Termites promote resistance of decomposition to spatiotemporal variability in rainfall

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Abstract. The ecological impact of rapid environmental change will depend on the resistance of key ecosystems processes, which may be promoted by species that exert strong control over local environmental conditions. Recent theoretical work suggests that macrodetritivores increase the resistance of African savanna ecosystems to changing climatic conditions, but experimental evidence is lacking. We examined the effect of large fungus-growing termites and other non-fungus-growing macrodetritivores on decomposition rates empirically with strong spatiotemporal variability in rainfall and temperature. Non-fungus-growing larger macrodetritivores (earthworms, woodlice, millipedes) promoted decomposition rates relative to microbes and small soil fauna (+34%) but both groups reduced their activities with decreasing rainfall. However, fungus-growing termites increased decomposition rates strongest (+123%) under the most water-limited conditions, making overall decomposition rates mostly independent from rainfall. We conclude that fungus-growing termites are of special importance in decoupling decomposition rates from spatiotemporal variability in rainfall due to the buffered environment they create within their extended phenotype (mounds), that allows decomposition to continue when abiotic conditions outside are less favorable. This points at a wider class of possibly important ecological processes, where soil-plant-animal interactions decouple ecosystem processes from large-scale climatic gradients. This may strongly alter predictions from current climate change models.

Key words: biotic feedback; decomposition; ecosystem engineer; extended phenotype; rainfall variability; resistance; robustness; stability; temperature; termites.

Introduction

Decomposition of dead organic matter is a key process in the recycling of carbon and nutrients in terrestrial ecosystems (Sayer 2006, Canadell et al. 2007), providing the primary input of nutrients for both plant and detritivore communities. A long history of research has identified climate (rainfall, temperature) as the main driver of decomposition rates, through determining vegetation composition (and hence, litter quality) and consumption by decomposers (Meentemeyer 1978, Aerts 1997, Cornwell et al. 2008, Makkonen et al. 2012). This strong dependence on (externally) environmentally imposed conditions makes decomposition (and hence ecosystem functioning) highly sensitive to changing environmental conditions, as demonstrated by model predictions of climate change effects on decomposition rates (Knorr et al. 2005, Bronson et al. 2008, Bond-Lamberty and Thomson 2010).

Macrodetritivores can strongly affect litter decomposition rates (Heemsbergen et al. 2004, Wall et al. 2008, Powers et al. 2009, Vos et al. 2011, Handa et al. 2014) through the consumption and digestion of dead organic

material. In addition, several groups of macrodetritivores, in contrast to bacteria and fungi, are capable of changing the local environmental conditions through biotic feedback mechanisms (Lavelle et al. 2006). Soil physical changes due to bioturbation, litter-soil mixing, grain size sorting or the formation of buffered environments within mounds by macrodetritivores (ecosystem engineering effects sensu Jones et al. [1994]) have been shown to stimulate litter decomposition and enhance nutrient cycling (Lavelle et al. 2007, Schrama et al. 2015). Ecosystem engineering effects may therefore loosen the connection between large-scale spatiotemporal climatic variability and decomposition due to improved local abiotic conditions for both microbes and macrodetritivores. Recent theoretical work (based on analysis of observed spatial patterns) indeed suggests that macrodetritivores, specifically termites, make dryland ecosystems robust to climate change (Bonachela et al. 2015). However, it is yet unclear how this "macrodetritivore-promoted robustness" holds across environmental conditions and across different functional groups, and whether it can be experimentally observed and tested.

Two contrasting hypotheses on how macrodetritivores can promote decomposition rates, when compared to microbes, are depicted in Fig. 1. Under the first hypothesis, macrodetritivore effects on decomposition may be subject to similar constraints as microbes, resulting in

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largest absolute effects under the most favorable environmental conditions (H1; Fig. 1A). Overall, the proportional effect of macrodetritivores on decomposition rates will then stay approximately constant across environmental conditions (H1; Fig. 1B). Under the second hypothesis, both absolute and proportional effect of macrodetritivores is largest under conditions unfavorable to microbes (H2; Fig. 1A, B). This is expected when macrodetritivores exert strong changes on local conditions, for example through the formations of biogenic structures, such as mounds that may act as "biological chemostats," incubators of microbial activity (Lavelle et al. 2006). Here, macrodetritivores buffer ecosystem decomposition towards spatiotemporal variability and monopolize the decomposition process under those conditions that are least favorable for microbial growth. Fungus-growing termites create such a buffered environment within their mound that is characterized by constant temperature and increased humidity, which enables the domestication of white rot fungi that live inside their nests. Therefore, through the environmental alteration by termites, their symbiotic fungi can remain active as decomposers when conditions outside the mound become unfavorable and therefore fungus-growing termites are able to outcompete free-living fungi in savanna environments (Aanen and Eggleton 2005). This is especially important in savanna ecosystems, that are known to have high spatiotemporal variability in rainfall, which has been identified as a key determinant of their structure and functioning (Olff et al. 2002, Sankaran et al. 2008, Davies et al. 2013b, Hempson et al. 2014).

We explored these alternative hypothesis by performing an experiment in which we separated the effects of two major groups of macrodetritivores on litter decomposition rates in an African savanna ecosystem: (1) fungus-growing termites with large elaborate nests (*Macrotermitinae*), and (2) non-fungus-growing macrodetritivores (earthworms, woodlice, millipedes, cockroaches, non-fungus growing termites), generally without extensive nest structures, and mostly interacting with free-living soil microbes. Most importantly, the first group cultivates basidiomycete fungi inside their nests in fungal gardens that have been suggested to function as "biological chemostats" (Rouland-Lefevre 2000) or "extended phenotypes" (Turner 2002).

METHODS

Study site

The study was conducted in Hluhluwe-iMfolozi Park (27.59°–28.26° S, 31.41°–32.09° E), a 900 km² game reserve in Kwa-Zulu Natal, South-Africa, from September 2013 to July 2014. The altitude of the park increases from 90 m a.s.l. in the south to 580 m a.s.l. in the north. Mean minimum temperature is 13°C (July) and mean maximum temperature is 35°C (January). Mean annual rainfall ranges from approximately 500 mm in the south to
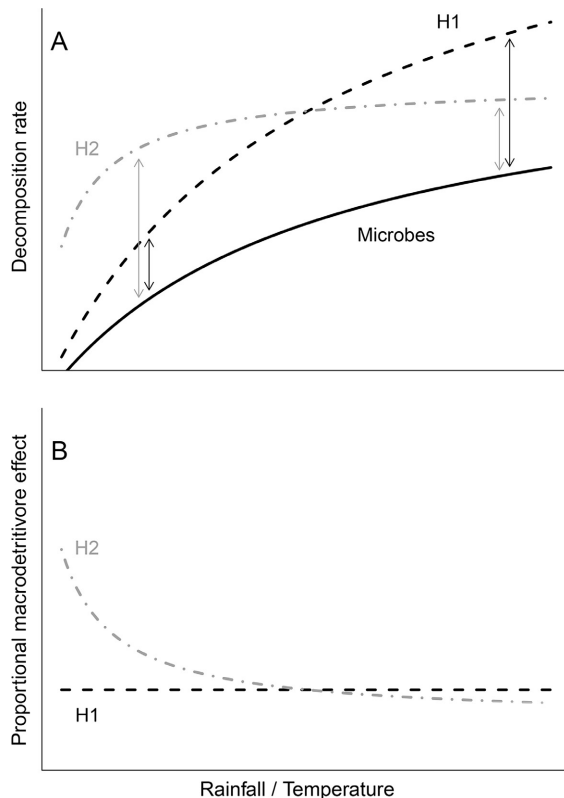

FIG. 1. Two alternative hypotheses on the effect of macrodetritivores on decomposition rates across environmental gradients of rainfall or temperature. H1: Macrodetritivores increase decomposition rates most compared to microbial decomposition under most favorable conditions resulting in the largest absolute "macrodetritivore effect" under higher rainfall and temperature conditions (A), but a constant proportional "macrodetritivore effect" (B) compared to microbial decomposition rates. H2: Absolute increase of decomposition by macrodetritivores is higher under more stressful conditions (i.e., lower temperature or rainfall) (A), which results in an exponential decrease of the proportional "macrodetritivore effect" (B) along the gradients (B).

900 mm in the north and is positively correlated with altitude (Balfour and Howison 2002). Most rain falls between October and March and is highly variable in both space and time (Bonnet et al. 2010). Vegetation structural types range from open grasslands to closed *Acacia* and broad-leaved woodlands (Whateley and Porter 1983).

We chose seven sites that span the rainfall gradient, but that were relatively similar in soil texture (median particle size: 0.05–0.15 mm), in order to avoid very clayey or sandy sites, that might affect macrodetritivore community composition and behavior. Rain gauges were installed at every site and emptied at least once every 2 weeks. A few ml of sunflower oil was poured into the rain gauge to prevent evaporation of collected rainwater. We used rain gauge data from nearby sites to fill gaps in rainfall data in those cases when rain gauges were destroyed by animals (elephants, monkeys) and subsequently installed new rain gauges at our sites.

Temperature

Data on daily mean temperatures (Sep 2013–July 2014) were obtained from the National Oceanic and Atmospheric Administration (NOAA, http://www.ncdc.noaa.gov/). The closest daily temperature measurements within our study period were available from the weather station at Charters Creek, SA (located −28.20° S, 32.42° E, ca. 30 km from our study area). We then obtained climate data layers from the WorldClim program (available from http://www.worldclim.org) generated through high resolution (1 km) spatial interpolation of average monthly data on mean temperature between 1960–90 (Hijmans et al. 2005) and extracted mean monthly temperatures for each of our seven sites and Charters Creek using ArcGIS Desktop 10.2 (ESRI 2011). For each site a linear model was constructed for mean monthly temperature as a function of mean monthly temperature in Charters Creek and proved highly accurate, with R^2 >0.99 obtained for all sites. Subsequently, these models were used to calculate the mean temperatures on a daily basis for all seven sites based on the daily measurements obtained from Charters Creek. Mean temperatures per time interval were then calculated per site and used for subsequent analyses.

Experimental design

At each site, we installed three decomposition station replicates with three different substrates (litter, dung, straw) in three vegetation structural types (lawn grass, bunch grass, shrub) ($3 \times 3 \times 3 = 27$ stations per site). One site only had two vegetation types present yielding a total of 180 ($27 \times 7 − 9$) decomposition stations. Decomposition was measured on approximately monthly intervals (32 ± 5.6 d) after which stations were emptied and refilled with new substrate for a subsequent measurement. This was repeated eight (litter and dung) and six (straw) times on all sites to cover the full growing season and start of the dry season, yielding decomposition measurements across a large variation in rainfall and temperature in both space and time, yielding a total of $180 \times 8 − 120 = 1,320$ stations.

Vegetation structural types

Decomposition stations were placed in lawn grass vegetation, bunch grass vegetation, and underneath shrubs to investigate the effect of microclimate. In general, lawn areas are driest and warmest, while microclimates below shrub are relatively wet and cool (Holdo and Mack 2014, Veldhuis et al. 2014).

Substrate

We explored the importance of substrate quality for decomposition rates by comparing three different substrate types. We used two substrates with constant quality: white rhino dung (high litter quality; C:N ratio = 23.6) and straw (low litter quality; C:N ratio = 38.7). As a third substrate we used litter originating from the site itself (dead grass/leaves collected from the topsoil), which therefore had variable quality both in space and time and represented the actual substrate for decomposition at that site and moment (variable quality; C:N ratio = 31.2 [±8.9]). Carbon (%C) and nitrogen (%N) content of substrates were estimated using a Bruker near-infrared spectrophotometer (NIR, Ettlingen, Germany) using a multivariate calibration of samples measured both on the NIR and CHNS EA1110 elemental analyzer (Carlo-Erba Instruments, Milan, Italy). Cross-validation showed these NIR predicted C and N contents to be highly accurate (R^2 = 92.9 for C, R^2 = 95.7 for N, N = 1,759).

Decomposition stations

Decomposition stations consisted of 10 cm diameter × 5 cm height, white PVC pipe segments. They were secured in place with a U-shape metal wire pushed into the soil at two sides (Appendix S1: Fig. S1). Decomposition stations had a 1.4 mm mesh cover to prevent litter falling in from above, while the bottom was open to allow macrodetritivores to enter the stations from below. Also, four additional 2 cm holes at ground level allowed macrodetritivores to enter the stations from aside. Stations were placed on bare patches in between vegetation after removal of all loose litter on the soil. We designed this method, instead of using the more standard litter bag approach, to prevent compaction of the substrate which potentially can increase water content and, subsequently, substrate mass loss. Furthermore, as the effect of macrodetritivores on changing local conditions is expected to increase with body size, we wanted to include the effect of larger sized macrodetritivores (body size >5 mm), but at the same time reduce the chance of loss of substrate due to physical transport (wind, water, large animals). The compacted, smooth nature of the soil in this savanna facilitated this approach, because it was easy to remove the natural litter layer and prevented mixing of experimental litter with natural litter. This allowed the collection of only experimental litter remaining after the monthly intervals.

Every station was filled with 5 g (±0.01 g) of dried (48 h at 70°C) substrate at the start of each measurement interval. Furthermore, a control treatment excluding large macrodetritivores (allowing only decomposition by microbes and smaller soil fauna) was placed within each station consisting of 10 × 3 cm double layered metallic litter bags (mesh size: 1 mm) containing 1 gram (±0.001 g) of the same substrate. We chose the mesh size of 1 mm (which is relatively large) because we were especially interested in the effect of the largest macrodetritivores (large termites, earthworms, woodlice, millipedes, cockroaches). Smaller mesh sizes increased the risk of creating a different microclimate, with increased moisture, which could affect the results. Furthermore, the material inside

these control bags was packed loosely to further reduce the risk of altered microclimate. Nevertheless, there will always be a small effect of such mesh. If so, it would most likely result in higher moisture inside control bags which would result in a type II error and therefore only reduce the effect size measured. It is therefore unlikely that the effect found in this study can be attributed to altered microclimate inside the control bags. Smaller species (colleboles, small soil-dwelling termites, protists) where therefore lumped in a category of microdetritivores. After ca. 32 d (±5.6 d), the remaining substrate was collected, oven dried (48 h at 70°C) and weighed. Then it was ashed (4 h at 550°C), to account for the possible collection of soil during the incubation or collection of the samples. Difference in weight before and after ashing was taken as a measure for remaining substrate mass at the end of the experiment.

Macrodetritivore effects

Distinction between the effects of the two groups of macrodetritivores, i.e., large fungus-growing termites (LFT) and other large macrodetritivores (OLM: earthworms, millipedes, woodlice, cockroaches, non-fungus-growing termites) was based on incidence (yes/no) of sheeting inside each decomposition station (Ndiaye et al. 2004). Fungus-growing termites typically construct runways and galleries and cover organic material with mineral particles (sheeting) to protect themselves against sun, as they lack pigmentation, and predation (Wood and Sands 1978). Nevertheless, this is an indirect method and some other (less abundant) groups of termites can also produce sheeting. However, fungus-growing termites have been shown to be the dominant termite group (ca. 77%) in the study system (Davies et al. 2013a). Therefore, we are confident that the effects found in this study can primarily be attributed to fungus-growing termites. Decomposition in non-sheeted stations was attributed to the OLM group. Mass loss inside control bags was allocated to decomposition by microdetritivores (everything smaller than 1 mm). Control bags with signs of sheeting were removed from analyses to reduce the possible influence of very small fungus-growing termites entering control bags.

In total we set out 1320 decomposition stations on seven sites along a rainfall gradient (500–900 mm yr^{-1}) throughout eight 1-month intervals spanning an 11-month period (September–July). 112 (8.4%) decomposition stations were damaged by the abundant large mammals in the ecosystem (as white rhino, elephant) during the study. Altogether, this yielded a relatively large experimental dataset (N = 2416 [stations + control bags]) to investigate the separate impacts of microbes + small soil fauna (microdetritivores), non-fungus-growing macrodetritivores (OLM) and fungus-growing termites (LFT) on decomposition rates for different substrate types, microclimates and a wide range of macroclimatic conditions.

Data analysis

Linear mixed effect models (LMM) were constructed with percentage mass loss as response variable within the "nlme" R package (Pinheiro et al. 2014). The percentage mass loss was arcsine square-root transformed prior to analyses to approach normal distributions. Due to spatial pseudoreplication within sites and control bags within decomposition stations, we used station ID nested within site as random variables. Explanatory variables were monthly rainfall, mean temperature, vegetation type (three levels, i.e. lawn, bunch, shrub), C:N ratio and detritivore group (three levels, i.e. microdetritivores, OLM, LFT). Quadratic terms were added for the explanatory variables monthly rainfall and mean monthly temperature, since we hypothesized that climatic effects had an optimum (Fig. 1A). Conditional and marginal R^2 for the mixed models were calculated following Johnson (2014). Assumptions of normality and equal variances were visually investigated by residual plots, with no apparent violations.

To investigate incidence of termite attack (sheeting) across gradients of monthly rainfall and temperature, we used generalized linear models (GLM) with a binomial probability distribution to deal with the binary response variable (i.e. logistic regression). For visual representation and further analyses, we divided our two main continuous explanatory variables (rainfall and temperature) into equal intervals based on visual inspection of histograms to obtain categories without low sample sizes (Appendix S1: Fig. S2). Minimum number of stations were 42 (mean temperature) and 59 (monthly rainfall) per category. Proportional macrodetritivore effect for each category was calculated as decomposition rates including macrodetritivores (OLM or LFT) divided by decomposition of microdetritivores only.

Subsequently, we used these same categories to determine the relative impact of both macrodetritivore groups on decomposition rates over gradients of monthly rainfall and mean monthly temperature. Impact of fungus-growing termites was calculated as the absolute difference between decomposition by LFT and decomposition by microdetritivores (representing effect size) multiplied by the incidence of termite attack (representing the probability of that effect to occur). For non-fungus-growing macrodetritivores it simply represents the absolute difference between decomposition by OLM and decomposition by microdetritivores (occurrence = 1, as we assume they were always present). These impacts of LFT and OLM on decomposition rates were then rescaled by setting the maximum to 1 and scaling the rest appropriately to obtain a relative impact of both macrodetritivore groups. We believe this is more informative than the absolute impact, because the latter is highly dependent on length of incubation, with increased probabilities of "termite attack" with longer periods, resulting in shifts in importance between fungus-growing termites and other macrodetritivores. Therefore, changing incubation times

will have a large effect on the absolute impact, while the relative effect is expected to be more robust. All statistical analyses were executed in R 3.1.2 (R Core Team 2016).

RESULTS

Three hundred and ninety eight of the 1208 intact stations showed signs of presence of fungus-growing termites (sheeting, 32.9%). All explanatory variables and most interactions significantly affected decomposition rates (Appendix S1: Table S1) and explained ca. 60% of the variation in mass loss (LMM: Marg. $R^2 = 0.57$, Cond. $R^2 = 0.60$). We therefore decided to include only the three most important predictors (highest F-values, Appendix S1: Table S1) in the further analyses: monthly rainfall ($F_{1,1807} = 1,229.6$), mean monthly temperature ($F_{1,1807} = 146.9$) and detritivore group ($F_{2,1807} = 367.2$). Removing all other variables from the LMM's only resulted in a decrease in conditional R^2 from 0.60 to 0.59, justifying their removal (LMM: Marg. $R^2 = 0.53$, Cond. $R^2 = 0.59$).

Decomposition by microdetritivores overall increased with both monthly rainfall (LMM: df = 631, $t = 12.2$, $P < 0.001$; Fig. 2A) and mean monthly temperature ($t = 6.01$, $P < 0.001$; Fig. 3A). In addition to this overall trend, the increase to some extent peaked at intermediate values of rainfall and leveled off toward higher mean temperatures (Figs. 2A and 3A), statistically supported by negative quadratic terms for both monthly rainfall ($t = -7.86$, $P < 0.001$) and mean monthly temperature ($t = -5.46$, $P < 0.001$).

Both macrodetritivores functional groups significantly increased decomposition rates, with on average 34% for OLM (LMM: df = 1840, $t = 9.03$, $P < 0.001$) and 123% for LFT ($t = 24.70$, $P < 0.001$; Fig. 2). However, the effect sizes differed across gradients of both rainfall and temperature (Figs. 2 and 3; Appendix S1: Figs. S3 and S4).

For OLM, absolute differences in decomposition rates compared to microdetritivores only increased with rainfall resulting in a significant positive interaction term (LMM: df = 1718, $t = 2.18$, $P < 0.05$), except for very high amounts of monthly rainfall (>120 mm) where their effect again decreased (Fig. 2A). Consequently, the proportional effect relative to decomposition rates without macrodetritivores remained constant with rainfall for OLM (LM: $F_{1,5} = 5.34$, $P = 0.07$; Fig. 2B). By contrast, absolute differences between LFT and decomposition by microdetritivores decreased with rainfall ($t = -2.39$, $P < 0.05$; Fig. 2A), resulting in a logarithmically decreasing proportional macrodetritivore effect for fungus-growing termites (LM: $F_{1,5} = 106.7$, $P < 0.001$, $R^2 = 0.95$; Fig. 2B).

In response to temperature, absolute differences in decomposition rates between OLM and decomposition by microdetritivores also increased (LMM: df = 1836, $t = 3.18$, $P < 0.01$; Fig. 3A). Not surprisingly, we therefore found no change in proportional macrodetritivore effect with temperature for OLM (LM: $F_{1,3} = 0.19$, $P = 0.69$; Fig. 3B). However, we found no significant LFT ×

temperature interaction ($t = 0.45$, $P = 0.65$), indicating that the absolute increase in decomposition rate by large fungus-growing termites compared to microdetritivores did not vary with study interval temperature. The proportional macrodetritivore effect of LFT decreased exponentially with temperature, but was just significant (LM: $F_{1,3} = 9.52$, $P = 0.05$, $R^2 = 0.76$; Fig. 3B).

Incidence of termite sheeting (overall ca. 32,9% of the stations) peaked around 60 mm rainfall month^{-1} and decreased towards both higher and lower amounts of rainfall (GLM: $X^2 = 31.2$, df = 2, $P < 0.001$; Fig. 4A). Furthermore, we found the proportion of sheeted stations to increase with temperature (GLM: $X^2 = 87.7$, df = 1, $P < 0.001$; Fig. 4B). When we combined these data with the absolute effects of LFT and OLM on decomposition, we found that the relative impact of LFT was highest between 40–60 mm rainfall month^{-1} whereas the relative impact of OLM peaked between 80–120 mm rainfall (Fig. 5A). Furthermore, relative impact on decomposition rates of both functional groups of macrodetritivores increased with temperature (Fig. 5B).

DISCUSSION

The main objective of this study was to test alternative hypotheses on the impact of different macrodetritivore functional groups on decomposition rates of different substrate types and microclimate under a wide range of spatiotemporal variability in rainfall and temperature (Fig. 1). Non-fungus-growing macrodetritivores increased decomposition rates by ca. 31% and this proportional effect did not vary with rainfall or temperature (H1 in Fig. 1). Thus, they strongly increased decomposition rates under optimal environmental conditions for decomposition by microbes and small soil fauna, whereas limited effects were found where temperature or moisture decreases activity of microbes and small soil fauna. By contrast, fungus-growing termites showed the opposite pattern, increasing decomposition most under water-limited conditions (both in absolute and proportional effect), thus stabilizing ecosystem processes by decoupling decomposition rates from spatiotemporal variability in rainfall (H2 in Fig. 1). However, the overall impact of termites (and their activity) on decomposition showed an optimum between 40–60 mm rainfall month^{-1} and decreased towards both drier and wetter conditions, indicating a limit of their buffering capacity. Although the proportional effect of large fungus-growing termites on decomposition rates was also increased at low temperatures, their decreased activity made their overall impact on decomposition rates under decreased temperatures negligible.

The experimental design of our study relied on the natural colonization of the decomposition stations by fungus growing termites and other large macrodetritivores that could only indirectly be observed through the presence of sheeting. Ideally, access of these two groups of
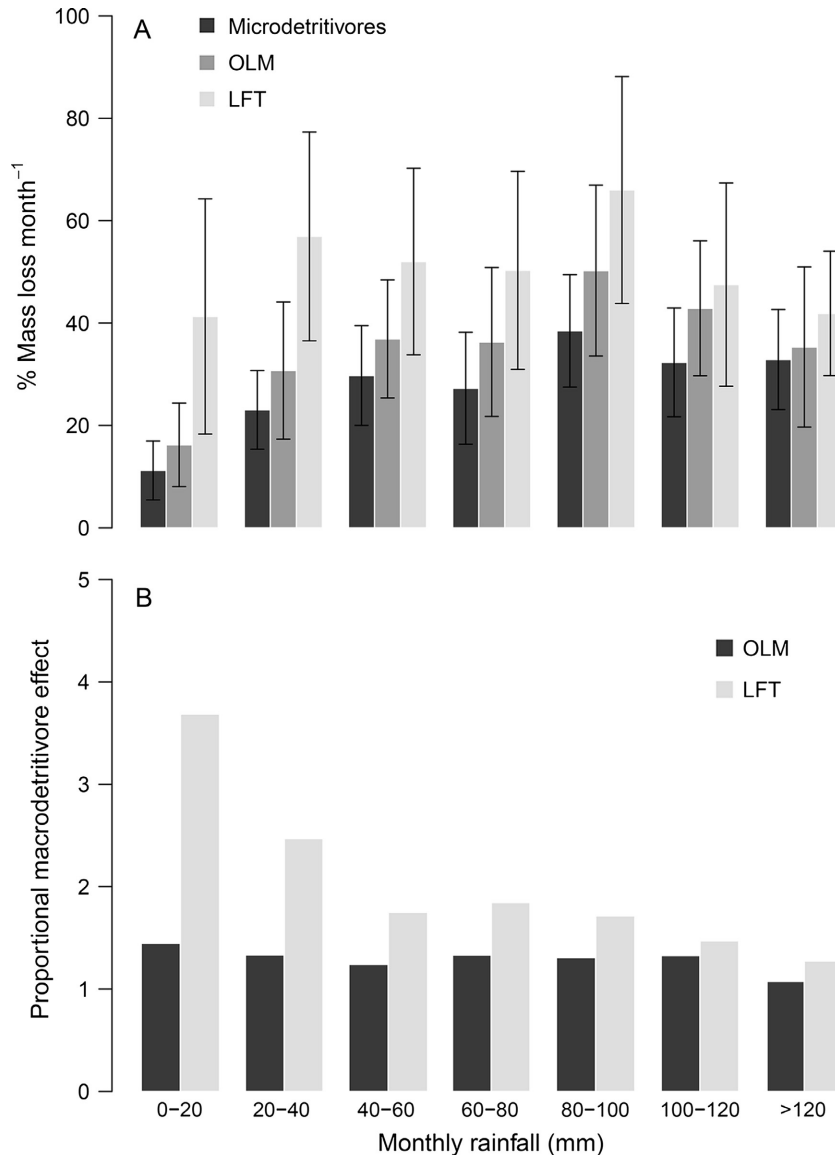
FIG. 2. (A) Monthly decomposition rates across a gradient of monthly rainfall for microbes and small soil fauna (microdetritivores), non-fungus-growing macrodetritivores (OLM) and large fungus-growing termites (LFT). Error bars indicate standard deviations. (B) Proportional "macrodetritivore effect" (relative to decomposition by microbes and small soil fauna) for large fungus-growing termites (LFT) and other macrodetritivores (OLM) over a gradient of monthly rainfall. A proportional "macrodetritivore effect" of 1 indicates no effect, >1 indicates increased decomposition and <1 indicates decreased decomposition.

macrodetritivores should have been controlled experimentally, but this is practically impossible in the field. Therefore, our study provides a best possible approach to study the effects of fungus-growing termites on savanna decomposition.

Our results on the decomposition rates of microdetritivores generally followed predictions from global decomposition studies (Meentemeyer 1978, Berg et al. 1993, Aerts 1997, Cornwell et al. 2008, Makkonen et al. 2012), with faster decomposition towards higher rainfall and temperatures. A notable exception to generally accepted patterns, however, is the relatively small observed effect of litter quality (i.e. F-value of C:N ratio was relatively small [Appendix S1: Figs. S3 and S4]) on decomposition rates. Perhaps, other litter quality traits, as concentrations of polyphenols, tannins or magnesium, would have shown stronger effects (Hättenschwiler and Vitousek 2000, Makkonen et al. 2012). Nevertheless, other recent studies on decomposition rates across climatic gradients in African savannas, using different quality indices, also did not find clear effects of substrate quality (Tian et al. 2007, Davies et al. 2013b). Possibly, low litter quality may be less limiting for microbial decomposition in warm tropical climates than in
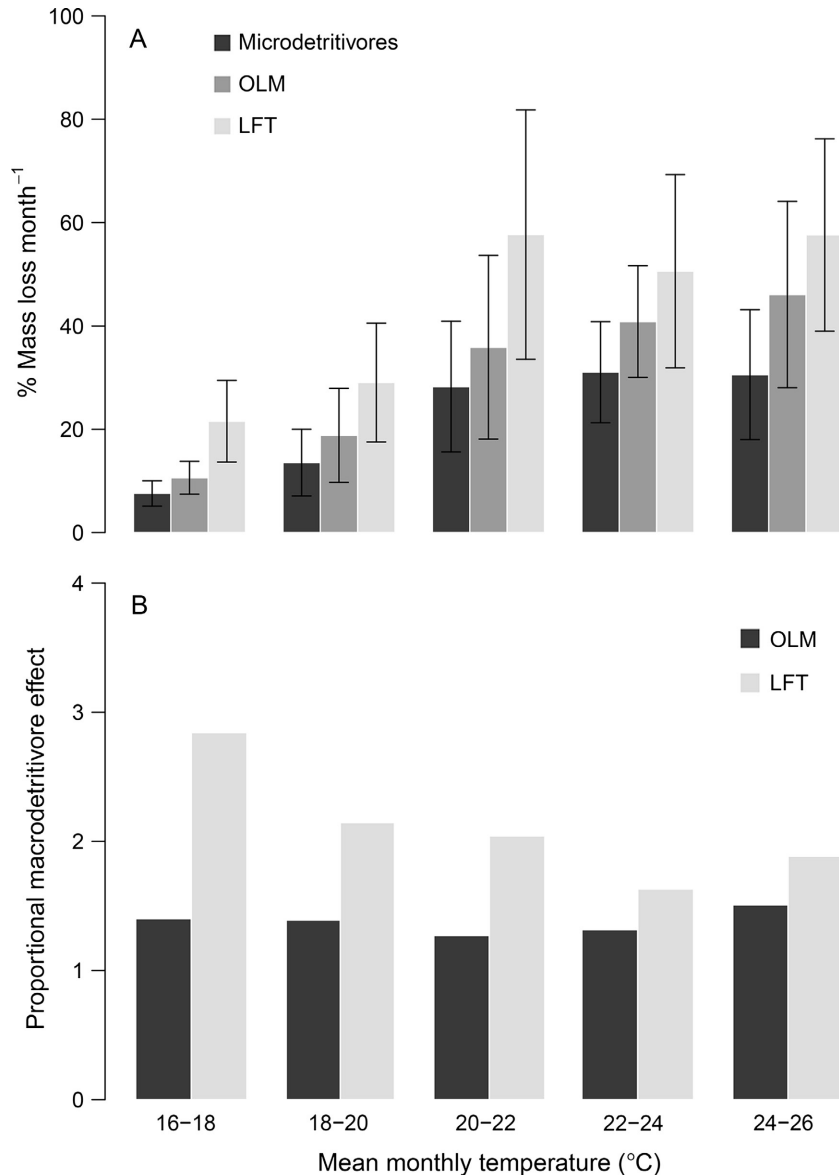
Fig. 3. (A) Monthly decomposition rates across a gradient of mean monthly temperature for microbes and small soil fauna (microdetritivores), non-fungus-growing macrodetritivores (OLM) and large fungus-growing termites (LFT). Error bars indicate standard deviations. (B) Proportional "macrodetritivore effect" (relative to decomposition by microbes and small soil fauna) for large fungus-growing termites (LFT) and other macrodetritivores (OLM) over a gradient of mean monthly temperature. A proportional "macrodetritivore effect" of 1 indicates no effect, >1 indicates increased decomposition and <1 indicates decreased decomposition in the presence of macrodetritivores compared to decomposition by microbes and small soil fauna.

temperate or arctic conditions. Alternatively, the importance of fire as a non-selective consumer in these ecosystems (Bond and Keeley 2005) increases the relative costs of secondary metabolite production in comparison to other ecosystems. In ecosystems where fire is scarce or absent, the production of secondary metabolites can be a viable strategy, as the investment of these molecules might be offset by a smaller loss of tissue to herbivory. However, the constant risk of losing these costly molecules due to burning favors alternative herbivore response strategies, like structural defenses (Wigley et al. 2015), or

strong regrowth capacity (Scogings et al. 2004), secondarily increasing litter quality for decomposition.

Non-fungus-growing macrodetritivores increased decomposition rates by 34% on average relative to free-living microbes. Recent global experiments found similar trends, with increased decomposition in wet and warm climates, but neutral effects of soil fauna when temperature or moisture conditions constrain biological activity (Wall et al. 2008), with largest positive effects of macrodetritivores in temperate and tropical biomes (Makkonen et al. 2012). These ectothermic invertebrate
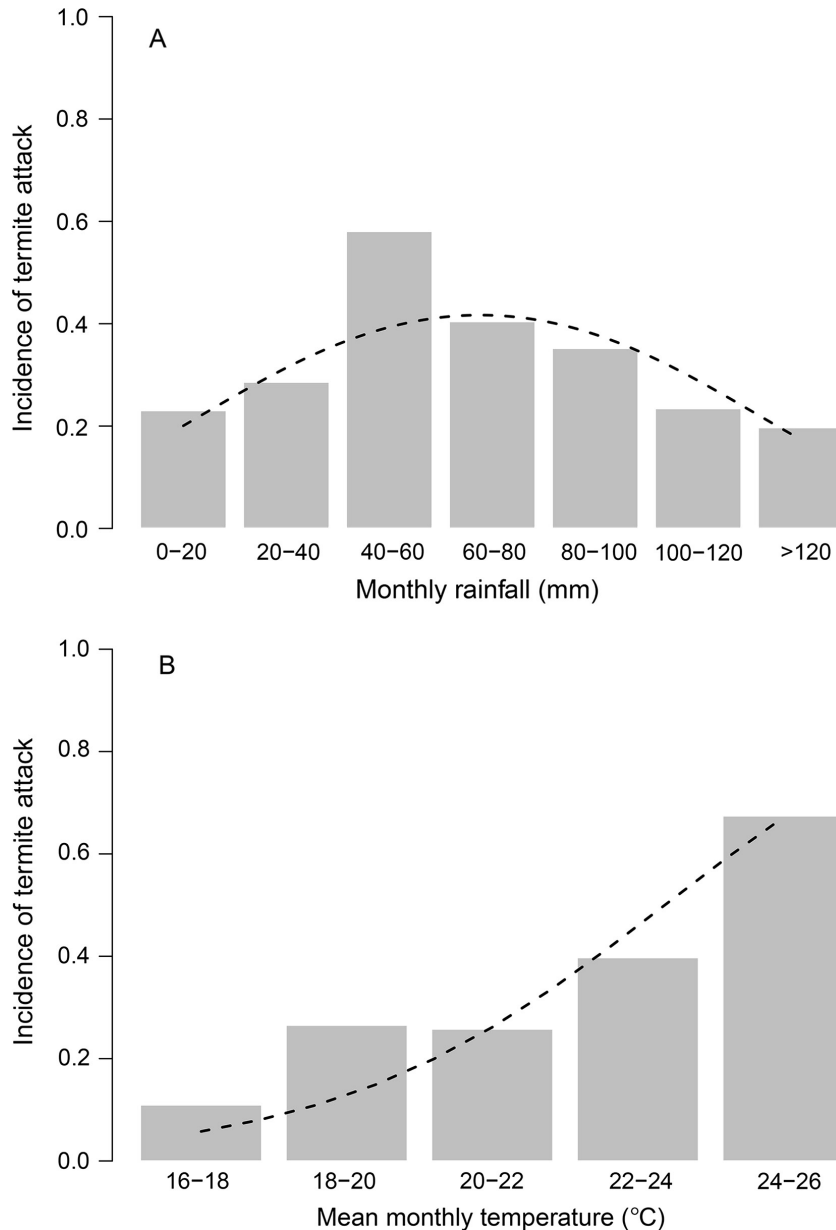
Fig. 4. Incidence of termite attack (sheeting) of the decomposition stations over gradients of monthly rainfall (A) and mean monthly temperature (B), at a particular site at a particular time. Dashed lines represent logistic regression lines based on 1208 stations (32.9% sheeted).

decomposers are sensitive to water- and temperature-limited conditions (Curry 2004, Hornung 2011), which explain their increased effects on decomposition across gradients of rainfall and temperature.

Large fungus-growing termites, on the other hand, increased decomposition rates relative to free-living microbes and small soil fauna most strongly under water-limited conditions, both in a relative and absolute manner, following Hypothesis 2 (Fig. 1). Their elaborate nests likely provide a physiological steady state with constant temperatures (ca. 30°C) and severely increased

moisture levels (ca. 100%) (Darlington et al. 1997, Korb 2003), that are ideal conditions for their fungal symbionts (Aanen and Eggleton 2005). By returning the substrates to their mounds, instead of locally decomposing the dead organic matter, they decouple the litter decomposition process from local environmental conditions at which the litter is produced. Therefore, in contrast to other macrodetritivores, fungus-growing termites may be viewed as "extended phenotype engineers" (Jones et al. 1994, Turner 2002, Jouquet et al. 2006), through creating a buffered environment within their extended phenotype
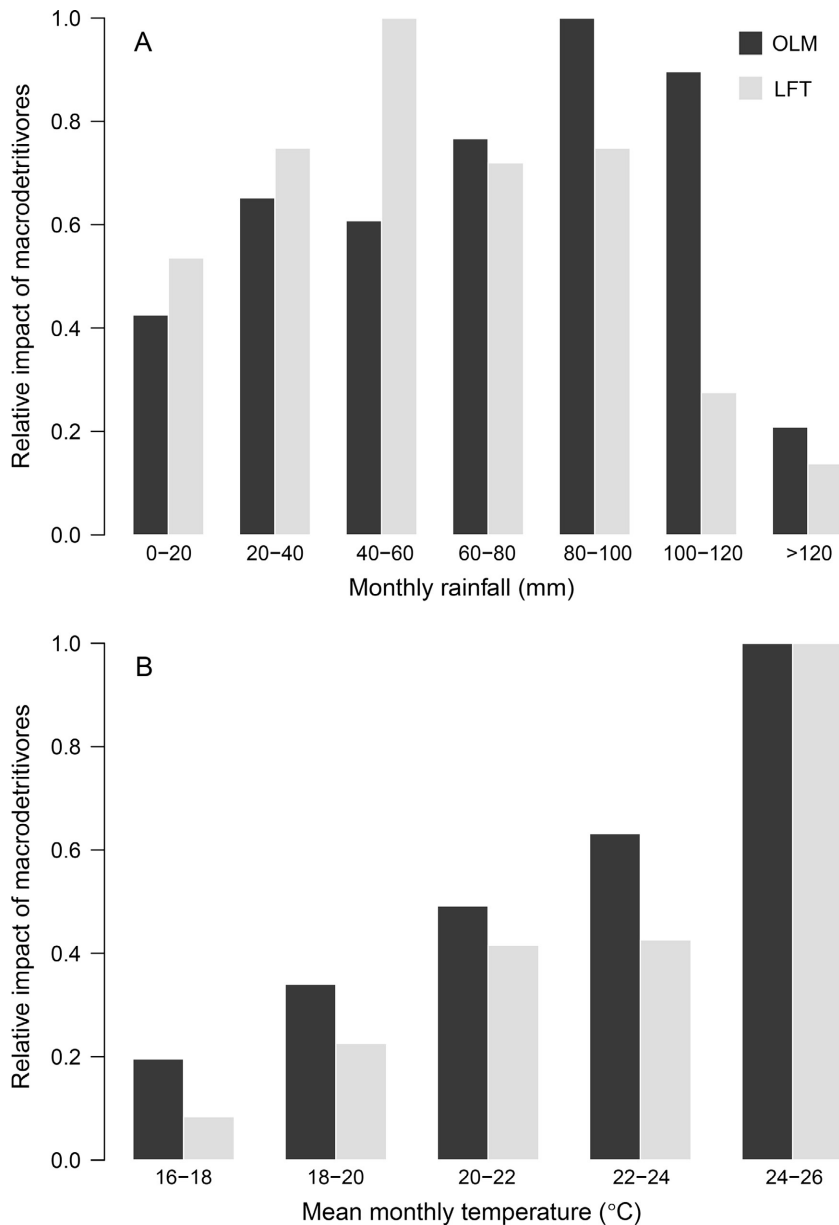
FIG. 5. Relative impact of non-fungus-growing macrodetritivores (OLM) and large fungus-growing termites (LFT) over gradients of monthly rainfall (A) and mean monthly temperature (B). Relative impact for termites is calculated as the absolute difference between termite decomposition and decomposition by microbes and small soil fauna multiplied by the incidence of termite attack (Fig. 4). For other macrodetritivores it represents the absolute difference between non-fungus-growing macrodetritivore decomposition and decomposition by microbes and small soil fauna. Both are rescaled by setting the maximum to 1 and scaling the rest appropriately.

(mounds), that allows decomposition to continue when abiotic conditions outside are less favorable (ecosystem engineering).

The relative impact of both groups of macrodetritivores changed across the rainfall gradient, with increased impact of fungus-growing termites towards drier conditions and larger effect of non-fungus-growing macrodetritivores under higher rainfall. This suggests niche segregation between fungus-growing termites and other

macrodetritivores and free-living fungi (Aanen and Eggleton 2005) and is supported by the inverse correlation between termite (dry) and earthworm (moist) biomass found in a global comparative study (Fragoso and Lavelle 1992). Therefore, decomposition rates in savanna ecosystems do not slow down with decreasing rainfall, temperature or both, as is often assumed in models predicting climate change effects on decomposition (Knorr et al. 2005, Bronson et al. 2008, Bond-Lamberty and Thomson

2010). Instead, due to the biotic engineering of termites in savanna ecosystems through their mound-building activities, decomposition rates are hardly affected by decreasing rainfall until a certain threshold (ca. 40 mm month^{-1}), after which it collapses.

Altogether our study provides empirical evidence that fungus-growing termites can increase the resistance of decomposition in dryland ecosystems under high spatio-temporal variability in rainfall, supporting recent theoretical investigations (Bonachela et al. 2015).

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SUPPORTING INFORMATION