedes, cockroaches and non-*Macrotermes* termites. We did not record earth tunnels here, as they are readily damaged by hoofed animals or washed away by 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 “photopriming”, 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 sites, they likely experience higher predation risk (Pringle et al. 2010). In addition, moisture is an important requirement for decomposition in dry environments (Gliksman, 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 microhabitats was supported. 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 on unprotected samples was about 1.3 times less in open compared to shaded sites. It seems the decomposition rates associated with active *Macrotermes* mounds are not dependent on moisture, this is consistent with Veldhuis et al. (2017). On a larger scale, however, Leitner et al. (2018) showed that shade resulting from increasing tree cover was associated with reduced decomposition because of reduced termite activity in the wooded areas.

Even when all organisms larger than 1mm were excluded, decomposition rates on mounds and in shadier sites were higher on-mounds than off them. 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-mounds 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 particular enzymes in particular 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. Bebber 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 wood density regardless of microhabitat type. It is surprising that this relationship between denser wood and slower decomposition does not hold when macro-detritivores are excluded. Other traits, such as wood nutrient concentrations can also influence decomposition rates (Hu et al. 2018 in press). 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 *Dichrostachys 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 macro-detritivores are excluded. In any case, our results indicate that the influence of wood density in determining decomposition rates depends on the organisms involved.

We have shown that active termites, their mounds and constituent vegetation, influence wood decomposition rates across the landscape together. Wood decomposed more rapidly on-mounds rather than off-mounds and on active versus inactive mounds. Wood mass loss was little affected by vegetation cover on active mounds, but on inactive mounds mass loss was 1.3 times lower in the open than shaded microhabitats. The marked spatial variation in decomposition rates found in this landscape underlines the important direct and indirect role of *Macrotermes*.

ACKNOWLEDGEMENTS

We thank the Uganda National Council for Science and Technology (UNCST) and Uganda Wildlife Authority (UWA) for permission to do field work. Paul Okullo provided crucial assistance with arrangements and logistics. Lawrence Kabiito and Rose Kentalo helped with data collection in the field. EA led on the data collection, laboratory measurements and analysis, while all three authors designed the study and contributed to writing this article.

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FIGURE LEGENDS

Figure 1. Mean (± 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 organisms having access to half the replicate wood samples (unprotected) and a 1-mm mesh around the other half (protected). The sample sets were placed in the shaded and open parts of the mounds, and in an open off-mound site between the active-inactive mound pairs

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

Figure 3. Mean (± 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. The open characters and symbols are mean values for individual species, while the filled circle are the overall mean values for species per microhabitat

Figure 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.

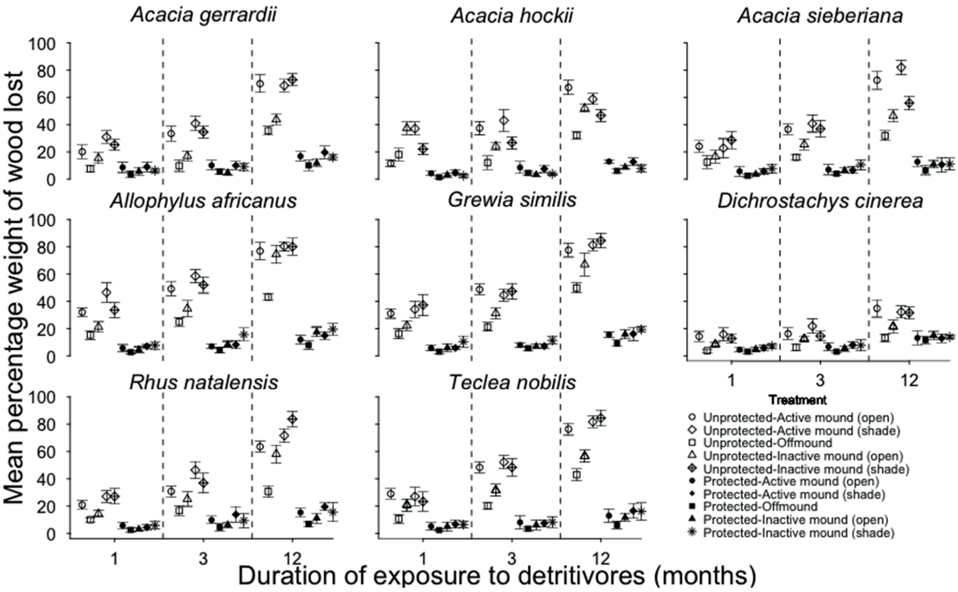
Acacia gerrardii
Acacia hockii
Acacia sieberiana
Allophylus africanus
Grewia similis
Dichrostachys cinerea
Rhus natalensis
Teclea nobilis
Mean percentage weight of wood lost
0
20
40
60
80
100
1
3
12
Treatment
Duration of exposure to detritivores (months)
Unprotected-Active mound (open)
Unprotected-Active mound (shade)
Unprotected-Offmound
Unprotected-Inactive mound (open)
Unprotected-Inactive mound (shade)
Protected-Active mound (open)
Protected-Active mound (shade)
Protected-Offmound
Protected-Inactive mound (open)
Protected-Inactive mound (shade)

Figure 1

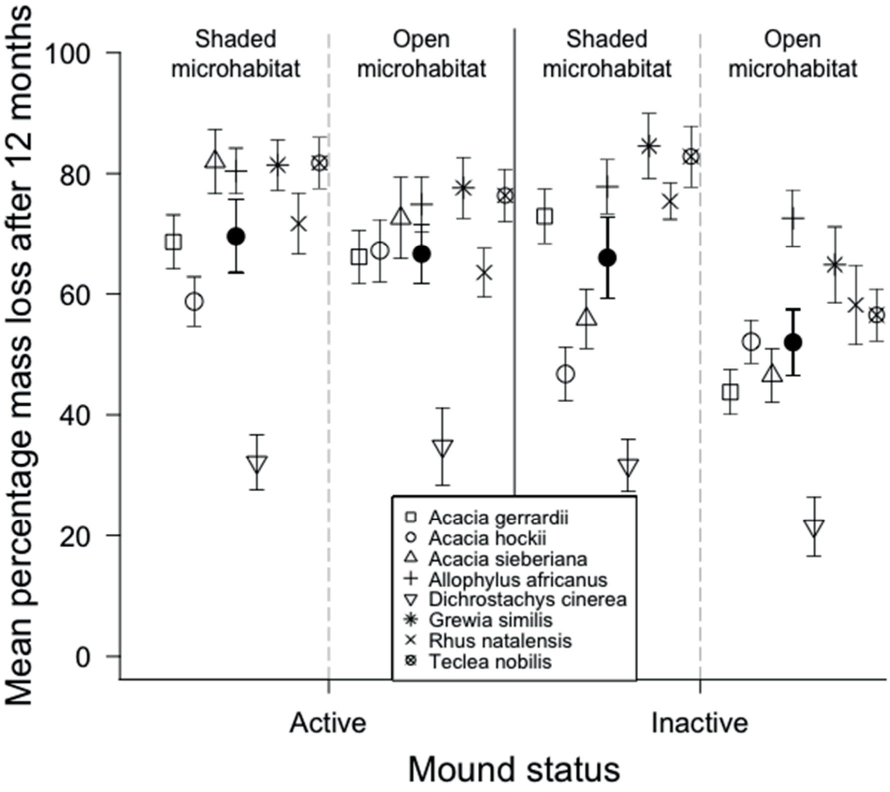
Shaded microhabitat
Open microhabitat
Shaded microhabitat
Open microhabitat
Mean percentage mass loss after 12 months
100
80
60
40
20
0
Active
Inactive
Mound status
Acacia gerrardii
Acacia hockii
Acacia sieberiana
Allophylus africanus
Dichrostachys cinerea
Grewia similis
Rhus natalensis
Teclea nobilis

Figure 2

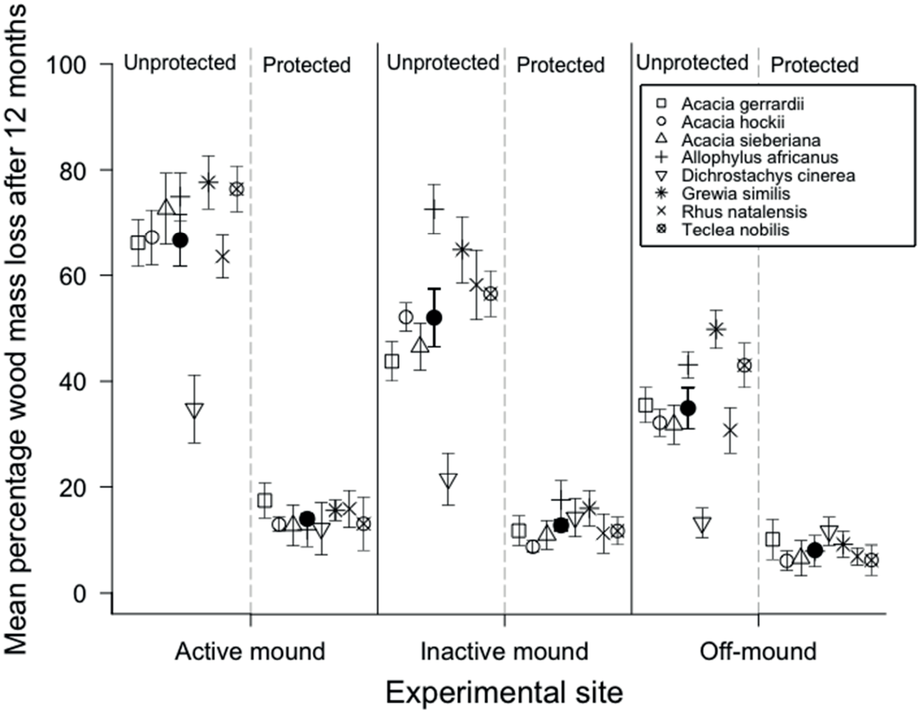
Mean percentage wood mass loss after 12 months
100
80
60
40
20
0
Unprotected
Protected
Unprotected
Protected
Unprotected
Protected
Acacia gerrardii
Acacia hockii
Acacia sieberiana
Allophylus africanus
Dichrostachys cinerea
Grewia similis
Rhus natalensis
Teclea nobilis
Active mound
Inactive mound
Off-mound
Experimental site

Figure 3

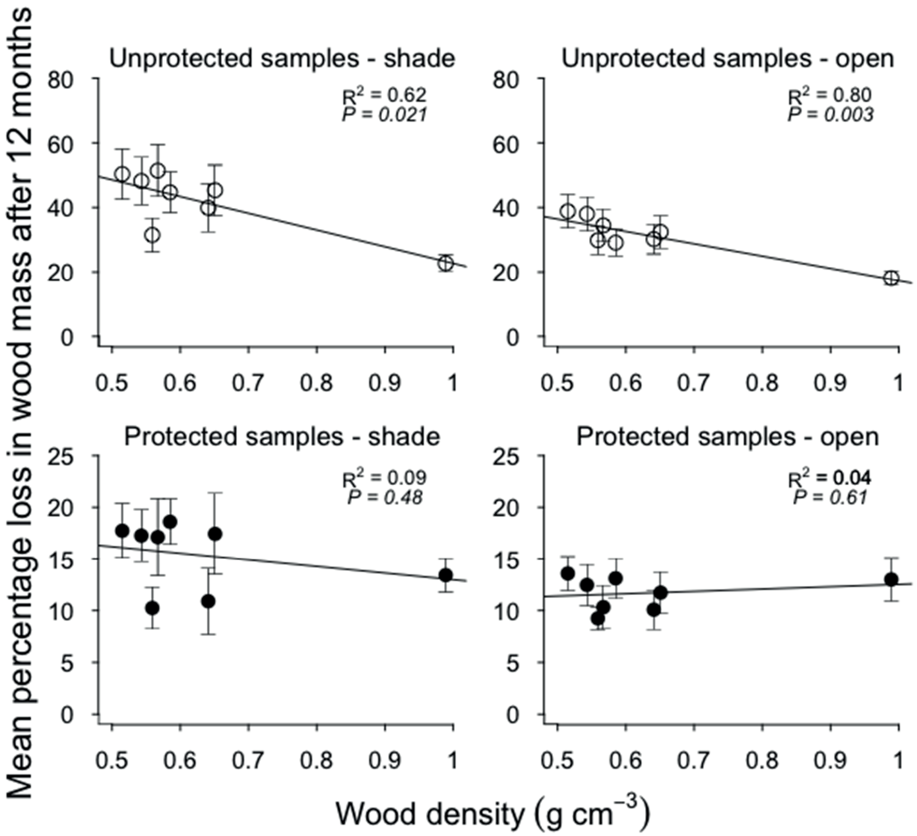
Mean percentage loss in wood mass after 12 months
Unprotected samples - shade
$R^2 = 0.62$
$P = 0.021$
Unprotected samples - open
$R^2 = 0.80$
$P = 0.003$
Protected samples - shade
$R^2 = 0.09$
$P = 0.48$
Protected samples - open
$R^2 = 0.04$
$P = 0.61$
0
20
40
60
80
0
5
10
15
20
25
0.5
0.6
0.7
0.8
0.9
1
Wood density ($g\ cm^{-3}$)

Figure 4

Appendix

Appendix S1: Supporting tables

Table S1. Habitat where woody plant species used in the study typically grow and their wood densities. Wood density was derived by dividing oven-dry wood mass by the mass of wood after soaking in distilled water for 24 hours.

Species	Typical habitat	Wood density ($g\ cm^{-3}$)
Acacia gerrardii	Off-mound	0.585 ± 0.003
Acacia hockii	Off-mound	0.559 ± 0.010
Acacia sieberiana	Off-mound	0.641 ± 0.005
Dichrostachys cinerera	Off-mound	0.989 ± 0.008
Grewia similis	On-mound	0.515 ± 0.002
Rhus natalensis	On-mound	0.651 ± 0.009
Allophylus africanus	On-mound	0.543 ± 0.004
Teclea nobilis	On-mound	0.567 ± 0.002

Table S2: Comparison of mean percentage wood mass loss per species with and without lost samples. Samples that were recorded as "100% wood mass loss" were not found in the field. We used Wilcoxon matched-pairs signed rank test to compare means between the two groups. *P* values were adjusted using *fdr* corrections

Species	Omitting lost samples	Including lost samples	Adjusted *P* value
Acacia gerrardii	21.9 ± 1.7	22.1 ± 1.7	0.319
Acacia hockii	20.4 ± 1.6	21.1 ± 1.7	0.098
Acacia sieberiana	22.0 ± 1.8	22.7 ± 1.9	0.093
Allophylus africanus	28.7 ± 2.1	29.5 ± 2.1	0.088
Dichrostachys cinerea	12.8 ± 0.9	13.4 ± 1.0	0.170
Grewia similis	27.9 ± 2.1	28.3 ± 2.1	0.319
Rhus natalensis	22.9 ± 1.9	23.1 ± 2.0	0.319
Teclea nobilis	26.2 ± 2.1	26.9 ± 2.1	0.087

Table S3. Model 1 result of analysis for the effect of woody species, mound cover (shade vs open), mound status (active vs inactive), duration of exposure and access to wood samples by large macro-detritivores (protected vs unprotected) on weight loss of wood samples after decomposition on active and inactive mounds. The reference categories are *A. gerrardii,* open part of mound, active mound, 1 month and unprotected wood sample-sets. Percentage weight loss is the response variable which was arcsine square-root transformed before analysis.

Fixed effects	Estimate	SE	df	t-value	P value
(Intercept)	0.502	0.026	909	20.11	< 0.001
A. hockii (vs. *A. gerrardii*)	0.021	0.032	909.0	0.662	0.508
A. sieberiana (vs *A. gerrardii*)	0.016	0.032	909.0	0.514	0.607
A. africanus (vs *A. gerrardii*)	0.111	0.032	909.0	3.494	< 0.001
D. cinerea (vs *A. gerrardii*)	-0.172	0.032	909.0	-5.408	< 0.001
G. similis (vs. *A. gerrardii*)	0.111	0.032	909.0	3.480	< 0.001
R. natalensis (vs. *A. gerrardii)*	-0.003	0.032	909.0	-0.078	0.938
T. nobilis (vs. *A. gerrardii*)	0.058	0.032	909.0	1.825	0.068
Shade (vs. Open)	0.070	0.014	909.0	5.029	< 0.001
Inactive (vs. active)	-0.122	0.014	909.0	-8.809	< 0.001
3 months (vs. 1 month)	0.1015	0.029	909.0	3.470	< 0.001
12 months (vs 1 month)	0.425	0.030	909.0	14.408	< 0.001
Protected (vs. unprotected)	-0.247	0.028	909.0	-8.909	< 0.001
A. hockii : 3 months	-0.003	0.039	909.0	-0.077	0.939
A. sieberiana : 3 months	0.030	0.039	909.0	0.772	0.440
A. africanus : 3 months	0.056	0.039	909.0	1.428	0.153
D.cinerea : 3 months	-0.027	0.039	909.0	-0.696	0.486
G. similis : 3 months	0.020	0.039	909.0	0.501	0.616

R. natalensis : 3 months	0.053	0.039	909.0	1.331	0.183
T. nobilis : 3 months	0.078	0.039	909.0	2.004	0.045
A. hockii : 12 months	-0.064	0.039	909.0	-1.624	0.105
A. sieberiana : 12 months	-0.015	0.039	909.0	-0.384	0.701
A. africanus : 12 months	-0.029	0.039	909.0	-0.753	0.452
D. cinerea : 12 months	-0.119	0.039	909.0	-3.047	0.002
G. similis : 12 months	0.031	0.039	909.0	0.800	0.424
R. natalensis : 12 months	0.040	0.040	909.0	1.007	0.314
T. nobilis : 12 months	0.046	0.039	909.0	1.172	0.241
A. hockii : Protected	-0.076	0.032	909.0	-2.372	0.018
A. sieberiana : Protected	-0.070	0.032	909.0	-2.182	0.0293
A. africanus : Protected	-0.124	0.032	909.0	-3.876	< 0.001
D. cinerea : Protected	0.185	0.032	909.0	5.803	< 0.001
G. similis : Protected	-0.127	0.032	909.0	-3.970	< 0.001
R. natalensis : Protected	-0.047	0.033	909.0	-1.433	0.153
T. nobilis : Protected	-0.125	0.032	909.0	-3.904	< 0.001
Shade : Inactive	0.051	0.016	909.0	3.202	0.001
Shade : Protected	-0.064	0.016	909.0	-3.976	< 0.001
Inactive : Protected	0.083	0.016	909.0	5.166	< 0.001
3 months : Protected	-0.0814	0.020	909.0	-4.163	< 0.001
12 months : Protected	-0.2575	0.020	909.0	-13.109	< 0.001

Table S4. Model 2 result of analysis for the effect of woody species, mound status (active, inactive, adjacent off-mound), duration of exposure and access to wood samples by large macro-detritivores (protected vs unprotected) on weight loss of wood samples after decomposition on- and off-mound. The reference categories are *A. gerrardii*, active mound, 1 month and unprotected wood sample-sets. Percentage weight loss is the response variable which was arcsine square-root transformed before analysis.

Fixed effect	Estimate	SE	df	t-value	P
(Intercept)	0.478	0.0222	675.0	21.494	<0.001
A. hockii (*vs A. gerrardii*)	0.057	0.0237	675.0	2.401	0.0166
A. sieberiana (*vs A. gerrardii*)	0.057	0.0237	675.0	2.440	0.0150
A. africanus (vs *A. gerrardii*)	0.133	0.0237	675.0	5.618	<0.001
D.cinerea (vs. *A. gerradii*)	-0.153	0.0237	675.0	-6.458	<0.001
G. similis (vs *A. gerrardii*)	0.153	0.0237	675.0	6.454	<0.001
R. natalensis (vs *A. gerrardii*)	0.044	0.0249	675.0	1.774	0.076
T. nobilis (vs *A. gerrardii*)	0.125	0.0237	675.0	5.267	<0.001
Adjacent_off-mound (vs Active)	-0.223	0.0204	675.0	-10.931	<0.001
Inactive (vs Active)	-0.118	0.0202	675.0	-5.804	<0.001
3 months (vs 1 month)	0.124	0.0202	675.0	6.085	<0.001
12 months (vs 1 month)	0.404	0.0205	675.0	19.708	<0.001
Protected (vs unprotected)	-0.254	0.0289	675.0	-8.804	<0.001
A. hockii : Protected	-0.106	0.0332	675.0	-3.189	0.001
A. sieberiana : Protected	-0.095	0.0332	675.0	-2.845	0.0046
A. africanus : Protected	-0.147	0.0332	675.0	-4.434	<0.001
D. cinerea : Protected	0.135	0.0332	675.0	4.074	<0.001
G. similis : Protected	-0.147	0.0332	675.0	-4.435	<0.001
R. natalensis : Protected	-0.062	0.0347	675.0	-1.776	0.076
T. nobilis : Protected	-0.162	0.0332	675.0	-4.871	<0.001

Adjacent_off-mound : 3 months	-0.035	0.0249	675.0	-1.407	0.160
Inactive : 3 months	-0.025	0.0248	675.0	-0.997	0.319
Adjacent : 12 months	-0.080	0.0251	675.0	-3.169	0.002
Inactive_off-mound:12 months	-0.031	0.0250	675.0	-1.229	0.220
Adjacent : Protected	0.180	0.0205	675.0	8.807	<0.001
Inactive : Protected	0.110	0.0203	675.0	5.415	<0.001
3 months : Protected	-0.061	0.0203	675.0	-3.014	0.003
12 months : Protected	-0.221	0.0204	675.0	-10.828	<0.001

ISBN: 978-82-575-1539-3
ISSN: 1894-6402

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