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Teatime for termites: Understanding the impact of human land-use and climate on termite and microbial litter decomposition

Master's thesis in Biology

Supervisor: Bente Jessen Graae, Stuart Smith, James D. M. Speed

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Photo: Per Harald Olsen

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1 Abstrakt

Nedbrytning av planter er en fundamental underliggende prosess for næringscyklus og økosystemproduktivitet. Nedbrytningshastigheten i savanneøkosystemene er avhengige av både jordmikrober og makrofauna, hvor termitter er kjent for å være viktige. Det er imidlertid lite kjent om hvordan balansen mellom disse nedbryterne påvirkes av et økende landskap dominert av mennesker. Her tar vi tak i dette kunnskapshullet ved å undersøke mikrober og termitters bidrag til nedbrytningsprosessen over tre savannelandbruk: landbruks-, kvegbbruks- og Villmark-forvaltet område i og utenfor Serengeti Nasjonal Park, Tanzania. Vi brukte en selektiv nett-metode til å sammenligne effekten av mikrobiell og termitt-drevet nedbrytning ved å bruke globalt standardiserte substrater: lett nedbrytbart grønn te og sakte nedbrytbart rooibos te, også kjent som Tea Bag Index. Teposene ble begravet i de forskjellige landbruks områdene i to ulike regnregioner i løpet av regn- og tørkesesongen. I tillegg etablerte vi en «common garden» for å vurdere hvordan jordforholdene påvirker nedbrytningen på tvers av landbruk og regnregimer. Vi fant ut at mikrober bryter ned den lett nedbrytbare grønne teen i langt høyere grad i den våte sesongen og i den våtregionen. I tillegg har termitter og andre makrofauna liten eller ingen innvirkning av denne teen. I motsetning til dette ble nedbrytningen av rooibos te sterkt påvirket av termitter, særlig resulterte dette i høyere nedbrytningsrate i tørr sesong og i tørre områder enn mikrobers' nedbryting av grønn te. Bidraget fra termitter og annen makrofauna var størst i landbruks- og kvegområder sammenlignet med Villmark-forvaltet område iløpet av tørkesesongen. Ved å bruke «common garden» fant vi ingen påvirkning av jordegenskaper på nedbrytning. Disse funnene illustrerer betydningen av termitter for en kontinuerlig næringscyklus i tørre savannemiljøer.

1 Abstract

Plant litter decomposition is a fundamental process underlying nutrient cycling and ecosystem productivity. Rates of decomposition in savannah ecosystems are dependent on both soil microbes and macrofauna, where termites are known to be important. However, little is known about how the balance between these decomposers is influenced by an increasing human dominated landscape. Here, we address this knowledge gap by investigating the contribution of microbes and termites to litter decomposition across three savannah land-uses: agricultural, pastoral and wildlife protected areas in and around the Serengeti National Park, Tanzania. We used a selective mesh approach to contrast the impact of microbial and termite driven decomposition on a global standard litter types: labile green tea and recalcitrant rooibos tea, also known as the Tea Bag Index. Teabags were buried across the different land-uses in two contrasting rainfall regions and during both wet and dry seasons. Additionally, we established a common garden to assess how soil conditions influence the decomposition across land-uses and rainfall regimes. Overall, we found that microbes decompose the labile green tea to a far higher degree in the wet season and wet region, and that termites and other macrofauna have little to no impact of labile litter decomposition. In contrast, the decomposition of the recalcitrant rooibos tea was strongly influenced by termites, in particular resulting in higher rates of decomposition in dry season and dry regions than microbial labile litter decomposition. Importantly, the contribution of termites and macrofauna was greatest in agricultural and pastoral areas compared to wildlife protected areas during dry season. Through the use of the common garden we found no influence of soil properties on decomposition. These findings illustrate the importance of termites for the continuous nutrient cycling during dryer savannah conditions with an previously undervalued importance of macrofauna on human modified savannah landscapes.

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1 Introduction

Plant litter decomposition is a fundamental process underlying nutrient cycling and ecosystem productivity (Van Der Heijden et al., 2008; Bardgett & van der Putten, 2014). This process is mainly driven by climate, soil properties, litter quality and the soil fauna (Couteaux et al., 1995; Aerts, 1997; Bardgett, 2005). Increasing anthropogenic activities severely alters ecosystems and cause changes in climate patterns. Further, land-use changes can drastically alter plant and soil communities which in turn affects the plant litter decomposition process (de Vries et al., 2013; García-Palacios et al., 2013; Fanin & Bertrand, 2016) Therefore it is crucial to understand how the decomposition process are affected by these changes.

Most decomposition studies have been carried out in temperate ecosystems in strong comparison to tropical ecosystems (Djukic et al., 2018). In tropical ecosystems, litter quality and moisture are the most important drivers for litter decomposition (Couteaux et al., 1995). In dry tropical ecosystems, such as savannahs, litter removal are mediated by fire, microbes and macro-invertebrates (Cornwell et al., 2008). These factors are influenced by the variable rainfall both spatially and temporally with pronounced wet and dry seasons (Frost et al., 1986). The litter decomposition is highly determined by these climate patterns. Where decomposition increases during wet seasons and soil moisture becomes limiting during the dry seasons (Ruess & Seagle, 1994)

Soil macro-invertebrates such as earthworms, termites and litter-feeding arthropods also takes a major part in the soil decomposition process (Lavelle et al., 1997). In humid savannahs earthworms have been estimated to decompose up to 30% of the annual litter production and termites may reach up to 20% of annual litter (Lavelle et al., 1997). In African savannahs, termites are a highly important as a dominant decomposer (Collins, 1981; Freymann et al., 2008). Termite-driven decomposition can be a soil-feeding, grass-feeding or wood-feeding process where they process digested litter with help from a symbiosis with gut bacteria (Brauman et al., 2000). Alternatively, they can indirectly decompose litter by cultivation of fungi within their mounds (Breznak & Brune, 1994). These fungus-growing termites (family: *Macrotermitinae*) creates a heterogenous savannah landscape due to their foraging behaviour. They translocate soil particles and concentrates clay particles and nutrients into their mounds (C. Jones et al., 1994). This behavior creates nutrient islands which are favorable soil conditions for plant growth and microbial activity (Sileshi et al., 2010).

Fungus-growing termites are the most dominant termite group in African savannahs (Buxton, 1981; Collins, 1981). This is largely due to the climatic stable mound throughout rainfall seasons, as they are dependent on their fungi association (T. Wood, 1988). These mound-properties benefits fungus-growing termites in terms of continuous foraging even in dry conditions (Schuurman, 2005; M. Veldhuis et al., 2017). This is in strong contrast to microbes' ability, which are strongly limited by soil moisture (Couteaux et al., 1995). Yet, studies report that termites are sensitive to both temperature and moisture (Houseman & Gold, 2003; Cornelius & Osbrink, 2010). Therefore, we would expect termite-driven decomposition to be influenced by temporal and spatial climate in savannah ecosystems. Studies using wood and paper litter indicate that termite forage activities are higher during the wet seasons in both African and Australian savannahs (Buxton, 1981; Dawes-Gromadzki & Spain, 2003). Yet, others report higher activities in dry African savannah conditions (Schuurman, 2005; M. Veldhuis et al., 2017). These mixed results seem attributed to the abundance of different termite functional groups in the context of each savannah habitat. For example Buxton et al (1981) reported that non-fungus growing termites was abundant and they increased forage activities as these savannahs receive large amount of rainfall (Buxton, 1981). It was also observed that the number of fungus-growers species decreased with higher rainfall. While Veldhuis et al (2017) conducted their study in a drier savannahs in South Africa which are often dominated by fungus-growing termites and resulted in an increased termite-driven decomposition during dryer conditions (Schuurman, 2005; M. Veldhuis et al., 2017). With such mixed results this indicates a need for more research on spatio-temporal climate effects to increase our understanding of climatic drivers on the termite activity.

Increasing human land-use is a major threat to soil biodiversity and ecosystem function. Protected wildlife areas across Africa are greatly influenced by the increasing human population growth (Joppa et al., 2008; Wittemyer et al., 2008). The Serengeti savannah ecosystem in Tanzania are no exception. Increasing livestock grazing in pastures and agricultural cropland are having a major influence on the savannah wildlife (M. P. Veldhuis et al., 2019). Which in turn results in changes in the soil community and nutrient cycling (de Vries et al., 2013; Fanin & Bertrand, 2016; G. Kagezi et al., 2016).

Livestock grazing can affect termites negatively through factors such as physical damage to mounds and increased bare-soil by trampling and overgrazing. Which in turn may reduce available food resources, especially vital for grass-feeding termites (Traoré & Lepage, 2008; Seymour et al., 2010; Mugerwa et al., 2011). However, livestock grazing may also lead to

positively effects. Where Hagan et al (2017) reported an increased mound density with livestock grazing. This could be attributed to an increase litter input since many termite species readily utilize dung as a food source (Freyman et al., 2008).

Studies on the impact of human land-use have shown that termite diversity decreases with less woodland cover (Eggleton et al., 2002; D. Jones et al., 2003). Studies have found that agricultural intensification decreases termite diversity (Kooyman & Onck, 1987; Okwakol, 2000; Coulibaly et al., 2013), while studies on livestock grazing have shown to either decrease (Tracy et al., 1998; Vasconcellos et al., 2010) or increase termite activity (Hagan et al., 2017). Such discrepancy could be due to that some termite families, such as fungus-growers, show more resiliency to light and moderate disturbance (Eggleton et al., 2002; Leitner et al., 2018). Therefore, it is important to understand the implications land-use changes exert on the regulation of litter decomposition and sustained nutrient cycling.

1.1 Teabag Index

The usage of litterbags to study decomposition and nutrient cycling has been an well-established procedure (Kampichler & Bruckner, 2009). However, many studies use different litterbag methods, which may induce non-comparable results (Makkonen et al., 2012) Therefore, a growing need of a standardized litterbag method has been required to compare litter decomposition across ecosystems (Didion et al., 2016). The Teabag Index (TBI) approach presented by Keuskamp et al. have sought to remedy this problem (Keuskamp et al., 2013). This approach is not only standardized, but also a cost-effective method using two contrasting litter types (Lipton green tea and Lipton rooibos tea) to measure decomposition rates at a single sampling time. Green tea has a high cellulose content and decompose faster than rooibos tea, which consists of higher ligning content (Keuskamp et al., 2013). These contrasting litter types makes it possible to estimate the stabilization factor S (the fraction of the labile material that is not decomposed after 90 days) and the decomposition rate, k .

Studies using TBI has often focused on alpine (Elumeeva et al., 2018; Petraglia et al., 2019) and temperate regions (Helsen et al., 2018; Houben et al., 2018; MacDonald et al., 2018). Some studies have also applied this method to arid ecosystems (Miatto & Batalha, 2016; Alsafran et al., 2017). The study by Alsafran et al (2017) reported a small issue regarding destruction of litter bags due to invertebrates. Thus, had to remove four out 46 tea bags. Nevertheless, the study concluded that TBI was suitable for studies on litter decomposition across biomes in arid environments (Alsafran et al., 2017). Mainly because the TBI showed high variation in k , S

and litter mass loss between local dryland ecosystems and therefore able to distinguish among ecosystems at local scales. As of now only one study applied the TBI within the African savannahs in the Kilimanjaro mountain region (Becker & Kuzyakov, 2018). Hence, further knowledge on the applicability of the TBI in savannah ecosystem are therefore needed.

TBI research on soil macro-fauna focuses predominately on earthworms and mesofauna communities (Zaller et al., 2016; Van Hoesel et al., 2017; Spiegel et al., 2018; Tresch et al., 2018). While, research with termites are, to our knowledge, non-existent. Traditionally approaches to study termite decomposition involves different plant litter, such as leaf, wood and roots (Eichenberg et al., 2017; Smith et al., 2018; Acanakwo et al., 2019), paper rolls (Davies et al., 2015; Leitner et al., 2018) and even wildlife dung (Freyman et al., 2010). Here, we introduce a novel approach to assess termite and microbial contribution to decomposition using the TBI.

The principal aim of this study is to understand the impact of human dominated land-uses (pastures and agricultures) on microbial and termite-driven decomposition compared to wildlife protected areas in the Serengeti savannah ecosystem. In addition, we want to know how these two decomposer groups are influenced by seasonal and regional rainfall differences.

Firstly, hypothesize that the human dominated land-uses exert negative ecosystem responses on the soil community. In turn, leading to lower litter mass loss in both soil groups. Specifically, we assume that agricultural areas will have the most negative impact on both decomposer groups due the agricultural practices such as cultivation and possibly termite mound destructions.

Lastly, we hypothesize that termite-driven mass loss will be less influenced by seasonal and regional rainfall relative to microbial litter mass loss. We assume that mass loss during dry conditions will be mediated by the fungus-growing termites due to their dominance throughout the Serengeti savannah ecosystem. Specifically, we predict that termites will contribute more to mass loss during dry season in dry rainfall region relative to microbial mass loss.

2 Method

2.1 Study site

The decomposition study was conducted inside and outside the Serengeti National Park, Tanzania (latitude 2°40' to 2°50'S and longitude 34° to 34°90'E). Across the ecosystem, mean annual rainfall ranges from ~450mm to 1300mm as a gradient from East to West. Rainfall

varies seasonally with mean annual rainfall up to ~800 mm in wet seasons (November-May) and ~150mm in dry seasons (June-October) (Norton-griffiths et al., 1975). Mean soil temperatures are 29°C (McNally et al., 2017) Mean soil temperatures are 29°C (McNally et al., 2017) and the general soil type across the northern and central regions consists of accumulative organic phaezoems with small patches of salt enriched solonchaks (ISRIC, 2018). Tree densities vary with treesless in the southeast to woodland dominated in the west which stretches north to the Loita Plains (Sinclair et al., 2007). The wildlife protected areas constitutes mainly of migrating wildebeest and zebras and low densities of other wild herbivores, such as elephant, buffalo, impala. While crop cultivation and livestock grazing by cattle, sheep and goat are the widespread outside the wildlife protected areas (McNaughton, 1985; M. P. Veldhuis et al., 2019). Within wildlife protected areas fires are managed with regular burning, while outside fires are almost non-existent (M. P. Veldhuis et al., 2019).

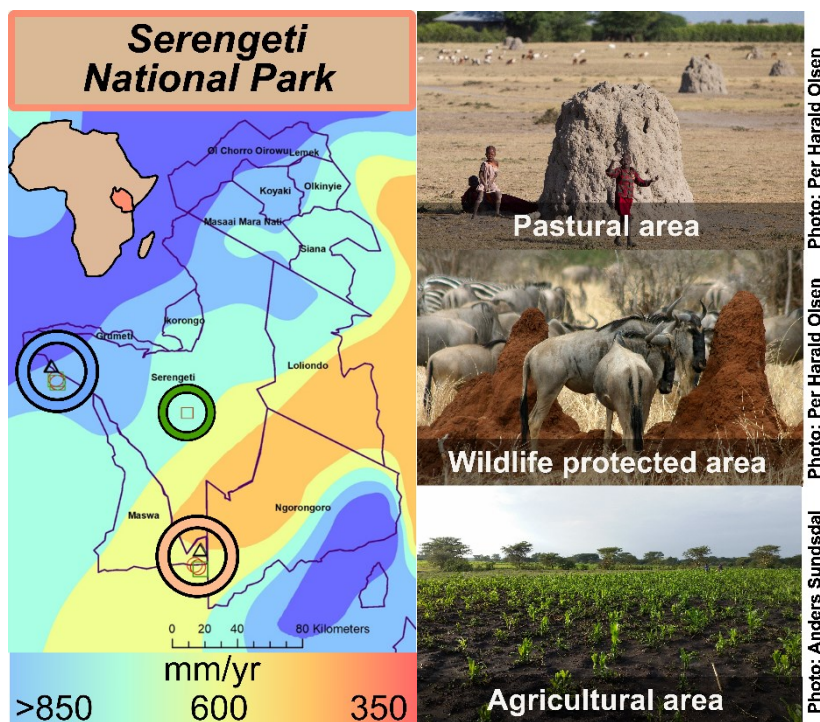


Figure 1 Rainfall map, Serengeti national park and surrounding wildlife protected areas. Additional illustrative pictures of each land-use. Blue circle=Wet rainfall region, Orange circle=Dry rainfall region, Green circle= common garden. Photo credit: Per Harald Olsen and Anders Sundsdal.

2.2 Site selection

Within the two extreme rainfall regions - wet and dry, three distinct land use types were selected: wildlife protected, pastoral and agricultural areas. Agricultural and pastoral areas are in Mwantimba in wet region and Makao in the dry region. Whereas wildlife protected areas are close to Handajega Gate in the wet region and within Maswa Game Reserve in the dry region (Fig. 1). Within each land-use area four sites were selected. These sites were approximately

500 m to each other to ensure the same land use effect. They shared same soil type where possible (Table 1) and had visible *Macrotermes* at all sites. Sites within wildlife protected areas were characterized as savannah woodlands and were either inside SNP or close to park border-posts to exclude any illegal livestock grazing. Pastoral sites are savannah woodland with human modifications such as removal trees and no fire which increase shrubbiness in this area. The pastures were regularly grazed by cattle, sheep and goats. All agricultural sites were maize fields adjacent to pastoral land. Fields with similar farming methods were selected: no pesticide, fertilizers or manure additions except for the use of livestock to remove stubble and plowing were done by hand or livestock with plow. Each agricultural fields was paired at each sites. Meaning that two agricultural fields were situated within on site. The intermediate region consists of one wildlife protected site at the Serengeti plains close to Seronera and categorized as savannah.

2.3 Study design

The study sites were situated close to the park border in the western and eastern region to assess spatial climate effects on decomposition (fig. 2). These regions are from now on referred to as wet region (west), dry region (east) as well as an intermediate rainfall region in the center of the Serengeti ecosystem.

To investigate the influence of rainfall season across rainfall regions and land-uses two campaigns were carried out during wet season (late-January to early March 2017) and dry season (July to September 2017). During each campaign two experiments were conducted simultaneously; the main experiment across wet and dry regions to assess the effect of land-use and spatial climate, and a common garden experiment in the intermediate rainfall region to control for effects of climate, land-use and macro-fauna community on rates of litter decomposition.

2.3.1 Main experiment

Sites in the main experiment were situated within the three major land-uses. Within each land-use, four sites of approx. 500m² were established, with each sites eight randomly placed plots with litterbags, meeting the requirements being more than 1m apart from each other and more than 2m away from the nearest termite mounds.

2.3.2 Common garden

The common garden was established in the intermediate rainfall region in the centre of Serengeti National Park, Seronera. The garden consisted of 4 blocks at least 5m apart and

facing north. Each block was 1m x 2m and included seven plots. Each common garden plot was 40cm apart and more than 2m away from termite mounds. Each common garden plot contained transplanted soil from each block used in the main experiment (above). Fresh soil had been collected from the main experiment stored in sealed buckets for a maximum of eight days before use in the common garden.

2.4 Litterbags

The Tea Bag Index (TBI) was used to estimate litter mass loss as a cost-effective, globally standardized method to gather data on decomposition (Keuskamp et al., 2013). This method uses specific commercially available Lipton tea as two contrasting litter types: Lipton Rooibos and Lipton Green tea. With Rooibos as the recalcitrant litter type and Green tea as the labile litter type. From now on referred to as recalcitrant litter and labile litter, respectively.

To assess the contribution of termite-driven decomposition compared to microbial decomposition an extra set of litterbags were wrapped in 0.3mm aperture size stainless metal mesh around existing nylon mesh, buried in all plots in both experiments. This mesh size was designed to exclude all macro-invertebrates of size >0.3mm, specifically aimed for termites (Smith et al., 2018) while soil organisms such as microbes and fungi and fine roots would still be able to access litter. This treatment of metal mesh wrapped litterbags is now referred to as excluded, while the non-metal meshed litterbags are referred to as open (Fig. 2).

At each plot one excluded and one open litterbag of each litter type, four in total, were buried. Litterbags were placed horizontally in each corner of a $\sim 20\text{cm}^2$ plot, $\sim 8\text{cm}$ deep (fig. 1). To help retrieve the litterbags, tent pegs were placed at each plot just visible at ground level and location of each plot was GPS referenced. A metal detector and GPS were used to relocate plots and litterbags.



Fig. 1 A picture of the example plot setup: One excluded and one open litterbag of each litter type (four litterbags in total) in a $\sim 20\text{cm}^2$ and $\sim 8\text{cm}$ deep hole.

Litterbags were incubated for two months following the TBI protocol for tropical conditions (Keuskamp et al., 2013). Two incubation periods were carried out in 2017. One during wet season in late January to early March and the second during dry season in late July to late September.

In the main experiment, the total sample size was 1488 litter bags (2 seasons x 2 regions x 3 land-uses x 4 blocks x 8 replicate plots (7 in dry season) x 2 treatments x 2 litter types). Sample size in the common garden was 224 litterbags (2 seasons x 4 blocks x 7 replicate plots x 2 treatments x 2 litter types).

2.5 Measurements

2.5.1 Decomposition measurements

After collection, metal mesh was removed, and the nylon meshed litterbags were air dried. Any adhered soil particles and ingrown roots on litterbags were brushed clean and removed. The bags were then oven-dried at 60°C for 48hrs and weighed with and without nylon meshed bag (± 0.001 g). Additionally, due to soil dust and termite intrusions during incubation litter mass was ash corrected. Decomposed litter and debris inside litterbags were homogenized by pestle and mortar. Subsamples of homogenized litter were burned in a furnace at 550°C for 4hrs to determine Loss of Ignition (LOI). The remaining inorganic minerals (ash) was then used to correct for amount of soil infiltration into the litterbags. Litter from 10 labile and three recalcitrant undecomposed litterbags were also burned using LOI to estimate the ash content in undecomposed litter. The weight differences of ash corrected undecomposed and decomposed litterbags was used to calculate percentage litter mass loss.

2.5.2 Rainfall and micro-climate spot measurements

At each plot soil temperature (°C) was measured to a depth of 10cm (HI 98501 Checktemp, Hanna instruments, Woonsocket, Rhode Island, U.S.A.) and soil moisture (%) to a depth of 5.5 cm (ML3, Delta-T, Cambridge, U.K.). Spot measurements were taken at start and end of each incubation period.

Rainfall for the incubation periods was obtained using satellite-based daily rainfall from NASA's Goddard Earth Sciences Data and Information Services Centre (Huffman & Savtchenko, 2017) and half-hourly measurements of cloud cover were taken using multi-satellite microwave data at 10 × 10 km spatial resolution. Daily rainfall estimates were averaged over the incubation period for each block.

2.5.3 Soil nutrients and texture

The soil from the upper 20cm soil layer from both seasons at all sites were analyzed for total soil carbon (C) and nitrogen (N). Soil was sieved through a 2mm sieve and grinded with pestle and mortar. Soil subsamples of between 16 and 22mg were then placed in small tinfoil cups and analysed carbon and nitrogen concentrations by dry-combustion via an elemental analyzer at 1800°C (vario MICRO cube, Langensfeld, Germany). The percentage of carbon and nitrogen was used in the analysis.

Soil texture for soil collected during the wet season was determined by sieving through a <2mm mesh sieve to remove stones. Then the soil was pulverized then haken in sodium hexametaphosphate 5% dispersing solution before being transferred to a sedimentation cylinder determining percentage of clay, silt and sand content by timed suspension of an ASTM 152H-Type hydrometer (Gee & Bauder, 1986). Due to possible over-estimation of sand content and underestimation of clay (Elfaki et al., 2016), we repeated 14 samples using pipette method, where 10mL deionized water and 10 mL of 35% hydrogen peroxide (H₂O₂) were added in 10 g of each soil sample. Additional 35 % H₂O₂ was added into the solution the following day and heated until the organic material was fully oxidized. Water was later added into the solution until the volume reached 200 ml followed by 45% volume reduction by heating, before left over night. Hydrochloric acid (HCL) was not added due to high pH in all samples indicating possible calcium carbonate (CaCO₃) compounds. The solution went through a sedimentation analysis the following day by repetitive removal and addition of water and 2-3 drops of magnesium chloride (MgCl₂) and then determining percentage of clay, silt and sand by the pipette method (Gee & Bauder, 1986).

Due to consistent biases between the soil texture hydrometer and pipette method, it was possible to convert texture values to pipette method equivalent soil texture, using the following conversion equations:

$$\text{Clay: } Y_{\text{pipette}} = 1.3392x - 10.4221, R^2 = 0.7338 \quad (1)$$

$$\text{Silt: } Y_{\text{pipette}} = 0.8139x - 12.6331, R^2 = 0.8072 \quad (2)$$

$$\text{Sand: } Y_{\text{pipette}} = 1.1281x - 17.9957, R^2 = 0.9093 \quad (3)$$

Studies show termite apply clay in both foraging and mound structuring (Jouquet et al., 2002; Oberst et al., 2016). Consequently, soil sand content was chosen as the only soil texture variable in the models. We assumed sand content to be more independent of termite behavior in terms of less reallocation of sand soil particles.

2.6 Statistical analysis

Initial data exploration showed substantial missing moisture data and a high correlation and colinear with temperature (PCC=0.6). Therefore, temperature was the only plot level climate variable used in further analysis.

2.6.1 Main experiment models

To test the effect of Season, Region, Land-use, Treatment, Temperature, C:N and Sand on percentage mass loss of each litter type, linear mixed effect model (LMM) using the lmer()-function within the lme4 package were used (Bates et al., 2015). Following the nested structure of the experimental design with plots within blocks within sites we used a random factor in the model (Crawley, 2007). The two litter types showed strong mass loss differences and since the purpose of this study was to explore interactions among the other variables we analyzed mass loss of each litter type in separate models: Mass loss_{Labile}^{Main} and Mass loss_{Recalcitrant}^{Main}

2.6.2 Common Garden models

To test the effect of Season, Region, Land-use, Treatment, Temperature, C:N and Sand on the percentage mass loss difference between Common Garden (CG) site and Main experiment sites of specific litter type, the response variable where transformed on a positive-negative scale. Where negative percentage indicate greater mass loss in Common Garden, positive values indicate greater mass loss in Main experiment and zero percentage means no difference in mass loss. A LMM using the lmer()-function within the lme4 package was used (Bates et al., 2015). Following the nested structure of the experimental design with blocks within sites we used a random factor in the model (Crawley, 2007). Mass loss of each litter type was evaluated in separate models: Mass loss_{Labile}^{CG} and Mass loss_{Recalcitrant}^{CG}.

2.6.3 Model selection and diagnostics

For all models, a saturated global model was first fitted with all possible two-way interactions and all combinations of three-way interactions among these factor terms: Season, Region, Land-use and Treatment. Then a Least-likelihood-ratio test (LRT) were executed using the drop1() function. Terms were removed sequentially by removing the least significant of terms ($p > 0.05$). After simplifying to the most parsimonious model with lowest Akaike's information criterion (AIC), removed terms were added back to test for better model fit. For the final model, p-values where generated for each term by contrasting models fitted with maximum likelihood (ML) with and without each terms (Zuur et al., 2009).

Model diagnostics were done by checking for heteroscedasticity and plotting model predictions against observed values. Due to constraints by rank deficiency in all models, predictions were based on simplified models. Recalcitrant model had poorer fit than labile model. With a tendency for the residual values to decline systematically with fitted values, likely due to high range in mass loss from 0 to 100%. Standardized terms improved model fit, however results were the same. Hence, the unstandardized original model results are presented here.

2.6.4 Model and data visualization

To identify the contribution of each fixed terms in explaining the variation in mass loss within each model marginal (R^2_m) coefficients of determination were calculated and plotted (Fig.5a-b). The function `r.squaredGLMM()` from the MuMIn package were used (Nakagawa et al., 2017). Additionally, conditional coefficients of determination (R^2_c) is provided, but will not be evaluated in this paper (Appendix A, Table A1, Table A2).

As a tool in ease of model interpretation, the `emmeans()` package were used to create contrasts within terms to determine significant factors of more than three levels and interactions as estimated marginal means (EMMs) (Searle et al., 1980). To visualize results graphically the `ggplot2` package were used (Wickham, 2016).

All data analysis were carried out in the statistical software R studio, version 1.1.463 (R Core Team, 2018)

3 Results

3.1 Climate and soil properties

The rainfall during the incubation spanned from 8mm-150mm in dry season and 175mm-197mm during wet season (Fig.1). Average soil temperatures in upper 10cm soil was 27°C and 29°C during incubation in wet and dry season, respectively. While average soil moisture of upper 5.5cm soil was 20.6% and 7.4% during wet and dry season. The agriculture fields within dry rainfall region differed with 61% sand and the agriculture fields within wet rainfall region differed with 33% sand between agriculture field (Table 1). Wildlife protected areas had 37% higher sand in the wet rainfall region and 41% higher sand in the intermediate rainfall region compared to same land-use in the dry rainfall region, whereas pastoral areas had 16% higher sand percentage in the dry rainfall region compared to the wet rainfall region (Table 1).

Tabell 1 Soil properties within the land-use (agriculture, pasture and wildlife protected area) across rainfall regions and seasons shown as means with $1 \pm SE$. Soiltype classification aquired from a soil reference base (TAXGWRB, 2006).

	C:N (%)		Soiltype	Sand (%)	Silt (%)	Clay (%)
	Dry season	Wet season				
Dry region						
Agriculture ^a	12.531	± 0.492	12.734	± 0.301		
Field 1&2			Planosol	73.521	± 3.481	14.285 ± 0.498 12.143 ± 3.309
Field 3&4			Arenosol	12.333	± 1.456	28.984 ± 0.550 60.582 ± 0.820
Pasture	13.130	± 0.424	12.334	± 0.504	Arenosol	62.799 ± 1.522 17.044 ± 0.910 20.326 ± 1.132
Wildlife	12.529	± 1.080	12.231	± 0.380	Vertisol/Planosol	21.914 ± 2.922 32.659 ± 0.460 43.169 ± 3.865
Wet Region						
Agriculture ^a						
Field 1&2			Planosol	30.259	± 2.381	26.530 ± 1.013 43.347 ± 4.492
Field 3&4			Arenosol	63.363	± 3.257	16.637 ± 0.000 20.326 ± 3.866
Pasture	12.727	± 0.512	12.899	± 0.893	Arenosol	46.523 ± 3.015 20.394 ± 0.930 34.136 ± 2.230
Wildlife	15.638	± 1.454	13.736	± 0.698	Planosol	59.415 ± 1.522 18.265 ± 0.615 22.335 ± 0.839
Intermediate Region						
Wildlife	13.039	± 0.419	12.923	± 0.598	Solochaks	62.548 ± 2.073 17.995 ± 0.299 19.064 ± 2.367

^a Agricultural sites consists of two fields and areis separated here due to distinct differences in soil texture.

3.2 Land-use effect on decomposition

The variation in litter decomposition was strongly dependent on rainfall season, rainfall region and land-use (Fig.3a-d). The impact of land-use on microbial decomposition was only significant during driest conditions (Fig.3a, Appendix A; table A1). Specifically, during dry season the microbial decomposition within the dry rainfall region was 13% more in agricultural areas than pastoral and wildlife protected areas (Fig.3a). However, this effect was only attributed to microbial decomposition of labile litter (Fig.3a). On the other hand, termite-driven decomposition was significantly influenced by land-use (Appendix A; table A1). There was no significant difference in termite-driven mass loss between pastoral and agricultural areas (Fig.3a-d). Termites decomposed about 20% more in human dominated land-uses compared to wildlife protected areas. Except during wet season in dry rainfall region (Fig.3c). Here, termite-driven mass loss was highest in wildlife protected areas (Fig.3c). These differences in land-use across season and region amount to a significant season and region interaction and season and region and land-use interaction in our models, although only a weak overall effect of land-use across season (Fig. 5).

3.3 Climate effect on decomposition

Decomposition by both termites and microbes was significantly lower during dry season compared to wet season (Fig.3, Appendix A; table A1). Specifically, during dry season microbial labile litter decomposition was 50% lower in dry rainfall region compared wet

rainfall region (Fig. 3a-b). While, termite-driven recalcitrant mass loss was 16% lower in dry rainfall region compared to wet rainfall region (Fig.3a-b). Microbial decomposition of recalcitrant litter followed same pattern as labile litter, but with consistently lower mass loss than labile litter across rainfall season and rainfall region (Fig.3a-d).

3.4 Termite and microbial contribution

Termites did not contribute substantially to labile litter decomposition (Fig.3e-h) However, the contribution was significant regarding recalcitrant litter mass loss (Fig.3e-h). Termites contributed the most to recalcitrant litter decomposition in driest conditions compared to microbes (Fig. 3e). Specifically, in human dominated land-uses termites contributed 12% more to recalcitrant decomposition than microbes in human dominated land-uses in dry rainfall region during dry season (Fig.3e). Additionally, there was only 1% difference in mass loss by microbial labile litter mass loss compared to termite recalcitrant mass loss (Fig.3e).

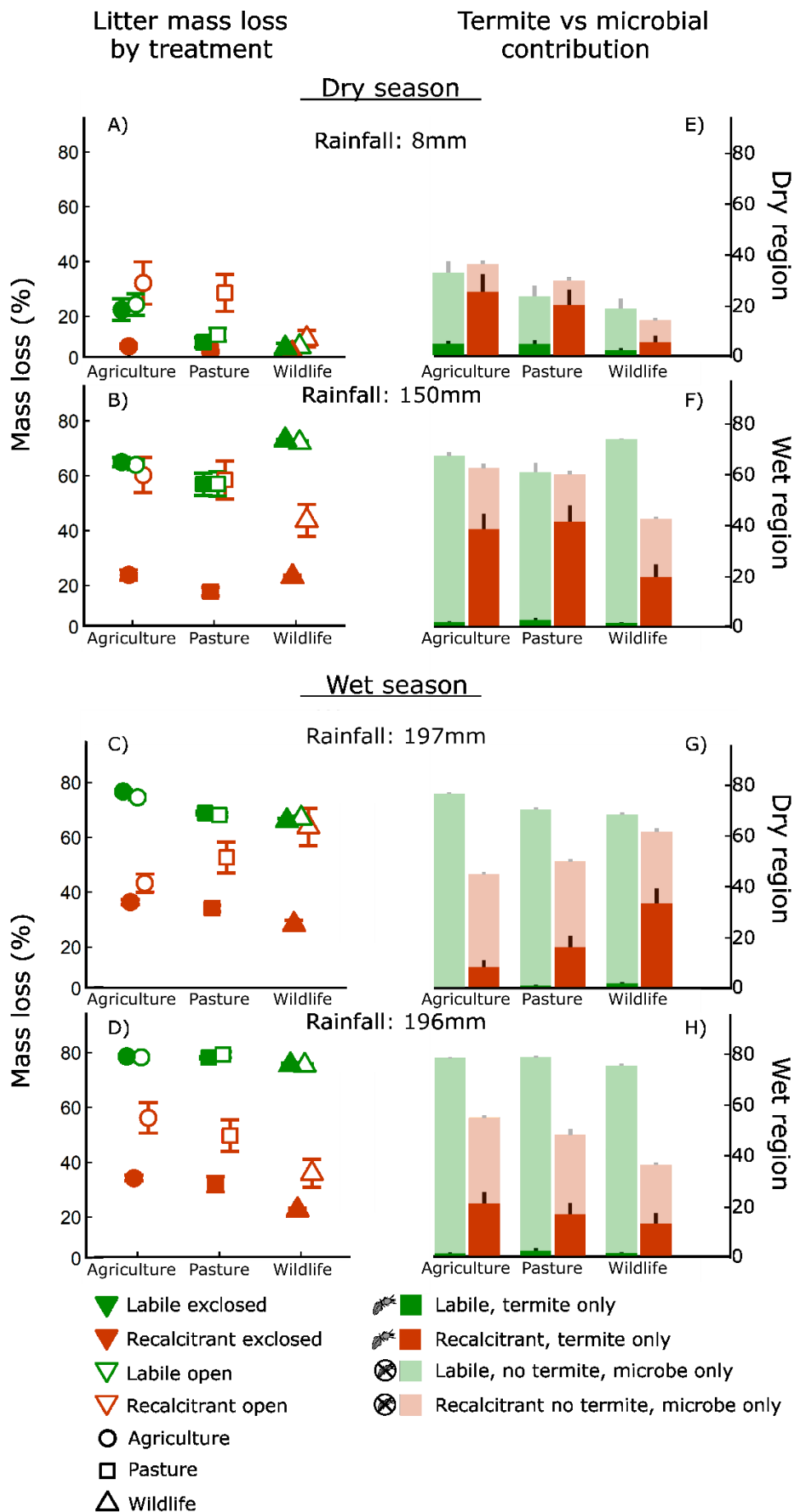


Fig. 3a-d Mean and SE mass loss of labile and recalcitrant litter in three major land-uses: Agricultural, Pastural and Wildlife areas across seasons and regions. Green (filled) = Labile (Green tea) in metal mesh enveloped litterbag. Green (unfilled) = Labile (Green tea) in standard nylon teabag. Red (filled) = Recalcitrant litter (Rooibos tea) in metal mesh enveloped teabag. Red (unfilled) = Recalcitrant (Rooibos tea) litter in standard nylon teabags.

Fig. 3e-h Mean and SE mass loss as termite contribution to mass loss relative to microbial contribution in three major land-uses: Agricultural, Pastural and Wildlife protected areas across seasons and regions. Shown as a stacked bar plot. Termite contribution is calculated as the difference of an open minus an enclosed litterbag. These open litterbags are assumed to have mainly termite intrusions. Any negative values were set to zero. "no termite" is the enclosed litterbag where we assume only microbial mass loss.

3.5 Effect of soil type on the decomposition

When moving soils from both regions to the common garden the soil properties (C:N and Sand) did not significantly influence the decomposition (Fig.4, Appendix A; table A1). The variation in mass loss between the common garden and each region was strongly dependent on rainfall season, rainfall region and land-use (Fig.4a-d). For instance, when moving soils from the dry regions to the common garden the decomposition increased by 59% and 15% during dry season for labile and recalcitrant litter respectively (Fig.4a). While soil moved from the wet rainfall region to the common garden did not significantly influence the decomposition during either the wet or the dry season (Fig.4b-d). In addition, with increasing temperatures labile litter mass loss significantly decreased in driest conditions (Appendix A; table A1). Specifically, in dry rainfall region (Appendix B; B1).

Further, soil moved from each land-use to the common garden showed inconsistent patterns in relation to termite-driven recalcitrant decomposition. Specifically, there was greater termite-driven mass loss of recalcitrant litter in certain land-uses across season and rainfall region than in the common garden (Fig.4b-c). For instance, during wet season there was higher termite-driven mass loss in the pastoral and wildlife protected areas in the dry rainfall region (Fig.4b). While, there was higher termite-driven mass loss in pastoral and agricultural areas in the wet rainfall region (Fig.5d). These differences amount to the significant season and region interaction and region and temperature interactions in our labile models, and significant season and region and land-use interaction and season and treatment interaction in our recalcitrant models (Fig.5)

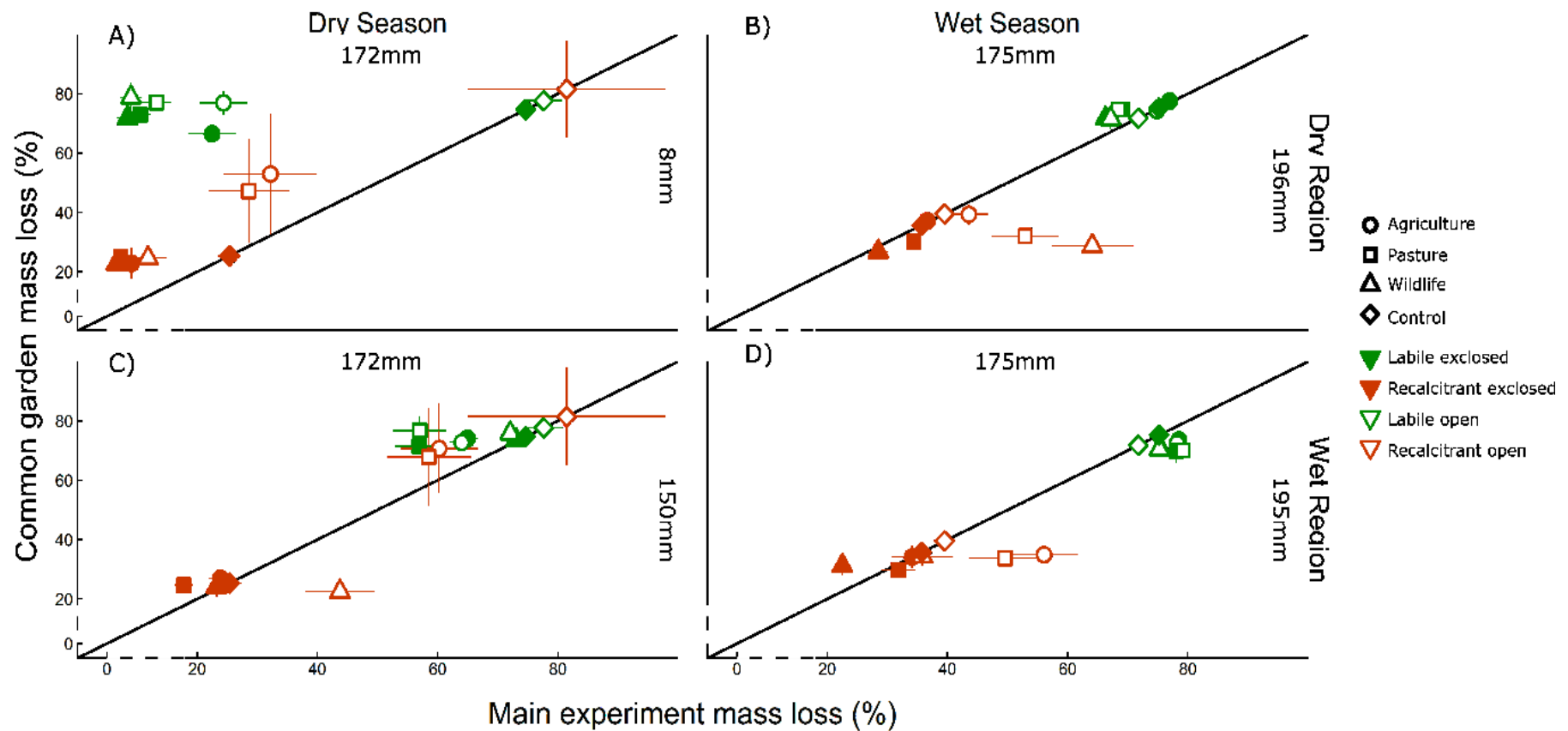


Fig. 4a-d Mean and SE mass loss as a comparison between Common garden (transplanted soil) and Main experiment (soil at source location). The 1:1 line represents when mass loss is equal across experiments. Vertical text describes which region and the amount of rainfall the Common Garden is comparing to. The control plots are local soil in the Common Garden.

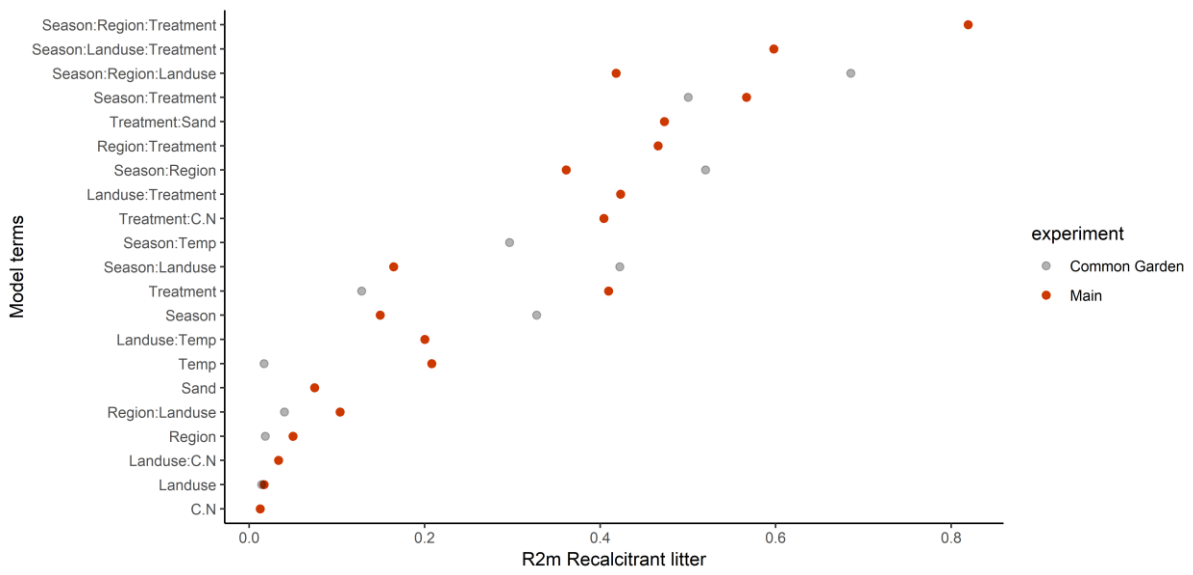


fig. 5 Marginal R^2 (R^2m) for each term describing how much of the variation in recalcitrant litter mass loss is explained by each fixed effect term in each of the models. R^2m of the full models: 0.368 R^2m and 0.287 R^2m for main and the common garden model respectively.

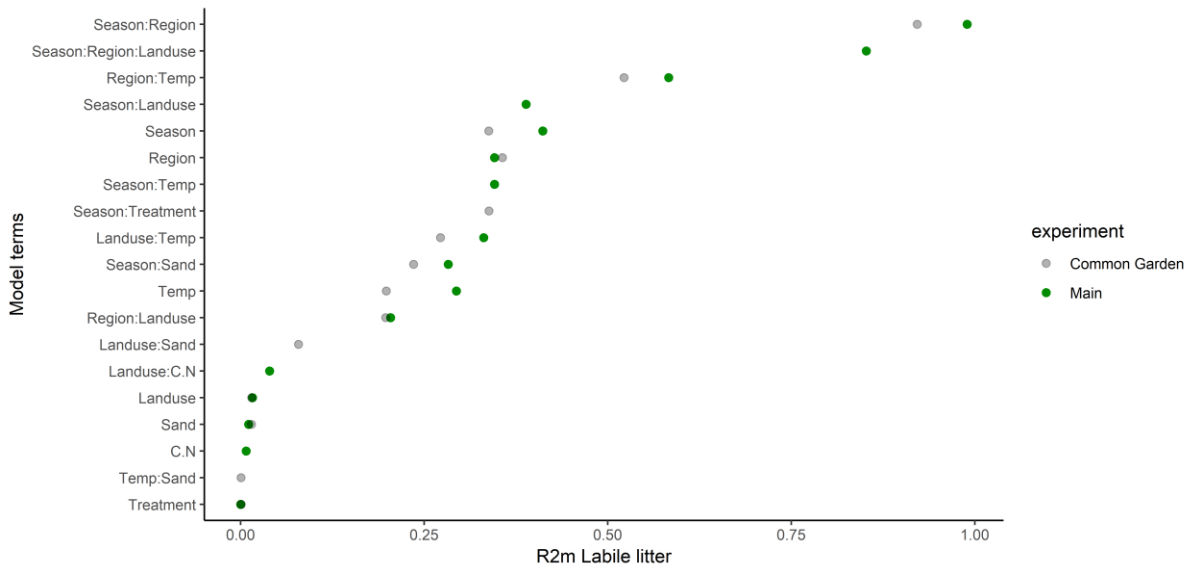


fig. 5 Marginal R^2 (R^2m) for each term describing how much of the variation in recalcitrant litter mass loss is explained by each fixed effect term in each of the models. R^2m of the full models: 0.944 R^2m and 0.970 R^2m for main and common garden model respectively.

4 Discussion

Our results demonstrate that termites play a greater role in recalcitrant litter decomposition in human dominated land-uses compared to microbes, especially during dry season. These findings illustrate the importance of termites for the continuous nutrient cycling during dryer conditions where microbial activity is inhibited. Further, the labile litter decomposition was predominantly decomposed by microbes. Additionally, we found the rainfall regimes and the difference in termite community to mediate the litter decomposition rather than the soil properties itself. These results underscore rainfall and termites (and other macro-fauna) as important factors explaining spatial and temporal heterogeneity on the decomposition process in the savannah ecosystem.

4.1 Land-use effects

4.1.1 Microbial litter decomposition

We predicted that microbial decomposition would be lower in human dominated land-uses. However, our study finds no indication that microbial decomposition is negatively or positively influenced by either pastoral or agricultural land-uses (Fig.3). Nevertheless, these finding are supported by a Geissnen et al 2006, who found no influence of pastures on microbial decomposition compared to a tropical forest (Geissen & Guzman, 2006). In addition, Wickings et al (2011) have reported that soil tillage increases decomposition rates (Wickings et al., 2011). Yet, our agricultural fields are predominantly plowed by livestock rather than tractors. We hypothesize that if tractors were to be used, microbial decomposition in the agricultural fields would increase. However, this is subject to discussion.

On the other hand, Veldhuis et al (2019) have reported that the increasing human land cultivation closer to the border of the Serengeti National Park are having an influence even further into the park by degradation of ecosystem functions, such as the microbial decomposition (M. P. Veldhuis et al., 2019). Therefore, it is possible that our wildlife protected areas, which are close to the park border, are influenced by the human land-use, such as illegal livestock grazing. Further studies should consider to separate human land-uses from wildlife areas by placing experiment to understand how impacts of human land-use are affecting the ecosystem function, such as the decomposition process.

4.1.2 Termite-driven litter decomposition

Our study finds that the human dominated land-uses have higher termite-driven mass loss of recalcitrant litter than wildlife protected areas (Fig.3). These findings contradict our hypothesis as we expected lower termite-driven decomposition in both human land-uses than in wildlife protected areas. This contrasts with other African studies showing a decrease in termite decomposition with human land-use change in Kenyan woodlands (G. H. Kagezi et al., 2011) and a decline in termite diversity in clear-cutting of forests in Uganda (Okwakol, 2000). However, both studies found fungus-growing termites to increase in abundance relative to other termite groups (Okwakol, 2000; G. Kagezi et al., 2016). Since fungus-growing termites are dominant in African savannahs (Buxton, 1981; Sileshi et al., 2010), further increase in their abundance could explain why our results show higher termite-driven decomposition in human dominated land-uses compared to wildlife areas. Additionally, with more available food resources such as maize and livestock dung, this could increase their forage activities and mound densities (T. G. Wood et al., 1980; Freymann et al., 2008; Hagan et al., 2017). For instance, Wood et al (1980) reported that the fungus-growing species *Microtermes* were highly abundant in cultivated maize fields in Nigeria due to their shallow and deep subterranean nests (T. G. Wood et al., 1980). These nests are easily overlooked and less vulnerable to human mound destruction (Sileshi et al., 2009). Therefore, we hypothesize that the fungus-growing termites in the Serengeti ecosystem favor the pastoral and agricultural land-use as they obtain more food resources (e.g. maize and dung) which in turn increases their forage activity and hence, increases termite-driven decomposition. However, we also observed greater termite-driven recalcitrant mass loss in the wildlife protected area compared to human dominated land-uses during the wet season in the dry rainfall region (Fig.3c). We assume this discrepancy to be attributed to the arrival of wildebeest following the annual migration pattern in the Serengeti-Mara ecosystem (Boone et al., 2006). Greater inputs of wildlife dung might explain the increased termite forage activities (Freymann et al., 2008), as observed with the greater termite-driven decomposition in this area (Fig.3c). To better understand how herbivores and cropland are influencing termite decomposition, more research on their interactions with termites are needed.

4.2 Climate effect on decomposition

In line with our hypothesis, we found a strong influence of season and rainfall region on microbial and termite-driven decomposition. Interestingly, microbial labile litter mass loss was substantially lower (50%) than termite-driven recalcitrant litter mass loss (16%). This suggests,

with support from Veldhuis et al (2017), that termites are more resistant to drought (M. Veldhuis et al., 2017). Since fungus-growing termites process litter within their mounds they can, in strong contrast to microbes (and other macro-invertebrates), decouple the litter decomposition from the local environment (Lavelle et al., 1997; M. Veldhuis et al., 2017). Additionally, Lys et al (1994) found that fungus-growing termites have the ability to absorb water from sandy soil with low water content (Lys & Leuthold, 1994) Thus, further supporting our suggestion that the fungus-growing termites works as a mediator for the continuous nutrient cycling when microbial decomposition become limited during the dry seasons.

We recognize that the open litterbags in our study are not explicitly differentiating termites from other macro-invertebrates. These macro-invertebrates are likely to over-estimate the termite-driven mass loss. Yet, most savannah macro-invertebrates have low tolerance to drought, such as earthworms (Lavelle et al., 1997). Therefore, it is most likely that the high recalcitrant litter mass loss, especially during dry season are predominantly due to termites. However, to further increase reliability of macro-faunal litterbag methods, body size-partitioning by mesh aperture and/or eDNA sampling from bags are possible improvements.

4.3 Effect of soil type on decomposition

Our results found that the rainfall regimes and the difference in macro-fauna community was the primary determinant for the litter decomposition rather than the soil property itself (Fig.4). Specifically, labile and recalcitrant litter decomposition in all soils was strongly dependent on rainfall, with increased mass loss with higher rainfall irrespectively of land-use. In addition, recalcitrant litter decomposition increased in areas with higher termite activity, but inconsistently with land-use. These findings, which are supported by Ruess et al (1994), suggest that the decomposition in the different soils in the Serengeti are predominantly driven by savannah rainfall patterns (Ruess & Seagle, 1994). Additionally, when termites are present, decomposition of recalcitrant litter are higher irrespectively of soil type. These results highlight the importance of including rainfall and termites in explaining spatial and temporal heterogeneity on the decomposition process. However, it should be noted that herbivores and fire are likely to influence these patterns as they are important drivers of savannah ecosystem processes (Scholes & Archer, 1997; Cornwell et al., 2009). Further investigation on how these factors together influence the decomposition are needed to increase our understanding of spatio-temporal patterns influencing savannah decomposition.

4.4 Assessment of teabag index for savannah ecosystems

The TBI was used as it is an easy applicable method to measure decomposition while also contribute to the creation of a global soil decomposition map (Keuskamp et al., 2013). However, the decomposition rate using standard litter types rather than local litter may not necessary give information about the full decomposition potential in a given ecosystem. The idea that some litter have home-field advantages due to adaptations of soil decomposers for particular litter traits (Ayres et al., 2009) could possibly induce different decomposition rates of local compared to standardized litter (Didion 2016). Didion et al showed similar decomposition patterns for labile local versus labile green tea and recalcitrant local litter versus recalcitrant rooibos, but with greater mass loss of local litter. Therefore, the mass loss presented in our study are likely to only show the decomposition potential and not its actual natural potential. Hence, further studies, such as Smith et al (2008), on the decomposition in the Serengeti savannah should include local litter types (Smith et al., 2018).

Savannahs which have variable rainfall, both spatially and temporally, could experience different leaching levels from litterbags placed in dry or wet rainfall regions (Cousteaux et al., 1995). As such, mass loss of litterbags during wet season and wetter regions could be overestimated compared to dry season. How much the litterbags are affected by leaching in savannah ecosystems is not known. Green and rooibos teabags have been estimated to leach about 20% and 40% (Pouyat et al., 2017), but how comparable this is to savannahs during wet seasons are uncertain. Effects of leaching could also be attributed to soil texture where higher clay percentages and soil moisture reduces leaching effects (Jenkinson, 1977; Cousteaux et al., 1995).). It is therefore, as stressed by Edwartz et al (2018), important to acknowledge and possibly account for leaching in the TBI method to improve comparability among ecosystems in future research (Keuskamp et al., 2013). Methods such as pre-leaching of teabags or incubate an extra set of pre-leached litterbags have been proposed (Pouyat et al., 2017; Edwartz, 2018).

In this study, substantial amount of our teabags was destroyed by termites. This made the calculations of decomposition rates impossible. We find it surprising that so few study reports problems with soil macro-fauna (Alsafran et al., 2017). Since we altered the litterbags with metal mesh we successfully excluded all macro-invertebrates and solved our problem. As for the TBI, such a method would firstly reduce the TBI's ease of use and secondly make the TBI unstandardized across ecosystems if we were to envelope teabags in metal mesh only in selected ecosystems with high soil macro-fauna activity. This could also induce microclimate

effects within the metal meshed bags in contrast to standard teabags (Bradford et al., 2002). Therefore, we conclude that the TBI is not suitable for savannah ecosystems, as it is, where soil-macrofauna considerably destroys the litterbags. Further improvements to the TBI are therefore needed to safely conduct decomposition experiments in the savannah ecosystems.

5 Conclusion

Our study demonstrates that termites and other macrofauna are the main decomposers of recalcitrant litter decomposition in human-dominated land-uses compared to soil microbes, especially during the dry season. In previous studies, termites have been shown to have a higher resilience against drought and becomes important for the continuous nutrient cycling throughout the dry season (M. Veldhuis et al., 2017). Meanwhile, rainfall regimes are determinant for microbial labile litter decomposition where decomposition is higher with higher rainfall irrespectively of land-uses. In our system, soil properties, such as texture and carbon to nitrogen ratio, did not seem to significantly influence decomposition in either rainfall regions. Instead difference in termite community and rainfall regime regulates the decomposition. Understanding the impacts of human land-use and climate on microbial and termite litter decomposition is key to recognize how the nutrient cycling in savannah ecosystems. In an increasingly human dominated landscape termites may play as vital role as decomposer for the continuous nutrient cycling in pastural and agricultural lands.

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Appendix A

Table A1 Least Likelihood Ratio-test output for the four models showing significance of each term in each model.

	The common experiment						Main experiment					
	Labile			Recalcitrant			Labile			Recalcitrant		
	F-ratio	Df	Pr(>Chisq)	F-ratio	Df	Pr(>Chisq)	F-ratio	Df	Pr(>Chisq)	F-ratio	Df	Pr(>Chisq)
Season	62.09	1,12	0.000 ***	7.34	1,11	0.007 **	485.13	1,13	0.000 ***	28.18	1,14	0.000 ***
Region	20.98	2,12	0.000 ***	1.55	2,11	0.460	22.37	2,13	0.000 ***	7.14	2,14	0.028 *
Landuse	6.57	2,12	0.037 *	1.17	2,11	0.558	8.97	2,13	0.011 *	1.11	2,14	0.573
Treatment	0.34	1,12	0.561	4.54	1,11	0.033 *				137.50	1,14	0.000 ***
Temp	7.25	1,12	0.007 **	0.68	1,11	0.408	124.67	1,13	0.000 ***	13.33	1,14	0.000 ***
Sand	11.13	1,12	0.001 ***				20.05	1,13	0.000 ***	8.48	1,14	0.004 **
C.N							27.12	1,13	0.000 ***	0.10	1,14	0.750
Season:Region	131.59	1,24	0.000 ***	5.20	2,19	0.074	299.45	2,27	0.000 ***	54.12	2,31	0.000 ***
Season:Landuse				2.65	2,19	0.265	45.52	2,27	0.000 ***	2.73	2,31	0.256
Season:Treatment	5.72	1,24	0.017 *	2.46	1,19	0.117				5.51	1,31	0.019 *
Season:Temp				1.03	1,19	0.311	0.71	1,27	0.400			
Season:Sand	40.18	1,24	0.000 ***				93.97	1,27	0.000 ***			
Region:Landuse	33.80	2,24	0.000 ***	0.16	2,19	0.924	12.04	2,27	0.002 **	9.41	2,31	0.009 **
Region:Treatment										3.40	2,31	0.183
Region:Temp	43.79	1,24	0.000 ***				4.46	2,27	0.108			
Landuse:Treatment										0.27	2,31	0.875
Landuse:Temp	55.35	2,24	0.000 ***				19.42	2,27	0.000 ***	3.08	2,31	0.215
Landuse:Sand	9.48	2,24	0.009 **									
Landuse:C.N							39.75	2,27	0.000 ***	9.92	2,31	0.007 **
Treatment:Sand										2.94	1,31	0.086
Treatment:C.N										4.44	1,31	0.035 *
Temp:Sand	11.23	1,24	0.001 ***									
Season:Region:Landuse				14.51	2,21	0.001 ***	13.91	2,29	0.001 ***	13.02	2,37	0.001 **
Season:Region:Treatment										16.29	2,37	0.000 ***
Season:Landuse:Treatment										11.02	2,37	0.004 **

Table A1 Marginal R^2 (R^2m) and Conditional R^2 (R^2c) for each term describing how much of the variation in Labile litter mass loss is explained by each specific term in the two models. Marginal R^2 considers only the variance by the fixed effects, and the conditional R^2 by both the fixed and random effects.

Labile litter			
Model terms	R2m	R2c	Experiment
<i>Full model</i>	0.829	0.944	<i>Main</i>
Season	0.411	0.775	Main
Region	0.346	0.353	Main
Landuse	0.016	0.476	Main
Treatment	0.000	0.403	Main
C.N	0.008	0.429	Main
Temp	0.294	0.911	Main
Sand	0.011	0.367	Main
Season:Region	0.989	0.950	Main
Season:Landuse	0.389	0.811	Main
Season:Temp	0.346	0.922	Main
Season:Sand	0.283	0.608	Main
Region:Landuse	0.204	0.650	Main
Region:Temp	0.583	1.052	Main
Landuse:C.N	0.039	0.474	Main
Landuse:Temp	0.331	0.928	Main
Season:Region:Landuse	0.852	0.979	Main
<i>Full model</i>	<i>0.921</i>	<i>0.970</i>	<i>Common Garden</i>
Season	0.338	0.733	Common Garden
Region	0.356	0.338	Common Garden
Landuse	0.015	0.476	Common Garden
Treatment	0.001	0.392	Common Garden
Temp	0.198	0.846	Common Garden
Sand	0.015	0.353	Common Garden
Season:Region	0.922	0.946	Common Garden
Season:Treatment	0.338	0.730	Common Garden
Season:Sand	0.236	0.576	Common Garden
Region:Landuse	0.197	0.670	Common Garden
Region:Temp	0.522	1.026	Common Garden
Landuse:Temp	0.272	0.910	Common Garden
Landuse:Sand	0.079	0.384	Common Garden
Temp:Sand	0.001	0.383	Common Garden

Table A2 Marginal R^2 (R^2m) and Conditional R^2 (R^2c) for each term describing how much of the variation in Recalcitrant litter mass loss is explained by each specific term in the two models. Marginal R^2 considers only the variance by the fixed effects, and the conditional R^2 by both the fixed and random effects.

Model terms	Recalcitrant litter		
	R2m	R2c	Experiment
<i>Full model</i>	0.368	0.432	Main
Season	0.149	0.305	Main
Region	0.050	0.192	Main
Landuse	0.017	0.198	Main
Treatment	0.410	0.536	Main
C.N	0.013	0.160	Main
Temp	0.208	0.601	Main
Sand	0.075	0.189	Main
Treatment:Sand	0.473	0.543	Main
Treatment:C.N	0.404	0.509	Main
Landuse:Temp	0.200	0.703	Main
Landuse:C.N	0.034	0.306	Main
Landuse:Treatment	0.423	0.563	Main
Region:Treatment	0.466	0.557	Main
Region:Landuse	0.104	0.319	Main
Season:Treatment	0.567	0.676	Main
Season:Landuse	0.165	0.330	Main
Season:Region	0.361	0.465	Main
Season:Region:Landuse	0.418	0.599	Main
Season:Region:Treatment	0.819	0.866	Main
Season:Landuse:Treatment	0.598	0.719	Main
<i>Full model</i>	0.287	0.342	Common Garden
Season	0.328	0.275	Common Garden
Region	0.018	0.015	Common Garden
Landuse	0.014	0.012	Common Garden
Treatment	0.128	0.108	Common Garden
Temp	0.017	0.014	Common Garden
Season:Treatment	0.500	0.419	Common Garden
Season:Region	0.520	0.484	Common Garden
Season:Landuse	0.422	0.354	Common Garden
Season:Temp	0.297	0.249	Common Garden
Region:Landuse	0.040	0.118	Common Garden
Season:Region:Landuse	0.685	0.776	Common Garden

Appendix B

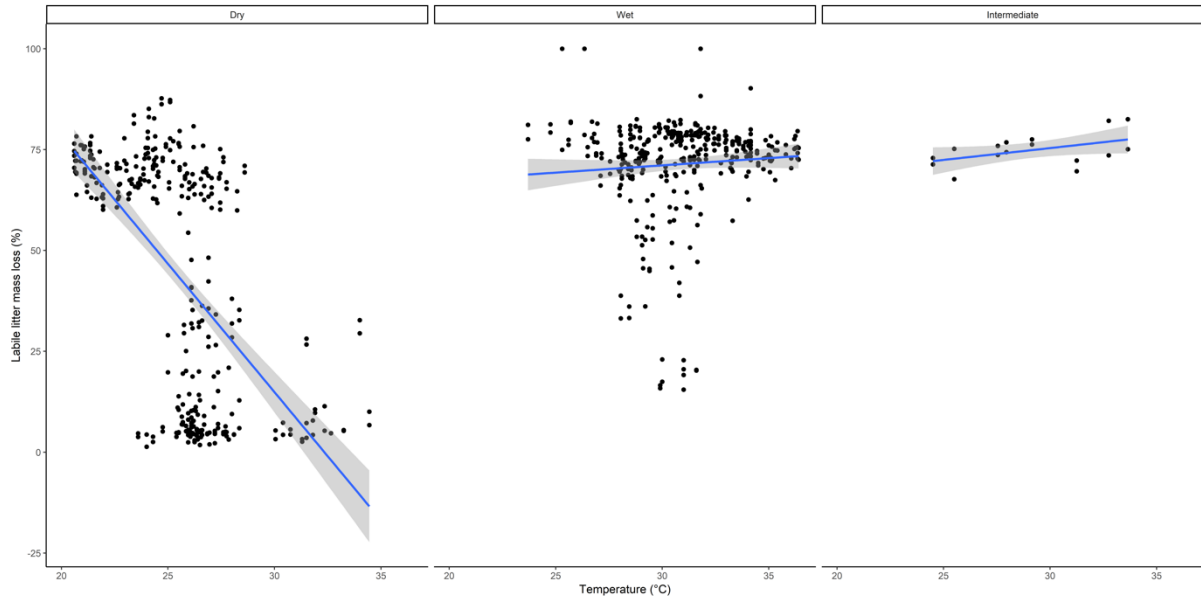


fig. B1 Mass loss of labile litter across the rainfall regions. A simple regression line is fitted to highlight trends in mass loss with increasing temperature.

