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Land-use diversity within an agricultural landscape promotes termite nutrient cycling services in a southern African savanna

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ABSTRACT

Soil macrofauna provide key supporting ecosystem services by transporting nutrients against physical and chemical gradients. In the semi-arid savannas of southern Africa, termites are the dominant macrofauna whose foraging activities increase nutrient availability, soil aeration and water infiltration. With increasing land-use conversion, savanna landscapes are becoming surrounded by a matrix of agricultural landscapes. We tested how compositional and configurational landscape heterogeneity influenced the presence of soil sheetings, a termite foraging activity, within savanna habitat patches embedded in a heterogeneous agricultural landscape in north-east Eswatini. We found that landscape heterogeneity most strongly influenced termite foraging activity at smaller spatial scales (1- to 2-km surrounding the savanna patch). Within this spatial scale, high compositional heterogeneity, which was indicative of diverse habitat patches, promoted termite foraging activity, yet high configurational heterogeneity, indicative of a fragmented landscape, reduced termite foraging activity. At larger landscape scales (5-km), the heterogeneity of the landscape no longer influenced termite foraging activity, yet low to moderate proportions of sugarcane surrounding savanna patches promoted termite foraging activity within those patches. Our results provide novel insights in how the structure of the landscape affects termite foraging activity, demonstrating that diverse, intact landscapes are a critical buffer in maintaining positive nutrient cycling services within an agricultural landscape.

1. Introduction

Nutrient cycling is a critical supporting service in ecosystems which influences nutrient storage, decomposition, and nutrient translocation (Costanza et al., 1997). Diverse biological taxa play key roles in nutrient cycling by moving material against physical and chemical gradients (Weathers and Ewiing, 2013), and contributing to the regulation of long-term ecosystem productivity through their control over energy and nutrient pathways and flow rates (Schuurman, 2005). These organisms exist in and interact with complex landscapes where their populations and ecosystem functions both respond to

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and cause heterogeneity (Turner and Cardille, 2007). As human-induced land-use change continues to modify natural landscapes, it is critical that we understand how those modifications affect the biological processes that influence key ecosystem functions so that they may be conserved through land use planning or regulation.

Land use changes have led to rapid alterations in ecosystem composition and structure, as well as biophysical and biochemical processes, improving or damaging the quantity and quality of services those systems provide (Wang et al., 2018). Land use change alters both compositional heterogeneity which is defined as the type and diversity of land-cover, and configurational heterogeneity which is defined as the shape and arrangement of the different land-cover types in space. Agricultural landscapes interspersed with natural landscapes have been highlighted as landscapes with high heterogeneity that can positively influence biodiversity by increasing compositional diversity (Fahrig et al., 2011), though empirical evidence suggests that responses are taxon specific (Reynolds et al., 2018). On the other hand, high configurational heterogeneity can lead to fragmentation effects where small isolated land use patches may not sustain ecosystem service providers, may prohibit recolonization of extinct patches, or may favor disturbance resilient species to the exclusion of other species (Tscharntke et al., 2005).

In southern Africa, landscape conversion to cropland from 1900 to 1990 increased by 1.34% per year with an absolute increase of 28.8 million hectares (Goldewijk, 2001), resulting in landscapes where patches of agricultural land-use vary in intensity from subsistence rain-fed agriculture to irrigated monoculture and are interspersed among 'natural' habitat patches (Reynolds et al., 2018). To sustainably manage these landscapes, we need to understand how the composition and configuration of these heterogenous landscapes affect the biological agents in savanna systems that maintain nutrient cycling services.

Dominated by a spatially and temporally variable mix of grass and tree growth forms, tropical savanna systems are inherently heterogenous patches of natural vegetation limited by disturbance, water, and nutrient concentrations (Lehmann et al., 2011; Scholes and Walker, 2004). On a regional scale, geology and rainfall are important constraints on nutrient dynamics in savanna systems (Tongway and Ludwig, 2005), however local biotic interactions and feedbacks play a significant role in nutrient availability within the local context (Veldhuis et al., 2016). Soil macrofauna are key facilitators to organic matter decomposition, bioturbation, and nutrient cycling in arid and semi-arid systems (Tongway et al., 1989). Termites are among the main soil macrofauna in savannas across Africa (Jouquet et al., 2011; Okullo and Moe, 2012; Sileshi et al., 2010). Through their foraging activity, up to 60% of annual litter decomposition has been attributed to termites in some savanna systems (Buitenwerf et al., 2011). Termites also translocate large quantities of soil by building biogenic structures such as nests, soil sheetings, and galleries. Soil sheetings are surface structures formed by termite workers, and are a mixture of mineral soil and saliva that are used to cover the food source and protect the termites during foraging. In these soil surface structures, nutrients contained in soil sheetings are recycled quickly and hence can alter soil nutrients (Sileshi et al., 2010). The majority of these biogenic structures are constructed by a few dominant, fungus-growing species (Macrotermitines) which have been found to be the main drivers of decomposition rates within arid systems (Schuurman, 2005). Because soil sheetings are used primarily for foraging, they are ephemeral and erode quickly. Experimental studies have found a positive relationship between the amount of vegetal material removed and the quantity of termite sheetings present, thus the abundance of termite sheetings is a direct indicator of foraging activity and an index of nutrient cycling (Cheik et al., 2019; Pomeroy, 2005; Rouland et al., 2003). Despite the significance of ecosystem services provided by termites, the effects of land-use heterogeneity on termite foraging activity remains poorly understood. Here we test how compositional and configurational heterogeneity in land-use affects termite foraging activity within this savanna ecosystem.

Termite activity is driven by both abiotic and biotic factors where abiotic factors are more important predictors of decomposition at the larger spatial scale and biotic factors are more important predictors at smaller spatial scales (Gosling et al., 2016). Biotic determinants such as vegetation structure and food availability have been highlighted as important influences on termite foraging intensity and decomposition rates at the local scale (Leitner et al., 2018; Mugerwa et al., 2011). At large spatial scales, geological characteristics drive termite activity by influencing both the spatial patterns of termite mounds as well as foraging rates, where sandier soils increase tunneling rates and reduce energy expenditure during foraging (Davies et al., 2014; Muvengwi et al., 2018a; Pequeno et al., 2015).

In addition to biotic and abiotic drivers, multiple studies have indicated that anthropogenic disturbance and land-use intensification have resulted in decreased termite richness and altered community assemblages (Hausberger and Korb, 2016; Jones et al., 2003; Muvengwi et al., 2017; Olugbemi, 2013; Schyra and Korb, 2017). However, some dominant functional groups, such as fungus-growing termites, exhibit high resilience to disturbance (Six et al., 2011), which can decouple the relationship between diversity and activity. For example, Olugbemi (2013) found both a decrease in termite diversity yet an increase in decomposition activity along a disturbance gradient and attributed those changes to an increase in abundance of Macrotermitinae which can dominate termite assemblages after a disturbance (Six et al., 2011). Thus, the response of termite guilds and their ability to cycle nutrients is context dependent and may depend both on the scale at which they are studied as well as on the dominant components of disturbance including land-use composition and its configuration on the landscape. In this study our objectives were to: (1) assess and quantify how agricultural landscape heterogeneity at different scales alters termite foraging activity within savanna patches; and (2) disentangle the influence of configurational heterogeneity of land use from the diversity and composition of land-use types on termite foraging activity, as these two metrics of landscape heterogeneity can differentially influence taxon diversity and ecosystem services (Reynolds et al., 2018).

To address these objectives, we quantified termite soil sheetings as a measure of termite foraging activity in savanna patches embedded across a gradient of agriculture land-use intensification in southern Africa. In our sampling sites, we varied both the composition of the landscape from high to low habitat diversity, and the configuration of the landscape from highly fragmented to larger, contiguous patches of habitat. Due to the influence of soil characteristics on termites, we expected that at the largest landscape scale, geology would be the dominant predictor of termite foraging activity. In contrast, at an intermediate landscape scale, we expected that termite foraging activity would increase with greater land use diversity. In this system, land use diversity increased with increasing agricultural patches which can provide alternate food resources for termites. Because of the previously observed negative impacts of fragmentation, we further predicted that high configuration would decrease termite foraging activity.

2. Material and methods

2.1. Study area

We conducted the study in the lowveld savanna of northeastern Eswatini (formerly Swaziland), located within the Maputaland-Pondoland-Albany biodiversity hotspot (Mucina and Rutherford, 2006). The region experiences mild, dry winters (8–26 °C; 0–50 mm; April – Mid-October) and hot, wet summers (15–33 °C; 200–500 mm; October–March) (Goudie and Price Williams, 1983). There were four dominant geology types across the study area; sandstone, limestone, basalt and rhyolite (Burger, 2013). We identified three land use types: sugarcane plantations, communal grazing lands, and rainfed subsistence agriculture that created a matrix around patches of savanna habitat (Hurst et al., 2014). The resulting landscape was composed of savanna patches of different sizes and shapes within a matrix of different agricultural intensities.

2.2. Site selection

Sixteen, 500 × 500 m savanna sites were selected *a priori* based on metrics of surrounding compositional and configurational landscape heterogeneity. We used a previously published land cover dataset from which landscape heterogeneity metrics were derived using a moving window analysis within a 2-km radius from each cell in the land-cover dataset in order to select the 16 sites (Reynolds et al., 2018). These landscape metrics included the Shannon diversity index of land-cover types (SHDI), land-cover richness (LCR), total length of edge between land-cover classes (TE), total number of patches (NP), large patch index (LPI) which quantifies the percentage of total landscape area comprised of the largest patch, patch cohesion (Cohesion) which quantified the clumpiness of a land-cover type, and patch division (DIVISION) which was the probability that two randomly chosen cells in the landscape were not situated in the same patch. In order to select sites that varied independently in composition and configuration, variables were reduced to represent a single metric of composition or configuration. The composition variable was derived from one orthogonal principle component that included SHDI and LCR. The configuration variable was a principal component derived from the remaining landscape variables.

The landscape surrounding savanna sites varied across a gradient of composition and configuration based on the quantiles of the rank scores of the two principle components that represented compositional or configurational heterogeneity (<33%, 34–66%, >67%). Each site was categorized as having low, medium, or high heterogeneity surrounding it, based on the respective quantiles of either compositional and configurational components, resulting in eight representative categories of heterogeneity that surrounded the savanna site: low composition, low configuration (LL, $n = 2$); low composition, medium configuration (LM, $n = 2$); low composition, high configuration (LH, $n = 2$); medium composition, low configuration (ML, $n = 2$); medium composition, medium configuration (MM, $n = 1$); high composition, low configuration (HL, $n = 2$); high composition and medium configuration (HM, $n = 2$); and high composition, high configuration (HH, $n = 3$).

2.3. Estimating the abundance of termite sheetings

Soil sheetings are short lasting structures that are continuously reconstructed as termites forage, resulting in a positive relationship between the amount of vegetal material removed and the quantity of termite sheetings present (Cheik et al., 2019; Pomeroy, 2005; Rouland et al., 2003). Therefore, for this study, the presence of soil sheetings was regarded as a direct measure of termite foraging activity and an indirect measure of soil turnover rates within a patch.

Within each of the 16 savanna sites we selected 2 locations for 50 × 50 m plots (Fig. 1). One plot was selected to represent a shrub encroached savanna habitat, and the other plot was selected for openness and lack of shrubs and bushes. These plots were selected via visual inspection to represent the extremes of habitat complexity at each site. Within each plot, we established two transects perpendicular to one another. We oriented one 50 m transect down the center of the plot and oriented the second transect perpendicular to the first forming a 'T' shaped pattern (Fig. 1). At 5 m intervals along each 50 m transect, we placed a 1 m^2 quadrat (21 quadrats per transect). Each 1 m^2 quadrat was divided into twenty 25 × 20 cm sections and the presence or absence of termite sheetings in each section was recorded (Fig. 1). The number of sections with sheetings present was then summed for each transect and site. The response variable was the total number of sections per site ($n = 20$ sections x 21 quadrats x 2 transects x 2 plots = 1680 sections per site) that had termite sheetings present per site and were inferred as an index of the abundance of sheetings on each site.

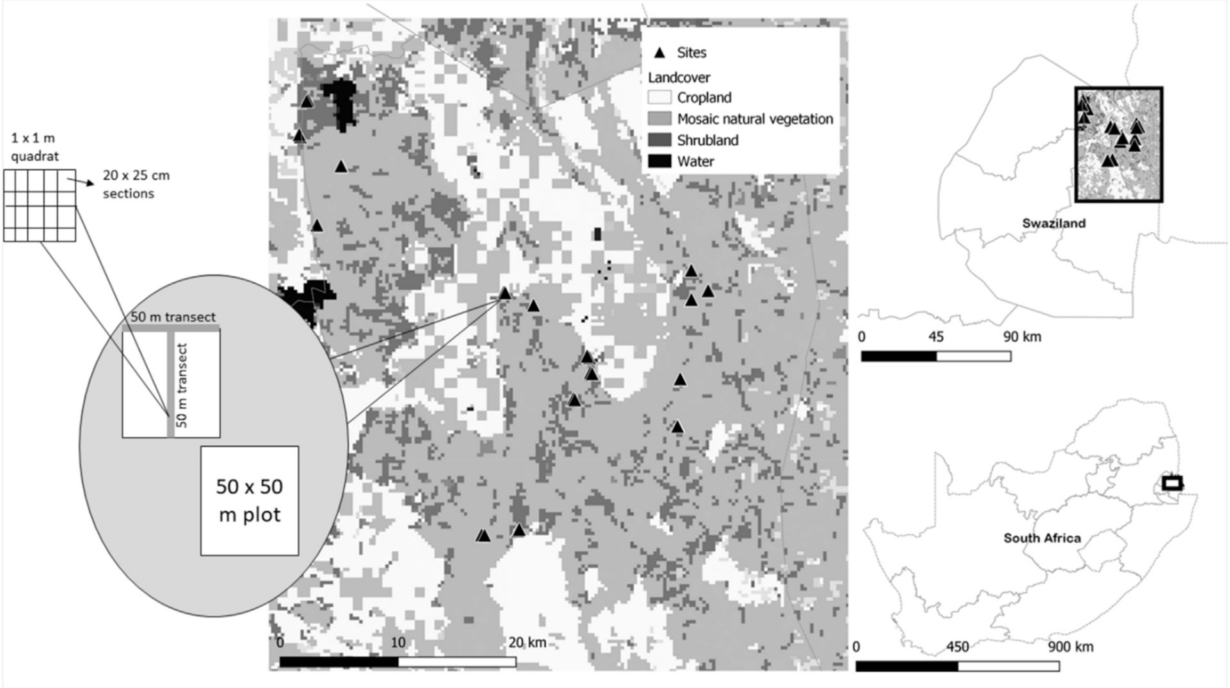

Fig. 1. Experimental design of field sampling for termite sheetings at 16 sites within Eswatini lowveld. Presence or absence of sheetings were determined for twenty 20 × 25 cm sections per quadrat. Twenty one quadrats were located at 5 m intervals along two perpendicular transects within a plot. Two plots were sampled per site. Termite sheetings were quantified as the number of sections with sheetings present per site.

2.4. Landscape covariates

We used parametrized metrics of configuration and composition rather than rank scores of principle components as covariates in our analyses to aid in interpretation of survey results. We also included as covariates the proportion of subsistence agriculture and the proportion of commercial agriculture surrounding each of our 16 savanna sites. For these landscape covariates, we calculated values at 1-, 2- and 5-km buffers surrounding each of the 16 savanna sites. We also included the geology type at each site as a covariate.

At each of the three spatial scales, we calculated a Shannon diversity index of landcover types (SHDI) as the single metric of compositional heterogeneity (Table S1), as it is commonly used to represent compositional landscape diversity (Cushman et al., 2008). The rest of the predictor variables for configurational heterogeneity were selected based on correlation coefficients that were less than or equal to 0.80 to remove variables that were highly correlated. (Table S2). To represent configurational heterogeneity, we selected total edge (TE) and number of patches (NP) at each spatial scale (Table S1). We also calculated proportions of subsistence (rural) and commercial (sugarcane) agriculture at the three spatial scales (Table S1).

2.5. Data analysis

We created three sets of generalized-linear mixed effects models to test for the effect of the landscape on the total number of sections with termite sheetings present; one set for each calculated scale (1-, 2-, and 5-km). Because the response variable was not normally distributed, we fitted the model to a Poisson distribution (Bolker et al., 2009). We tested the response variable of termite sheetings to the fixed effect variables of SHDI, TE, and NP for landscape heterogeneity as well as the proportion of each land-use type, rural and sugarcane and soil type. Site was included in the models as a random effect. All predictors were scaled and centered so that model estimates were comparable. The exception was geology type, which was a categorical variable. We tested a candidate set of 15 models comprising single and multiple fixed effects and included a null and global model.

We used R statistical software v 3.5.1 (R Core Team, 2018) with the lme4 package (Bates et al., 2015) for analysis of models and the MuMIn package (Barton, 2018) for model comparison. We compared all models within each candidate set using the Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002). We considered the model with the lowest ΔAICc score as the best model but considered all models that fell within <2 ΔAICc of the best model as competing models. If the best model fell within <2 ΔAICc of the null model, then these models were considered to have predictive power similar to the null (Burnham and Anderson, 2002). We then compared the best model of each subset within each scale to determine if heterogeneity or land-use type had a more dominant effect on termite sheetings presence. The parameters of competing models were considered significant if their 95% confidence interval did not overlap zero. For graphical representation, compositional diversity was factored to the categorical scale of −1 through 2 to the configuration metrics of the amount of edge at the 1-km scale and the number of patches at the 2-km to compare the effects of these different metrics against each other to the response variable of number of sections per site with termite sheetings present.

3. Results

We recorded the presence of termite sheetings at 4908 of the 26,880 total sections over the 16 sites that we surveyed. The percent of sections with sheetings presence ranged from 11% to 77% with an average of 37% per sampling plot. Throughout the results we refer to the response variable, number of sections with sheetings present, as foraging activity.

3.1. *Response to landscape heterogeneity*

The best model of each candidate set demonstrated that the scale of effect was important to drivers of termite foraging activity, with termite foraging activity having the strongest response to aspects of landscape heterogeneity at the 1-km and 2-km scales (Table 1; Fig. 1). Across all scales compositional diversity (SHDI), configurational heterogeneity in the form of total amount of edge (TE) and total number of habitat patches (NP), and geology were important predictors on termite foraging activities (Table 1). At the 1-km scale termite foraging activity was highest in savanna patches when surrounded by rhyolite derived soil. Termite foraging activity declined as the amount of limestone derived soils increased across all spatial scales (Table S3). At the 1-km scale termite foraging activity increased with increasing compositional diversity but decreased as the total amount of edge in the surrounding matrix increased (Table S3; Fig. 2a). At the 2-km scale, compositional diversity again caused an increase in termite foraging activity, but the total number of habitat patches surrounding the surveyed savanna reduced the amount of termite foraging activity (Table S3; Fig. 2b). Therefore, as the surrounding agricultural landscape became more fragmented with many small land-use patches, termite foraging activity decreased within the savanna patches. At the smaller spatial scales, the landscape heterogeneity metrics exhibited a stronger effect than the geology of the landscape (Table S3). At the 5-km scale, geology within the savanna patch became the dominant factor in predicting termite foraging activity, complimented with the surrounding land-use type of sugarcane, which demonstrated a significant positive relationship with termite foraging activity (Table S3, Fig. 3).

4. Discussion

We predicted that landscape heterogeneity would have mixed effects on termite foraging activity such that compositional heterogeneity would have a positive influence and configurational heterogeneity would have a negative influence. We also expected that at the larger landscape scale, geology would be the determinant factor on termite foraging activity. Based on our results, these expectations were supported by the data. Landscape compositional and configurational heterogeneity were the most important factors influencing termite foraging activity in savanna at 1- and 2-km scales. At these smaller scales, high compositional diversity promoted termite foraging activity, but high configurational heterogeneity hindered termite foraging activity within the savanna site. At the 5-km scale, termites in savanna patches surrounded by low to moderate proportions (up to 50%) of high intensity sugarcane monocultures had higher levels of foraging activity, however the geology of the landscape was the strongest predictor of termite foraging activity at this scale.

Compositional diversity consistently exhibited a significant positive relationship with termite foraging activity in each of the best and competing models at the 1- and 2-km spatial scale. This trend may occur because habitat diversity tends to increase resource diversity (Tews et al., 2004), which may feedback to termites by providing a greater breadth of resources

Table 1
Generalized linear mixed models investigating the effects of landscape heterogeneity on termite foraging activity. Included are models with delta AICc <2 at the 1, 2, and 5-km scale as well as the null models.

Model	DF	AICc	ΔAIC	Weight
1-km scale				
Geology + TE + SHDI	7	378.8	0	0.538
Geology + TE + SHDI + rural	8	380.1	1.3	0.281
Null	2	407.4	28.59	0
2-km scale				
Geology + NP + SHDI	7	391.3	0	0.467
Null	2	407.4	16.16	0
5-km Scale				
Geology + sugarcane	6	394	0	0.288
Geology + SHDI + sugarcane	7	395	0.95	0.179
Geology	5	395.9	1.94	0.109
Geology + rural	6	395.9	1.94	0.109
Null	2	407.4	13.43	0

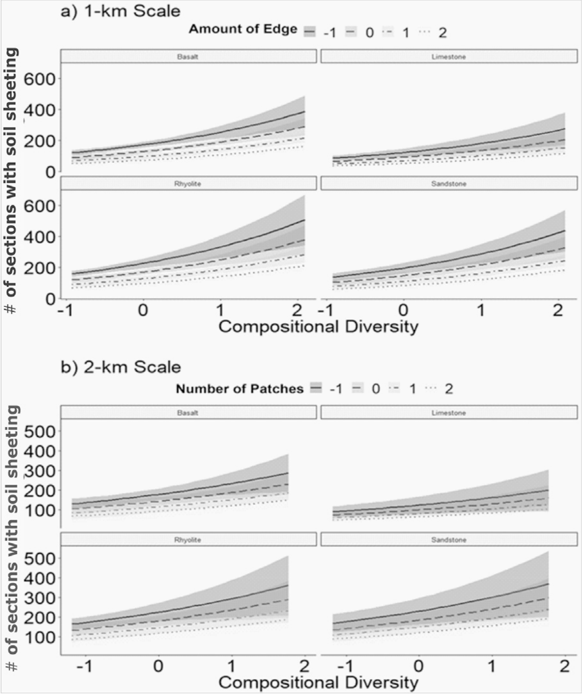

Fig. 2. Predicted curve of the total number of sections with termite sheetings present within savanna sites compared to landscape factors at the 1- and 2-km scales. Compositional diversity, the amount of edge at the 1-km scale (a) and number of patches at the 2-km scale (b) and soil composition were regressed against the predicted sum of sections with termite sheetings for each of the 16 savanna site with the shading representing 95% confidence intervals.

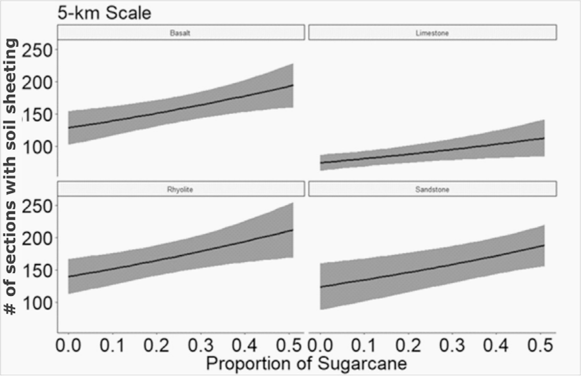

Fig. 3. Predicted sum of sections with termite sheetings present per site compared to the proportion of sugarcane surrounding the savanna site and geology type with the shading representing 95% confidence intervals.

that can be imported into a savanna patch (Jouquet et al., 2018). At the 5-km scale, however, the diversity of the landscape no longer had a significant effect and the geology and agricultural intensity became the significant drivers of the observed termite foraging activity. Geology is a dominant driver of termite diversity in African savannas at large spatial scales. High soil pH affects termite gut physiology by disrupting key physiological processes (Jones et al., 2010). In our study termite foraging activity was highest on acidic rhyolite soils with a lower pH than the basaltic and limestone soils. Termites also favor nutrient-poor soils, such as rhyolite, potentially due to reduced competitive exclusion of a few dominant species in nutrient-rich soils (Muvengwi et al., 2018b). Rhyolite also tends to have sandier soils compared to basaltic soils which aids in higher foraging rates (Pequeno et al., 2015).

In this study savanna patches with up to 50% of sugarcane surrounding the patch increased termite foraging activity. Sugarcane belongs to the grass family (*Poaceae*) and is therefore likely to contribute to termite food sources when sugarcane leaf litter is imported into the system. This increase in litter resource provides an alternate food source for litter-feeding termites, which are the functional guild responsible in producing soil sheetings (Ndiaye et al., 2004), and therefore can result in increased termite foraging activity. Macrotermitines, which are fungus-growing termites, will also migrate into disturbed areas from surrounding habitat, but their colonization depends on species already present and on the connectivity of the surrounding landscape matrix (Six et al., 2011). Therefore, low to moderate levels of sugarcane monoculture surrounding savanna patches can result in an increase in litter-feeding termite groups.

High configurational heterogeneity (which describes the shape and arrangement of patches) negatively impacted termite foraging activity at smaller spatial scales. As the amount of edge and number of patches surrounding the savanna patch increased, termite foraging activity within the patch decreased. In previous studies, measures of termite richness and abundance were resilient to habitat fragmentation; however, decomposition rates were decreased (Almeida et al., 2017; Genet et al., 2001). These previous findings suggest that specific species may drive decomposition rates in these systems and habitat fragmentation could result in the absence of these key species. Future research needs to be done to understand individual contributions of termite species to decomposition rates in savanna patches and how habitat fragmentation affects community composition, abundance and activity.

This study highlights the importance of interacting spatial scales and demonstrates that while low to moderate levels of agricultural intensity (up to 50% of the landscape) can promote termite driven processes, these positive interactions can only occur if the surrounding habitat matrix is not highly fragmented. We infer that large diverse patches of a mixture of high and low intensity agriculture along with savanna maintain healthy levels of termite foraging activity as well as soil turnover better than a landscape with small patches of these habitat types. Similar patterns of landscape heterogeneity have also been found to increase bee pollination in agricultural landscapes where the proximity to agriculture can boost pollinator abundance and/or diversity in natural habitat fragments, possibly due to floral resources provided in agricultural areas (Eltz et al., 2002; Winfree et al., 2007). Although not measured in our study, it should be noted that in other systems, smaller patches of natural habitat, although locally attractive may not be able to sustain positive reproduction, resulting in sinks or ecological traps (Kremen et al., 2007).

The altering of termite foraging activity due to landscape structure can have cascading effects on the nutrient cycling processes within these agricultural-savanna landscapes by affecting decomposition and nutrient translocation rates. In the semi-arid savannas of African landscapes, termites are the main litter decomposers in these systems, especially in the dry season where they are virtually the only active decomposers (Jouquet et al., 2011). Soil turnover by soil sheetings formation has a substantial effect on maintaining healthy land-use systems by helping to restore soils via increasing water infiltration and soil aeration (Kaiser et al., 2017). Nutrients that may be contained in these soil sheetings are also able to be recycled quickly and hence can increase nutrient content (Sileshi et al., 2010). Habitat fragmentation can disrupt these termite driven processes resulting in disrupted nutrient flows and soil restoration, affecting the productivity of the savanna system.

Termite sheetings as a proxy for termite foraging activity likely underestimates the nutrient cycling activity of this macrofaunal guild, as different termite species can exhibit different foraging patterns. However, the majority of surface soil sheetings comes from a few dominant, fungus-growing species which have been found to be the main drivers in decomposition rates within disturbed systems (Schuurman, 2005). More broadly, termite soil sheetings have only recently begun to receive attention in scientific research, with only a handful of studies measuring the soil characteristics and amount of soil translocation attributed to these structures (Harit et al., 2017; Kaiser et al., 2017; Rouland et al., 2003). More studies are needed to understand the fate of these structures and their influence on nutrient cycling processes.

4.1. Conservation implications

As anthropogenic land-use continues to develop in these systems, landscape planning needs to incorporate modification strategies that maintain and enhance these termite nutrient cycling services to manage sustainable, land-use landscapes. To accomplish this, understanding what drives termite foraging activity is a critical step. Based on this study, protecting large patches of savanna and low intensity agriculture within monoculture systems will aid in maintaining relatively high termite foraging activity and soil turnover. Land-use conservation strategies need to be multi-scaled when considering termite driven processes as termites respond to different drivers at different scales (Gosling et al., 2016). Termites have traditionally been perceived to be pests in agricultural landscapes, but both ants and termites have been found to increase crop yields in arid climates, suggesting that maintaining large savanna patches around monocultures can benefit the crops themselves (Evans et al., 2011).

4.2. Conclusion

The provision of ecosystem services has been a major topic in contemporary conservation. Previous works have quantified the critical services of termite activity on their respective systems (Bagine, 1984; Harit et al., 2017; Kaiser et al., 2017; Sileshi et al., 2010; Tongway et al., 1989) resulting in the classification of termites as key ecosystem service providers for both decomposition and soil generation services, according to the Millennium Ecosystem Assessment (2003) (Kremen, 2005). The objective of this study was to determine if the complexity of the landscape affects termite foraging activity. Our results provide novel insights in how the structure of the landscape affects termite foraging activity. Landscape heterogeneity may affect termite nutrient cycling services within these savanna mosaics, beyond local biotic and regional climatic factors, demonstrating that multiscale approaches in conservation management are necessary to maintain sustainable termite driven services within anthropogenic, land-use landscapes. However, further research needs to be done to determine the causal mechanisms that drive the relationship between termite activity and the landscape complexity observed here.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00885.

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