

A beneficial relationship: associated trees facilitate termite colonies (*Macrotermes michaelseni*) in Namibia

B. WILDERMUTH,† J. OLDELAND , AND N. JUERGENS 

Institute of Plant Sciences and Microbiology, University of Hamburg, Hamburg, Germany

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Abstract. In many tropical ecosystems, termites are important ecosystem engineers. Mound-building termite species often contribute to topographical landscape heterogeneity, and the associated accumulation of soil moisture and nutrients affects the spatial distribution of plant communities. Plants that grow next to the termite mound are known to benefit from the provided nutrients and water storage. The other way around, protection against erosion and cooling effects on the microclimate of the mounds imposed by associated trees have been described. However, little is known regarding the influence of tree parameters and the long-term effects on colony development. In an interval of 12 yr, we studied all *Macrotermes michaelseni* mounds occurring within one square kilometer of Namibian thornbush savanna in terms of morphology, life history, and associated plants, with a focus on the role of associated trees which grow directly adjacent to the termite mounds. Here, we present the results of a combined analysis of the character states recorded at the termite mound and the associated trees. More than 50% of all 345 recorded termite mounds were associated with a tree. Mounds with associated trees showed increased activity, growth, and height. Mound growth within the study period was correlated positively with the canopy coverage by the associated tree, while total mound heights were correlated non-linear with medium canopy coverage of about 40%. Mounds with a tree covering the sun's average zenith (north) were taller, grew most within 12 yr, and were more likely to be active than those with no northern canopy coverage. Mounds associated with the evergreen *Boscia albitrunca* attained highest average height (195.06 ± 11.76 cm). We conclude that vital parameters like growth, size, and activity of the termite colonies are facilitated by shading associated trees. These benefits were shown to take significant effect within the span of 12 yr. This indicates a proper long-term mutualism, not a loose alliance and not an obligative eu-symbiosis. Therefore, we propose to use the term “partner tree” for trees associated with *M. michaelseni* mounds.

Key words: associated trees; facilitation; *Macrotermes michaelseni*; mutualism; Namibia; plant-animal interaction; shading; termite mound.

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† **E-mail:** bmwildermuth6@gmail.com

INTRODUCTION

In the tropical regions of the world, termites constitute important decomposers (Khan and Ahmad 2018, Bignell 2019). Representing species with various feeding and nesting modes, they are major drivers of carbon mineralization with direct influence on soil properties and structure

(Bignell and Eggleton 2000). Termites of the fungus-cultivating, wood-feeding, and mound-building subfamily Macrotermitinae accumulate organic matter and soil particles by foraging and nest-building activities (Jones 1990, Holt and Lepage 2000). Hence, nutrients (N, P, C) and water storage capacities are increased in mound soils and the eroded surrounding (Fox-Dobbs

et al. 2010, Jouquet et al. 2016). Termite mounds therefore provide islands of highly fertile soils within nutrient-poor tropical ecosystems (Arshad 1982, Sileshi et al. 2010) and support plant diversity (Kirchmair et al. 2012, Gbefe et al. 2017). These characteristics contribute to habitat heterogeneity (Moe et al. 2009) and influence the distribution of plant communities (Okullo and Moe 2012, Erpenbach et al. 2017). Consequently, the term “ecosystem engineers” was adapted for termites (Jones et al. 1994, Dangerfield et al. 1998).

Within the Macrotermitinae, many studies started a significant difference in species composition between plant communities growing on termite mounds compared to the matrix vegetation (Moe et al. 2009, Joseph et al. 2013, Erpenbach et al. 2017). Specific tree species and traits, like broader and evergreen leaves, increased water requirement, and low nitrogen-fixing, were found to be linked to termite mounds (Van der Plas et al. 2013, Davies et al. 2016, Cuma Mushagalusa et al. 2020). Joseph et al. (2013) reported a correlation between mound size and occurrence of mound-linked woody plants. Furthermore, various studies found enhanced recruitment and reproduction success (Traoré et al. 2008, Brody et al. 2010, Støen et al. 2013) and enhanced growth of mound-associated trees (Yamashina 2010, Joseph et al. 2011).

Fungus-cultivating termites like *Macrotermes* are wood-feeding, but they are unable to digest lignin (Martin and Martin 1978, Mills et al. 2009). Therefore, they are cultivating fungi of the genus *Termitomyces* in a fungus garden which needs temperatures around 30°C and constant humidity of approximate 95% (Korb 2003, Bardunias et al. 2020). The termite mounds themselves constitute a ventilation system for the subterranean colony and maintain the stable microclimate of both temperature and humidity within the tunnels and the fungus garden (Lüscher 1961, Noirot and Darlington 2000, Korb 2003). The ventilation system of *Macrotermes michaelseni* colonies in southern Africa is kept enclosed and thus is a good indicator for the health and activity of the colony (Turner 2001, Grohmann et al. 2010). Increasing numbers of termites emit increasing metabolic heat, which demands bigger ventilation systems, and consequently, mound height is a common surrogate for colony

size estimations (Darlington and Dransfield 1987, Korb and Linsenmair 2000, Grohmann et al. 2010). However, this has to be applied with caution since the growth curve of *Macrotermes* mounds flattens in average after 6–12 yr (Collins 1981, Darlington and Dransfield 1987). Furthermore, some termite mounds are known to be colonized repeatedly over timespans up to 2200 yr (Erens et al. 2015) which makes the size even more error-prone when used as indicator for colony size. Nevertheless, mound heights can be a powerful parameter when analyzed over the time and together with data on colony activity. The mounds of *M. michaelseni* in Namibia can reach heights of ~4 m (Turner 2000). Although the intra-colonial coordination of the building behavior is not yet understood in detail (Korb 2011), empirical data suggest a building thermotaxis beside the upward pointed building gravitaxis (Turner 2000). This thermotaxis takes effect when exposed to high temperatures and direct sun radiation. In this case, the huge mounds of the Macrotermitinae are built with an inclination angle toward the sun’s average zenith; hence, they minimize sun-exposed mound surface (Turner 2000). Thus, overheating and loss of humidity can be prevented. A possible facilitation provided by associated trees could be the shade, which reduces the sun-exposed surface as well.

While the favorable conditions for trees are comprehensively researched and can be explained with the available water and nutrients in and around termite mounds (Goodland 1965, Jones 1990, Jouquet et al. 2016), possible reverse facilitative effects for the termite mounds are not understood in detail. Pullan (1979) pointed out the tree-provided erosion protection for termitaria which was confirmed recently (Nampa and Ndlovu 2019, Mugendi 2020). Schuurman and Dangerfield (1996) did not find a significant difference in *M. michaelseni* mound heights between woodland and grassland, thus did not support the theory of facilitative effects. Korb and Linsenmair (1998) even stated that the nest temperature of *Macrotermes bellicosus* mounds in gallery forest dropped below the optimal nest temperature. Turner (2000) reported that three quarters of *M. michaelseni* mounds in a Namibian thornbush savanna were associated with a tree. He did not observe any structural support for the termite

mounds but hypothesized that the trees provide shade and therefore support the survivorship of young colonies. Similarly, mounds of *M. bellicosus* and *Macrotermes subhyalinus* were found to be predominantly (~80%) linked to the shade in a Sahel and a Sudan savanna (Aiki et al. 2019). Large trees with central shade indeed lower the temperature of *Macrotermes* mounds in savanna ecosystems and thus mitigate against the extreme temperatures and drought (Joseph et al. 2016), resulting in a higher proportion of active mounds when associated with a tree (Joseph et al. 2018). A benefit which might especially come to play in case of young and small colonies which are less capable than large mounds to maintain a stable internal temperature (Ndlovu and Pérez-Rodríguez 2018). However, the latter study did not find a correlation between amount of received shade and mound size, neither did the amount of shade differ between active and inactive mounds. Overall, these outlined findings lack temporal data covering the supposed growth period of a rising termite colony. This should be considered since the absolute height of *Macrotermes* mounds can be built up over thousands of years by constant recolonization (Erens et al. 2015). Another factor that remains unclear is whether the leaf shedding of the respective associated trees influences mound parameters.

The aim of our study was to investigate possible facilitations provided by shading trees for *M. michaelseni* mounds. The spatial patterns of termitaria and associated trees were analyzed with special regard to the only present evergreen tree species in the observatory, *Boscia albitrunca* (Shepherd's tree, (Burch.) Gilg & Gilg-Ben.). Furthermore, the mound parameters of size, growth over 12 yr, and activity were examined for possible correlations to the presence, size, canopy coverage, relative cardinal direction, and leaf shedding of associated trees.

Our hypothesis was that the majority of termite mounds is associated with at least one tree above 1.50 m height and that the associated trees facilitate the termite mounds. Therefore, tree-associated mounds should grow faster, be taller and more likely to be active than solitary mounds. We examined the tree parameters of height, diameter, canopy coverage, and distance to the mound concerning their correlation to mound growth (2007–2019) and size. The key

hypothesis assumed that possible facilitation provided by associated trees results mainly from shading. Thus, we tested mounds associated with trees covering the sun's average zenith in the north and those associated with the evergreen *B. albitrunca* for increased growth over 12 yr, for height and for higher proportions of active mounds.

METHODS

Study site

The study was conducted in Central Namibia, 120 km north of Windhoek (21.596834° S 16.935106° E, altitude 1495 m a.s.l.). In 2001, the BIOTA Africa project (Biodiversity Monitoring Transect Analysis) established the observatory Otjiamongombe, encompassing 1 km² on the cattle farm Erichsfelde (Jürgens et al. 2010, 2012; Fig. 1). The vegetation of the observatory is dominated by *Vachellia* and *Senegalia* species and *Aristidoideae* grasses (Strohbach 2019) and represents a typical central Namibian thornbush savanna under the influence of cattle farming. In this summer rain area, the climate conditions are semi-arid with an average annual rainfall of 317 mm and a mean annual temperature of 20.6°C over the years 2010–2019 (Muche et al. 2018). Mounds built by the termites *M. michaelseni* occur all over the observatory. The western part of the observatory is dissected by a small riverbed in south-north direction. The soilscape can roughly be divided into a clayey northeastern half with luvisols and the southwestern half dominated by calcisols.

Mound mapping

In 2007 and 2019, a comprehensive ground truth mapping and measuring of all present termite mounds and mound remnants of *M. michaelseni* in the observatory was conducted by two different observer teams, following the approach of Grohmann et al. (2010). The diameter and foliage of the canopy of the associated trees effectively conceal more than 30% of all termite mounds when aerial or satellite images are used. Therefore, ground inspection was inevitable and applied. All mound locations were recorded with a handheld GPS (Garmin, Schaffhausen, Switzerland), having an accuracy of ±3 m. We considered termite mounds as visible above ground

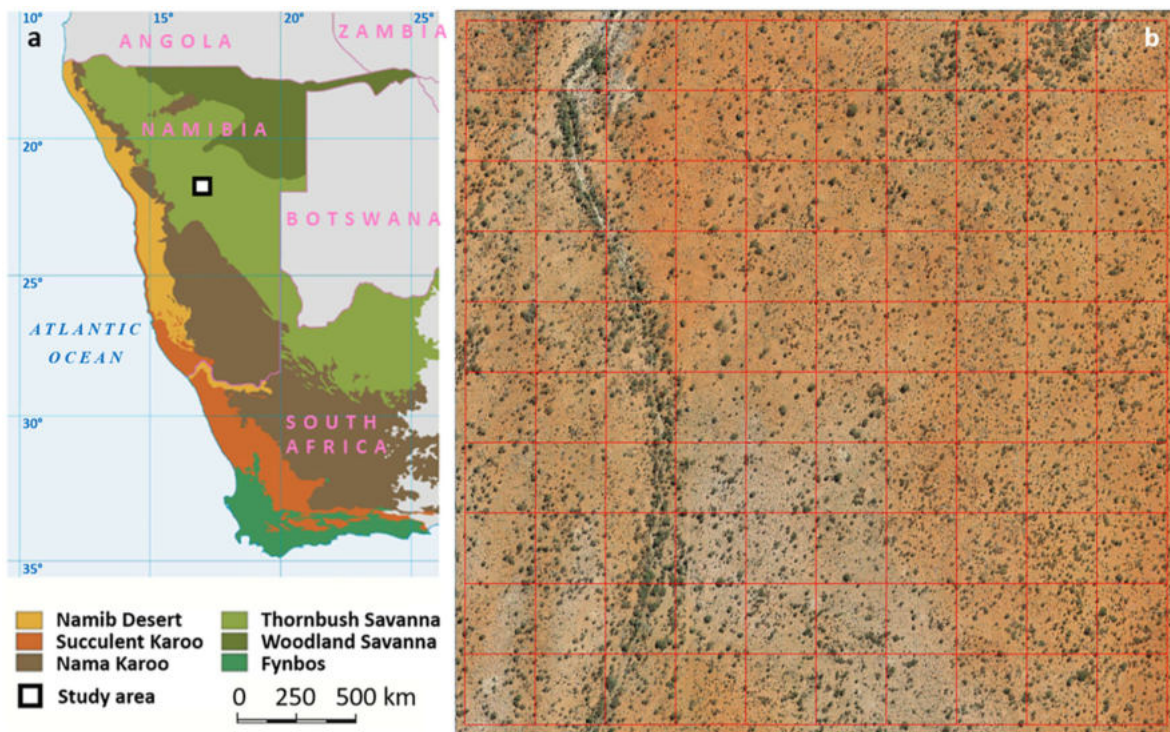


Fig. 1. (a) Biomes of southern Africa and location of the study area (modified after Jürgens et al. 2010). (b) Map of the study area Otjiamongombe, each grid cell covers 1 ha.

mounds and also any presence of remnants of the outwash pediment. Measurements were taken, starting with the outer elevation margin of the outwash pediment. The recorded data were coordinates, mound height, diameter of the conical mound base, and the outwash pediment and activity (active, inactive, or remnant) of the mounds. If only an outwash pediment was present, the mound was declared as remnant. Mounds with predominantly open ventilation systems were noted as inactive, and all mounds with closed or almost closed ventilation were tested for activity. Therefore, a hole was broken through the walls into the ventilation system using a chisel and a hammer. If either the hole was repaired the next day or the mound showed signs of recent building activity, it was assumed to be active.

Vegetation mapping

In 2019, the associated vegetation and every *B. albitrunca* above 1.50 m height in the observatory were mapped. Within the outwash pediment of a termite mound, every tree above

1.50 m total height was identified and measured. The collected dimensions were height, the distance of the tree center at breast height (1.30 m) to the conical mound center, and diameter at breast height (DBH). Furthermore, the perpendicular coverage of the mound cone and outwash pediment by the tree stem and canopy was estimated as percentage and the cardinal direction of the associated tree relative to the center of the mound was recorded with an accuracy of cardinal and intercardinal directions. In case of large branches or multiple stems covering other (inter)cardinal directions, it was noted.

Data analysis

All statistical analyses were conducted in R 3.6.1 (R Core Team 2020). The distributions of all mounds, associated trees >1.50 m height and all *B. albitrunca* specimens (>1.50 m) in the observatory were analyzed with pair correlation functions (PCF). Pair correlation function is one of the most important and regularly used tools in the analysis of point patterns (Illian et al. 2008) and a common method to classify spatial patterns into

random, regular, or clustered processes. Data preparation and upload to R was implemented with the aid of the R packages *maptools* (Bivand and Lewin-Koh 2019), *sp* (Bivand et al. 2013), and *rgdal* (Bivand et al. 2019). Then, *spatstat* (Baddeley et al. 2015) was used to apply the PCFs with the functions *PCF* and *PCFmulti* (marked PCF). The latter was used to assess the relationship of the *B. albitrunca* distribution to all termite mounds. Significance was tested with the *L* test, provided by the *Lest* function in *spatstat*. The *L* test examines whether the observed pattern is within or outside a 95% envelope of a theoretical random Poisson distribution curve. Since only 1 km² was analyzed, the default edge correction was applied to consider boundary effects.

Normality and variance homogeneity of the mound and tree parameter data were tested with the Shapiro-Wilks test, respectively, Levene's test provided by the R package *car* (Fox and Weisberg 2019). None of the datasets was normally distributed; hence, non-parametric tests were implied. Given variance homogeneity, Wilcoxon rank-sum test was chosen while Mood's median test was used for datasets with unequal variances. Mood's median test compares two samples and tests whether the observations of one sample which do not exceed the shared median of all observations differ significantly from half of the total observations (Brown and Mood 1951, Mood 1954). The median test was provided by the R package *agricolae* (De Mendiburu 2020).

Mound remnants of 2007 ($n = 124$) which did not show any presence of remnants of the outwash pediment or signs of termite activity in 2019 were excluded for further analysis. For new mounds (2019) and for the measurement of growth over 12 yr, the difference in height above the outwash pediment was chosen to avoid bias by relics of old pediment structures. Mound heights and the height difference over 12 yr (Δ height) were tested against tree presence via median tests. New mounds in 2019 were implied as 0 m height in 2007, whereas disappeared mounds were treated as 0 m height in 2019. For new mounds only, a Wilcoxon rank-sum test was run. The tests were run with both all associated trees and only living trees. The activity of the mounds was checked for possible dependencies to tree presence, relative cardinal direction, and leaf shedding of the associated trees by

performing a χ^2 test and visualizing the results in a mosaic plot with the package *vcd* (Meyer et al. 2017). A Wilcoxon rank-sum test was used to test whether the height of the associated trees differs significantly between active and non-active mounds.

Possible correlations between the mound parameters of height, Δ height (2007–2019), and pediment diameter and associated tree measurements (height, DBH, distance to the mound, canopy coverage) were examined by using a linear regression and Spearman's correlation test (for non-normally distributed data). If no significant linear correlation could be found, it was tested for non-linear regressions. For the correlation of mound heights and canopy coverage, a second-order polynomial was selected with Akaike's information criterion as the best-fitting regression over a linear or GAM-regression (generalized additive model). This was performed by using the R packages *visreg* (Breheny and Burchett 2017) and *mgcv* (Wood 2011).

All mounds with exclusive southern shading and all mounds with northern shading were tested for significant differences in height and Δ height (2007–2019) with Mood's median test (height), respectively, Wilcoxon's rank-sum test (Δ height), which was also applied to contrast those associated with the evergreen *B. albitrunca* as well as those associated with dead trees against the respective remaining mound–tree associations. These analyses were repeated with new mounds only (2019), using Mood's median test for the relative cardinal direction of the tree and Wilcoxon's rank-sum test to contrast associations with *B. albitrunca* against the remaining mound–tree associations.

RESULTS

A total of 345 mapped *M. michaelsoni* mounds and mound remnants in 2019 matched roughly the 388 mapped mounds and mound remnants in 2007. While 141 mounds had disappeared completely within the 12 yr, 98 new mounds had appeared. For further analyses, disappeared remnants of 2007 were excluded ($n = 124$), leaving a total n of 362 analyzed mound sites. While all *M. michaelsoni* mounds showed a random distribution, large and long-term active mounds (2007–2019) were distributed regularly (*L* test $P < 0.05$).

Out of all 362 analyzed mounds, 203 (56.08%) were associated with at least one tree. These associations were regularly distributed over the observatory. Within all 203 mound-tree associations, the evergreen *B. albitrunca* was present in 86 cases (42.36%). Other common associated trees were the deciduous *Senegalia mellifera* ($n = 43$), *Vachellia tortilis* ($n = 28$), *Vachellia hebeclada* ($n = 18$), and *Vachellia reficiens* ($n = 15$) or indeterminable dead tree remains ($n = 20$; Appendix S1: Table S1). New mounds, first recorded in 2019, were associated with trees in 60.2% of the cases (59/98) but only associated with *B. albitrunca* in 14 cases (23.73% of all new mound-tree associations).

In total, 334 individuals of *B. albitrunca* above 1.50 m height were recorded all over the observatory. The overall distribution of *B. albitrunca* showed a clustered spatial distribution with its highest density on the silty soils in the northeast (Appendix S1: Fig. S1). The marked PCF of the total mound distribution and the total *B. albitrunca* distribution in the observatory yielded a strongly clustered co-occurrence (L test $P < 0.05$).

Out of all 203 mounds with associated trees, 116 (57.14%) were active and within the total active mounds ($n = 163$), these 116 associated active mounds represent 71.17%. In contrast, only 29.56% (47/159) of all mounds without associated tree were active. 19.51% (16/82) of all remnant mounds were associated with a tree. The respective χ^2 test (Fig. 2) showed significance for interrelation of mound activity and tree presence ($\chi^2 = 60.585$, $P < 0.001$).

The height comparison of solitary mounds ($M = 94.94$ cm, standard error = ± 7.78 cm) vs. mounds with associated trees ($M = 169.29 \pm 8.1$ cm) revealed a significant difference ($P < 0.001$). A significant difference ($P < 0.01$) also occurred in contrasting the mean Δ height (2007–2019) between the mounds with associated tree ($M\Delta = +23.23 \pm 6.73$ cm) and without ($M\Delta = -0.57 \pm 5.75$ cm). This finding of increased growth in mounds with associated trees was even consolidated when treating all associations of mounds with dead trees as solitary mounds ($M\Delta = +32.19 \pm 6.77$ cm vs. $M\Delta = -7.56 \pm 5.77$ cm, $P < 0.001$; Fig. 3). Mounds associated with a dead tree had a negative and significantly lower Δ height ($M\Delta = -68.89 \pm 20.64$ cm, $P < 0.001$). Within the new mounds first recorded

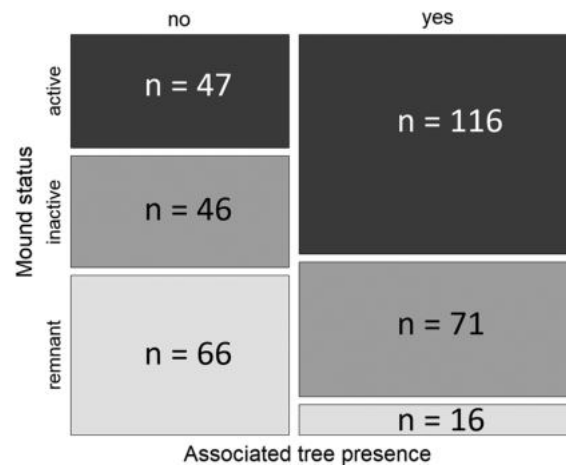


Fig. 2. Mosaic plot showing the proportion of activity statuses without and with associated tree. Mounds with associated tree are more likely to be active ($\chi^2 = 60.585$, $P < 0.001$).

in 2019, no association with a dead tree was found. New mounds associated with a tree ($n = 59$) showed an average growth of 91.86 cm (± 10.16 cm) while solitary new mounds grew 69.34 cm (± 10.97 cm) on average ($P > 0.05$). Trees associated with an active mound were significantly taller ($M = 520.78 \pm 17.5$ cm) than those associated with inactive or remnant mounds ($M = 457.3 \pm 17.08$ cm, $P < 0.05$).

Greatest average mound heights were reached at about 30–45% coverage by the associated tree canopy, while Δ height was positively correlated with the canopy coverage (Fig. 4). Mound height and distance of the associated tree to the mound center showed a positive linear correlation ($r = 0.15$, $P < 0.05$).

Tree height and DBH of the associated tree were both positively correlated with the corresponding mound height, as well as the mound diameter (Appendix S1: Table S2).

Interrelationships between the tree parameters of relative cardinal direction and leaf shedding and the respective mound heights, Δ height, and activity are summarized in Table 1. Striking results are that termite mounds associated with trees which cover the north grew more (Fig. 5) and were taller and more likely to be active. Furthermore, mounds associated with the evergreen *B. albitrunca* were the tallest (Table 1). Within the new mounds, first recorded in 2019, the relative

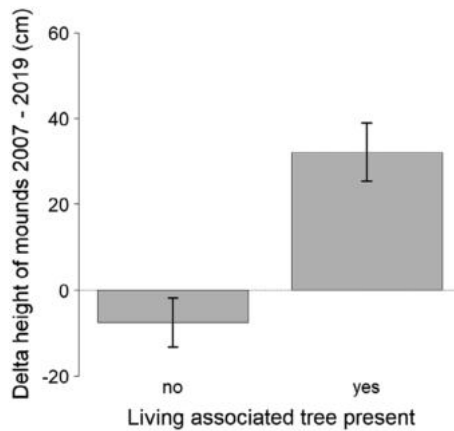


Fig. 3. Barplot comparing the mean Δ height of mounds without living associated tree ($M\Delta = -7.56$ cm) with the mounds with living associated tree ($M\Delta = 32.19$ cm; $P < 0.001$).

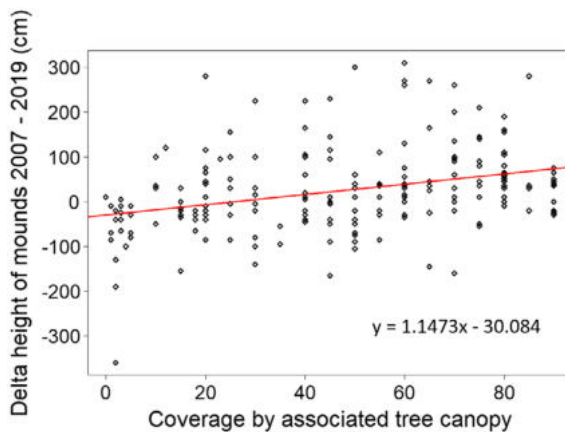


Fig. 4. Spearman's correlation of the coverage by associated trees and mound Δ height t ($\rho = 0.375$, $P < 0.001$).

cardinal direction of the associated tree also showed a significant impact on mound growth. New mounds which were covered in the north by the associated tree ($n = 41/98$; 41.84%) grew 105.73 cm (± 13.36 cm) on average, while those only covered in the south were lower in abundance ($n = 8/98$; 8.16%) and grew significantly less on average (48.13 cm \pm 7.38 cm, $P < 0.05$). When associated with *B. albitrunca*, new mounds showed a mean growth of 100.71 cm (± 21.92 cm). This did not differ significantly

from new mound–tree associations with deciduous tree species ($M\Delta$ height = $+89.11 \pm 11.33$ cm) but contrasts the low growth of mound–*B. albitrunca* associations when looking at all mound–tree associations ($M\Delta$ height = $+5.17$ cm; Table 1).

DISCUSSION

The present study focused on possible mutualistic and facilitating relationships between associated trees and *M. michaelsoni* mounds in the Namibian thornbush savanna. Apart from analyses of the mound parameters of size and activity, we now contribute data on mound growth over 12 yr and show impacts of tree presence and parameters of size, canopy coverage, relative cardinal direction, and leaf shedding of associated trees.

Our results complement the findings of previous studies on mound-associated trees. Over 50% of all 345 mounds in the observatory were associated with at least one tree. The evergreen *B. albitrunca* constituted almost half of all mound–tree associations and has typical mound-linked traits like low nitrogen-fixing, increased water requirement, and evergreen and broad leaves (Van der Plas et al. 2013, Davies et al. 2016, Cuma Mushagalusa et al. 2020), compared to, for example, ex-*Acacia* species (Alias et al. 2003, Burke 2006). The favorable conditions as there are available water and nutrients are well known (Wood 1988, Jouquet et al. 2006, Abe et al. 2009). Konaté et al. (1999) already showed that leaf shedding of evergreen shrubs in dry seasons was significantly lower, when growing on a termite mound. Even though large *B. albitrunca* trees were shown to have root lengths up to 70 m (Canadell et al. 1996) and thus may not rely on water provided by termites, small seedlings of woody species cannot reach such depths and show lower mortality and higher growth rates when growing on mound soils (Traoré et al. 2008, Traoré and Jouquet 2020).

Now, the results of this study additionally reveal the key role of mound activeness when supporting tree growth. Associated trees of active mounds were significantly taller than those of inactive or remnant mounds: a factor which predominantly should be linked to the water supply provided by active colonies, since

Table 1. Mound height, growth (Δ height 2007–2019), and activity (number, with percentage in parentheses) regarding the cardinal direction of the associated tree and leaf shedding.

Parameter	Associated tree covers		<i>P</i>	χ^2	Evergreen	Deciduous	<i>P</i>	χ^2
	North	Only south						
Mound height (cm)	184.52 \pm 10.79	104.44 \pm 13.99	<0.001***		195.06 \pm 11.76	152.93 \pm 12.27	<0.05*	
Δ height (cm)	+42.98 \pm 10.06	−13.89 \pm 12.73	<0.05*		+5.17 \pm 9.75	+55.66 \pm 8.79	<0.005**	
Active mounds	83/114 (72.81)	7/27 (25.93)	<0.001***	22.02	52/86 (60.47)	59/99 (59.6)	>0.05	0.9

Notes: In case of significance, higher values are shown in bold.

Values for height and Δ height are expressed as mean \pm standard error. Height and Δ height were tested with Wilcoxon's rank-sum test and the activity of the mounds with a χ^2 test. Mound height vs. cardinal direction was tested with a median test due to unequal variances.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

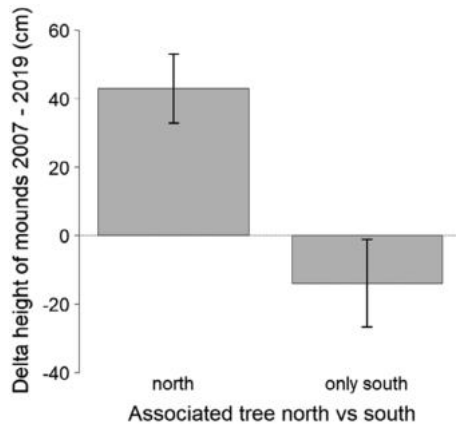


Fig. 5. Barplot comparing the mean Δ height of mounds with coverage in the north by associated trees ($M\Delta = +42.98$ cm) with mounds with exclusive southern coverage by associated trees ($M\Delta = -13.89$ cm; $P < 0.05$).

aggregated nutrient-rich soils in hard nest structures may be stable for decades (Bottinelli et al. 2015). The water supply is partly enabled by high water storage capacities and increased preferential water flow due to galleries and tunnels (Bargués Tobella et al. 2014) but also by the active transport of water from lower depths by the termites (Chen et al. 2019, Turner 2019).

Reverse facilitations for the termite mounds provided by associated trees are erosion protection (Pullan 1979, Nampa and Ndlovu 2019, Mugendi 2020) and cooling effects by the shade (Joseph et al. 2016, Ndlovu and Pérez-Rodríguez 2018). These benefits result in higher mound sizes and proportions of active mounds, when associated with trees (Joseph et al. 2018, Nampa and Ndlovu 2019). Our results show a

remarkable impact of associated trees on the activity and growth of termite colonies. Almost 60% of the mounds with associated trees were active and they comprised imperious three quarters of all active mounds. In contrast, barely 20% of all remnant mounds were associated with a tree. Mounds with associated trees were almost 80% taller than those without trees. Mound size and colony growth of rising *Macrotermes* mounds are correlated in the first 6–12 yr (Collins 1981, Darlington and Dransfield 1987) but afterward, mound growth flattens and the mound structures can be recolonized repeatedly (Erens et al. 2015). Thus, the absolute mound heights cannot be used unambiguously as colony size and health indicator. However, our measurements of mound growth over 12 yr cover the supposed time of correlated mound and colony growth and give insights into the dynamics of mound building and erosion. Over the 12 yr, on average, mounds with associated trees gained in height, in stark contrast to mounds without trees, which became smaller. This gives strong support that colony growth and ultimately colony size are promoted by associated trees. We assume that the negative Δ height of solitary mounds also displays the lack of tree-derived erosion protection (Nampa and Ndlovu 2019). In recognition of these results which indicate a proper long-term mutualism, we established the term “partner trees” for mound-associated trees in our study. Nevertheless, this mutualism is no obligative eusymbiosis.

Our study furthermore examined various tree parameters concerning their correlation to the mound growth and size. Tree height and DBH were correlated positively with both mound height and mound diameter, which hints at long-

term advantages of bigger partner trees, respectively, the mutual benefits of a mound–tree association. Even though mound growth over 12 yr did not show any correlation with tree size, we found a strong positive correlation of mound growth and percentage of coverage by the tree canopy. Apart from the mentioned erosion protection, we assign this effect to the shade provided by the canopy, which then helps to mitigate against extreme temperature in the savanna (Joseph et al. 2016, 2018). The correlation of mound height and coverage by the associated tree though was not linear. Coverage by the tree canopy of about 40% accompanied the tallest mounds, while low and high coverage values were found at smaller mounds. This indicates that shading above the level of 40% coverage by the canopy may be disadvantageous in the long run as well. Korb and Linsenmair (1998) already showed that *M. bellicosus* mounds in gallery forests occur in much lower densities than in the shrub savanna and that artificial total shading increases the mortality rate of the termite mounds. Hence, too much shade seems to lower the nest temperature under the optimal temperature of 30°C (Korb and Linsenmair 1998). Temperatures below the ideal temperature were also observed in *Macrotermes natalensis* mounds under savanna trees, especially if the mounds were inactive (Ndlovu and Pérez-Rodríguez 2018). This may be due to the fact that soil temperatures under isolated trees in African savannas can be 5–12°C lower than in the open (Belsky et al. 1993). However, we did not measure internal mound temperatures; thus, this conclusion remains speculative.

Within the mounds with partner tree, those which were covered by the tree in the north were significantly taller, grew more (2007–2019), and were more likely to be active than those which were covered exclusively in the south. The latter in contrast were significantly smaller, lost in height (2007–2019), and were less likely to be active. As the sun's average zenith is in the north in the southern hemisphere, these findings support the theory that the partner trees are sun protectors for the termite mounds, so the colony can grow larger. Turner (2000) reported that *M. michaelseni* mounds are built with an inclination angle toward the sun's average zenith to minimize the sun-exposed surface. Thus,

overheating and loss of humidity can be prevented and the stable microclimate of both temperature and humidity within the tunnels and the fungus garden is secured (Lüscher 1961, Noirot and Darlington 2000, Turner 2001). When transferring this principle to the discovered phenomenon of provided shade being beneficial to termite mounds, it is highly likely that the shading trees contribute buffering of the extremely high temperatures during the day.

The positive correlation between mound height and distance of the associated tree remains without a clear explanation, but here, the angle of the sun's zenith and the perfect shading angle might come to play. Further analyses of the ideal cardinal direction, angle, and distance of the associated tree should clarify this question.

Termitaria associated with the only present evergreen tree, *B. albitrunca*, were in average almost a third (27.55%) taller than all other tree-associated mounds. This supports the theory of advantageous shading, since evergreen leaves provide perennial shading and *B. albitrunca* leaves are broader and therefore provide more shade than, for example, ex-*Acacia* species (Alias et al. 2003). In contrast, and not reliably explained, this study discovered a significantly higher growth rate within the termitaria with deciduous partner trees, while average-wise, all termitaria with *B. albitrunca* barely grew (+5 cm) over the 12 yr. The answer may be the high average size of *Boscia*-associated termite mounds. The mean height of 195.06 cm constitutes the highest average in all investigated subsets and may represent a mean growth limit. This needs to be confirmed over longer time periods and with larger sample sizes. However, when looking at new mounds only (in 2019), this result is contrasted by high growth rates (+100 cm) of *Boscia*-associated mounds.

More temporal studies of mound-associated woody plants are needed to get reliable data whether the mutualism is initiated by the mound or the partner tree. Nampa and Ndlovu (2019) observed a mutualistic association between termite mounds and num-num plants but could not answer the question which one comes first. Our data do neither allow a concluding interpretation of the temporal sequence. However, the following observations may be helpful for future research and discussion: Over 60% of the newly built mounds in our study were associated with

a tree, and remarkably, they were never found under a dead tree. In over 50% of new mound–tree associations, the mound was covered by the tree canopy in the north, while only 8% were covered exclusively in the south. Considering that, for example, swarming *M. natalensis* alates prefer sheltered areas with plant litter cover for nesting (Mitchell 2007) and the survivorship of young *M. michaelsoni* colonies may increase when shaded by trees (Turner 2000), colony establishment under shading trees might be favored. On the other hand, only 14% of new tree-associated mounds in our study were associated with *B. albitrunca*—contrasting the finding that *B. albitrunca* constitutes almost 50% of all partner trees. This in turn indicates that *B. albitrunca* benefits from established termite mounds and thus occurs subsequently. Reports of *Macrotermes* mound-linked enhanced recruitment of various woody species (Traoré et al. 2008, Støen et al. 2013) as well as the observation that woody indicator species of *Macrotermes* mounds increasingly occur with bigger mound size (Joseph et al. 2013) support this theory. We consider it is possible that a mutual and self-reinforcing combination of all mentioned factors and temporal sequences causes a constant percentage of termite mound–tree associations (Nampa and Ndlovu 2019).

Aiki et al. (2019) observed up to 80% of *Macrotermes* mounds associated with trees, and in our study, 56% of all mounds were associated with at least one tree. Nonetheless, our results also suggest that the spatial patterns of long-term active and large mounds are determined by intraspecific competition and not by favorable partner trees. Thus, mounds which have been active in both 2007 and 2019 as well as tall mounds (>2 m) were distributed regularly over the observatory, while the overall distribution of the potentially most favorable partner tree, *B. albitrunca*, was clustered in the northeast of the observatory, both in the matrix and as partner tree. It should be noted that the canopies of the associated trees effectively conceal more than 30% of all termite mounds when aerial or satellite images are used. Therefore, ground inspection was necessary for spatial pattern analyzes of termite colonies.

In summary, this study found evidence that the shade provided by associated woody plants

has a facilitative effect on *M. michaelsoni* mounds in a Namibian thornbush savanna. Over 50% of all termite mounds in the study observatory were associated with a tree and this association was shown to increase colony growth over 12 yr, mound size, and activity. We regard this interaction as a long-term mutualism with obvious advantages for both, the termite colony and the tree. In this context we consider the tree to be a partner tree of the termite mound.

Mound growth over 12 yr was correlated positively with coverage by the partner tree canopy. Termite mounds which were covered in the north by a tree grew more and were taller and more likely to be active. Size of the partner trees, medium coverage by the canopy, and evergreen leaves (*B. albitrunca*) were correlated positively with the height of the termite mounds. Thus, the shade by the partner tree was identified as a key factor, which increases termite colony size and vitality. However, to draw these findings as more general conclusions, similar studies should be conducted across a larger spatial scale. Further temporal studies are also needed to understand more details of the succession of the mutualistic relationship between trees and termite mounds and to test for possible facilitating factors beyond the provided shading for the mounds.

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LITERATURE CITED

- Abe, S. S., S. Yamamoto, and T. Wakatsuki. 2009. Physicochemical and morphological properties of termite (*Macrotermes bellicosus*) mounds and surrounding pedons on a toposequence of an inland valley in the southern Guinea savanna zone of Nigeria. *Soil Science and Plant Nutrition* 55:514–522.
- Aiki, I. P., C. W. W. Pirk, and A. A. Yusuf. 2019. Thermal regulatory mechanisms of termites from two

- different savannah ecosystems. *Journal of Thermal Biology* 85:102418.
- Alias, D., S. Milton, A. E. Herrmann, and C. Seymour. 2003. A collation and overview of research information on *Boscia albitrunca* (shepherd's tree) and identification of relevant research gaps to inform protection of the species. 2003:089. Department of Water Affairs and Forestry, Pretoria, South Africa.
- Arshad, M. A. 1982. Influence of the termite *Macrotermes michaelseni* (Sjöst) on soil fertility and vegetation in a semi-arid savannah ecosystem. *Agro-Ecosystems* 8:47–58.
- Baddeley, A., E. Rubak, and R. Turner. 2015. *Spatial point patterns: Methodology and applications with R*. Chapman and Hall/CRC Press, London, UK.
- Bardunias, P. M., D. S. Calovi, N. Carey, R. Soar, J. S. Turner, R. Nagpal, and J. Werfel. 2020. The extension of internal humidity levels beyond the soil surface facilitates mound expansion in *Macrotermes*. *Proceedings of the Royal Society B: Biological Sciences* 287:20200894.
- Bargués Tobella, A., H. Reese, A. Almaw, J. Bayala, A. Malmer, H. Laudon, and U. Ilstedt. 2014. The effect of trees on preferential flow and soil infiltrability in an agroforestry parkland in semiarid Burkina Faso. *Water Resources Research* 50:3342–3354.
- Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* 30:143–155.
- Bignell, D. 2019. Termite ecology in the first two decades of the 21st century: a review of reviews. *Insects* 10:60.
- Bignell, D. E., and P. Eggleton. 2000. Termites in ecosystems. Pages 363–387 in T. Abe, D. E. Bignell, and M. Higashi, editors. *Termites: evolution, sociality, symbioses, ecology*. Springer Netherlands, Dordrecht, The Netherlands.
- Bivand, R., T. Keitt, and B. Rowlingson. 2019. rgdal: Bindings for the 'geospatial' data abstraction library. R package version 1.4-4. <https://CRAN.R-project.org/package=rgdal>
- Bivand, R., and N. Lewin-Koh. 2019. maptools: Tools for handling spatial objects. R package version 0.9-5. <https://CRAN.R-project.org/package=maptools>
- Bivand, R. S., E. Pebesma, and V. Gomez-Rubio. 2013. *Applied spatial data analysis with R*. Second edition. Springer, New York, New York, USA.
- Bottinelli, N., P. Jouquet, Y. Capowiez, P. Podwojewski, M. Grimaldi, and X. Peng. 2015. Why is the influence of soil macrofauna on soil structure only considered by soil ecologists? *Soil and Tillage Research* 146:118–124.
- Breheeny, P., and W. Burchett. 2017. Visualization of regression models using visreg. *R Journal* 9:56–71.
- Brody, A. K., T. M. Palmer, K. Fox-Dobbs, and D. F. Doak. 2010. Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*. *Ecology* 91:399–407.
- Brown, G. W., and A. M. Mood. 1951. On median tests for linear hypotheses. Pages 159–166 in J. Neyman, editor. *Proceedings of the Second Berkeley Symposium on Mathematical Statistics and Probability*. University of California Press, Berkeley, California, USA.
- Burke, A. 2006. Savanna trees in Namibia – Factors controlling their distribution at the arid end of the spectrum. *Flora – Morphology, Distribution, Functional Ecology of Plants* 201:189–201.
- Canadell, J., R. B. Jackson, J. B. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108:583–595.
- Chen, C., J. Wu, X. Zhu, X. Jiang, W. Liu, H. Zeng, and F.-R. Meng. 2019. Hydrological characteristics and functions of termite mounds in areas with clear dry and rainy seasons. *Agriculture, Ecosystems & Environment* 277:25–35.
- Collins, N. M. 1981. Populations, age structure and survivorship of colonies of *Macrotermes bellicosus* (Isoptera: Macrotermitinae). *Journal of Animal Ecology* 50:293–311.
- Cuma Mushagalusa, F., D. Bauman, M. Ngoy Shutcha, and P. Meerts. 2020. Trait divergence of woody species in relation to affinity for termite mounds in Upper Katanga (DR Congo). *Journal of Vegetation Science* 31:162–172.
- Dangerfield, J. M., T. S. McCarthy, and W. N. Ellery. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* 14:507–520.
- Darlington, J. P. E. C., and R. D. Dransfield. 1987. Size relationships in nest populations and mound parameters in the termite *Macrotermes michaelseni* in Kenya. *Insectes Sociaux* 34:165–180.
- Davies, A. B., C. A. Baldeck, and G. P. Asner. 2016. Termite mounds alter the spatial distribution of African savanna tree species. *Journal of Biogeography* 43:301–313.
- De Mendiburu, F. 2020. agricolae: Statistical procedures for agricultural research. R package version 1.3-3. <https://CRAN.R-project.org/package=agricolae>
- Erens, H., M. Boudin, F. Mees, B. B. Mujinya, G. Baert, M. Van Strydonck, P. Boeckx, and E. Van Ranst. 2015. The age of large termite mounds—radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo.

- Palaeogeography, Palaeoclimatology, Palaeoecology 435:265–271.
- Erpenbach, A., M. Bernhardt-Römermann, R. Wittig, and K. Hahn. 2017. The contribution of termite mounds to landscape-scale variation in vegetation in a West African national park. *Journal of Vegetation Science* 28:105–116.
- Fox, J., and S. Weisberg. 2019. *An R companion to applied regression*. Third edition. Sage, Thousand Oaks, California, USA.
- Fox-Dobbs, K., D. F. Doak, A. K. Brody, and T. M. Palmer. 2010. Termites create spatial structure and govern ecosystem function by affecting N₂ fixation in an East African savanna. *Ecology* 91:1296–1307.
- Gbeffe, A. K., T. D. Houehanou, M. Habiyaemye, E. S. P. Assede, A. S. Yaoitcha, L. Janssens de Bisthoven, E. A. Sogbohossou, M. Houinato, and B. A. Sinsin. 2017. Effects of termite mounds on composition, functional types and traits of plant communities in Pendjari Biosphere Reserve (Benin, West Africa). *African Journal of Ecology* 55:580–591.
- Goodland, R. J. A. 1965. On termitaria in a savanna ecosystem. *Canadian Journal of Zoology* 43:641–650.
- Grohmann, C., J. Oldeland, D. Stoyan, and K. E. Linsenmair. 2010. Multi-scale pattern analysis of a mound-building termite species. *Insectes Sociaux* 57:477–486.
- Holt, J. A., and M. Lepage. 2000. Termites and soil properties. Pages 389–407 in T. Abe, D. E. Bignell, and M. Higashi, editors. *Termites: evolution, sociality, symbioses, ecology*. Springer Netherlands, Dordrecht, The Netherlands.
- Illian, J., A. Penttinen, H. Stoyan, and D. Stoyan. 2008. *Statistical analysis and modelling of spatial point patterns*. John Wiley & Sons Ltd, Chichester, UK.
- Jones, C. O., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Pages 130–147 in *Ecosystem management*. Springer, New York, New York, USA.
- Jones, J. A. 1990. Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. *Journal of Tropical Ecology* 6:291–305.
- Joseph, G. S., G. S. Cumming, D. H. M. Cumming, Z. Mahlangu, R. Altwegg, and C. L. Seymour. 2011. Large termitaria act as refugia for tall trees, deadwood and cavity-using birds in a miombo woodland. *Landscape Ecology* 26:439–448.
- Joseph, G. S., C. L. Seymour, B. W. T. Coetzee, M. Ndlovu, A. De La Torre, R. Suttle, N. Hicks, S. Oxley, and S. H. Foord. 2016. Microclimates mitigate against hot temperatures in dryland ecosystems: termite mounds as an example. *Ecosphere* 7: e01509.
- Joseph, G. S., C. L. Seymour, B. W. T. Coetzee, M. Ndlovu, L. Deng, K. Fowler, J. Hagan, B. J. Brooks, J. A. Seminara, and S. H. Foord. 2018. Elephants, termites and mound thermoregulation in a progressively warmer world. *Landscape Ecology* 33:731–742.
- Joseph, G. S., C. L. Seymour, G. S. Cumming, D. H. M. Cumming, and Z. Mahlangu. 2013. Termite mounds as islands: woody plant assemblages relative to termitarium size and soil properties. *Journal of Vegetation Science* 24:702–711.
- Jouquet, P., N. Bottinelli, R. R. Shanbhag, T. Bourguignon, S. Traoré, and S. A. Abbasi. 2016. Termites: the neglected soil engineers of tropical soils. *Soil Science* 181:157–165.
- Jouquet, P., J. Dauber, J. Lagerlöf, P. Lavelle, and M. Lepage. 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* 32:153–164.
- Jürgens, N., et al. 2012. The BIOTA Biodiversity Observatories in Africa—a standardized framework for large-scale environmental monitoring. *Environmental Monitoring and Assessment* 184:655–678.
- Jürgens, N., U. Schmiedel, T. Hoffman, and BIOTA Southern Africa (Project), editors. 2010. *Biodiversity in Southern Africa*. Klaus Hess Publishers, Göttingen, Germany.
- Khan, M. A., and W. Ahmad, editors. 2018. *Biology, social behaviour and economic importance*. Springer, Cham, Switzerland.
- Kirchmair, I., M. Schmidt, G. Zizka, A. Erpenbach, and K. Hahn. 2012. Biodiversity Islands in the savanna – Analysis of the phytodiversity on termite mounds in Northern Benin. *Flora et Vegetatio Sudano-Sambesica* 15:3–14.
- Konaté, S., X. L. Roux, D. Tessier, and M. Lepage. 1999. Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. *Plant and Soil* 206:47–60.
- Korb, J. 2003. Thermoregulation and ventilation of termite mounds. *Naturwissenschaften* 90:212–219.
- Korb, J. 2011. Termite mound architecture, from function to construction. Pages 349–373 in D. E. Bignell, Y. Roisin, and N. Lo, editors. *Biology of termites: a modern synthesis*. Springer Netherlands, Dordrecht, The Netherlands.
- Korb, J., and K. E. Linsenmair. 1998. The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. *Insectes Sociaux* 45:51–65.
- Korb, J., and K. E. Linsenmair. 2000. Thermoregulation of termite mounds: what role does ambient

- temperature and metabolism of the colony play? *Insectes Sociaux* 47:357–363.
- Lüscher, M. 1961. Air-conditioned termite nests. *Scientific American* 205:138–145.
- Martin, M. M., and J. S. Martin. 1978. Cellulose digestion in the midgut of the fungus-growing termite *Macrotermes natalensis*: the role of acquired digestive enzymes. *Science* 199:1453–1455.
- Meyer, D., A. Zeileis, and K. Hornik. 2017. vcd: Visualizing categorical data. R package version 1.4-4. <https://CRAN.R-project.org/package=vcd>
- Mills, A. J., A. Milewski, M. V. Fey, A. Groengroeff, and A. Petersen. 2009. Fungus culturing, nutrient mining and geophagy: a geochemical investigation of *Macrotermes* and *Trinervitermes* mounds in southern Africa. *Journal of Zoology* 278:24–35.
- Mitchell, J. D. 2007. Swarming and pairing in the fungus-growing termite, *Macrotermes natalensis* (Haviland) (Isoptera: Macrotermitinae). *African Entomology* 15:153–160.
- Moe, S. R., R. Møbak, and A. K. Narmo. 2009. Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology* 202:31–40.
- Mood, A. M. 1954. On the asymptotic efficiency of certain nonparametric two-sample tests. *Annals of Mathematical Statistics* 25:514–522.
- Muche, G., et al. 2018. SASSCAL WeatherNet: present state, challenges, and achievements of the regional climatic observation network and database. *Biodiversity & Ecology* 6:34–43.
- Mugendi, D. G. 2020. Temporal patterns in *Macrotermes* mound occupancy in a savanna ecosystem. Thesis. Norwegian University of Life Sciences, Ås, Norway.
- Nampa, G., and M. Ndlovu. 2019. Association benefits between harvester termites (*Trinervitermes trinervoides*) and num-num plants (*Carissa bispinosa*) in a semi-arid savanna setting. *Journal of Arid Environments* 171:104005.
- Ndlovu, M., and A. Pérez-Rodríguez. 2018. Temperature fluctuations inside savanna termite mounds: Do size and plant shade matter? *Journal of Thermal Biology* 74:23–28.
- Noiroi, C., and J. P. E. C. Darlington. 2000. Termite nests: Architecture, regulation and defence. Pages 121–139 in T. Abe, D. E. Bignell, and M. Higashi, editors. *Termites: evolution, sociality, symbioses, ecology*. Springer Netherlands, Dordrecht, The Netherlands.
- Okullo, P., and S. R. Moe. 2012. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation: herbaceous species composition in savannas. *Journal of Ecology* 100:232–241.
- Pullan, R. A. 1979. Termite hills in Africa: their characteristics and evolution. *Catena* 6:267–291.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Schuurman, G., and J. M. Dangerfield. 1996. Mound dimensions, internal structure and potential colony size in the fungus growing termite *Macrotermes michaelseni* (Isoptera: Macrotermitinae). *Sociobiology* 27:29–38.
- Sileshi, G. W., M. A. Arshad, S. Konaté, and P. O. Y. Nkunika. 2010. Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns: termite-induced heterogeneity in African savanna vegetation. *Journal of Vegetation Science* 21:923–937.
- Støen, O. G., P. Okullo, T. Eid, and S. R. Moe. 2013. Termites facilitate and ungulates limit savanna tree regeneration. *Oecologia* 172:1085–1093.
- Strohbach, B. J. 2019. Vegetation of the thornbush savanna of central Namibia: baseline description of the present vegetation at Farm Erichsfelde, Otjozondjupa Region. *Namibian Journal of Environment* 3:A-36.
- Traoré, S., and P. Jouquet. 2020. Growth performance and adaptive strategy of early seedlings of three savanna woody species in pots as feedback to the soil of *Macrotermes subhyalinus* mound. *European Scientific Journal* 16:1857–7881.
- Traoré, S., M. Tigabu, S. J. Ouédraogo, J. I. Boussim, S. Guinko, and M. G. Lepage. 2008. *Macrotermes* mounds as sites for tree regeneration in a Sudanian woodland (Burkina Faso). *Plant Ecology* 198:285–295.
- Turner, J. S. 2000. Architecture and morphogenesis in the mound of *Macrotermes michaelseni* (Sjöstedt) (Isoptera: Termitidae, Macrotermitinae) in northern Namibia. *Cimbebasia* 16:143–175.
- Turner, J. S. 2001. On the mound of *Macrotermes michaelseni* as an organ of respiratory gas exchange. *Physiological and Biochemical Zoology* 74:798–822.
- Turner, J. S. 2019. Termites as mediators of the water economy of arid savanna ecosystems. Pages 401–414 in P. D’Odorico, A. Porporato, and C. Wilkinson Runyan, editors. *Dryland ecohydrology*. Springer International Publishing, Cham, Germany.
- Van der Plas, F., R. Howison, J. Reinders, W. Fokkema, and H. Olff. 2013. Functional traits of trees on and off termite mounds: understanding the origin of biotically-driven heterogeneity in savannas. *Journal of Vegetation Science* 24:227–238.
- Wood, T. G. 1988. Termites and the soil environment. *Biology and Fertility of Soils* 6:228–236.

- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semi-parametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73:3–36.
- Yamashina, C. 2010. Interactions between termite mounds, trees, and the Zemba people in the Mopane savanna in Northwestern Namibia. *African Study Monographs. Supplementary Issue* 40:115–128.

DATA AVAILABILITY

Data are available from Pangaea at: <https://doi.org/10.1594/PANGAEA.931642>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3671/full>