Research article

Land use effects on termite assemblages in Kenya

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ABSTRACT

Termites perform key ecological functions and they also cause crop damage. Land use change resulting from agricultural intensification can result in changes in termite species diversity and abundance. Termite species occurring in natural vegetation, maize monocrop and maize-beans intercrop macrohabitats were investigated in Embu and Machakos Counties, Kenya. Influence of soil properties and seasons was also evaluated. Across the two Counties, seven termite species were recorded with Machakos County having the highest number. Additive diversity partitioning of species richness and Simpson diversity showed that, α component contributed to 98.3% and 99.1% of the total diversity, respectively. Population densities of three termite species significantly varied between land use types in Machakos County but there were no differences in termite species abundance in Embu County. In addition, there were no significant differences in species richness between macrohabitats within each County. In Embu, season significantly influenced the abundance of *Macrotermes subhyalinus, M. herus,* and *Coptotermes formosanus* which occurred in greater numbers during the wet season. There was a significant influence of land use on *Trinervitermes gratiosus* and *C. formosanus* in Machakos with both species occurring in higher numbers in natural vegetation. *Trinervitermes gratiosus* was negatively associated with Mn and positively correlated to pH and sand. *Macrotermes subhyalinus* and *M. herus* showed a positive association with P and silt while *C. formosanus* was positively correlated to Ca and Mg. These findings provide an insight into the effects of land use change from natural vegetation to maize agro-ecosystems on termite diversity. It also provides a baseline for further studies on termite diversity in Kenya and their ecological significance.

1. Introduction

Termites form an important component of the soil invertebrate community and they contribute to different ecosystem services (Jouquet et al., 2011). Like most biodiversity, they are threatened by agricultural intensification (Zabel et al., 2019) which is on the rise in sub-Saharan Africa (SSA) (Haggar et al., 2020). In the last decade, conversion of natural ecosystems to agricultural land has been observed in SSA in order to cater for the increased demand in supply of key staple crops (Kuyah et al., 2021). In Kenya, maize is widely consumed by both rural and urban population and the area of production has increased in the last decade (FAOSTAT, 2021). Loss of biodiversity, including termites, that results from unsustainable agricultural production can have implications on functioning of agro-ecosystems (Jouquet et al., 2011).

Termite populations can be high, reaching up to 15,000 individuals/m^2. They play an important role in ecosystem functioning through their involvement in organic matter decomposition, soil pedogenesis and nutrient cycling. They also influence microbial, plant and animal diversity through landscape modifications in water and nutrient distribution (Jouquet et al., 2011). In Uasin Gishu plateau, Kenya, Jungerius et al. (1999) reported that termites improved soil structure by producing stable microaggregates in the sub-soil. Importance of termites in key ecosystem functions was demonstrated in a study in the Kenyan Laikipia plateau whereby subterranean termites influenced N fixation by *Acacia drepanolobium* and subsequently affected spatial distribution of the *Acacia* which had ecological implications on the entire community (Fox-Dobbs et al., 2010). At the same site, Pringle et al. (2010) observed that mounds built by *Odontotermes* species improved plant productivity while Baker et al. (2020) reported that *Odontotermes montanus* affected the diversity of fungi and bacteria at localized points within mounds. The effect was scaled up to the entire savanna community at regular spatial points which increased fungal and bacterial diversity with implications for ecosystem functioning.

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In tropical agro-ecosystems, termites are perceived as pests with no consideration for the important ecosystem services that they provide; exploring potential utilization of these ecosystem services in cropping systems is proposed (Jouquet et al., 2011). In some African countries, farmers have utilized the ecosystem engineering function of termites in improving productivity of farmland and restoration of degraded land through the use of Zaï pits (Kaiser et al., 2017; Nyantakyi-Frimpong, 2020; Roose et al., 1999). Apart from the ecological role that they perform, termites can also reduce crop yields (Govorushko, 2019) and damage their quality (Black and Okwakol, 1997). Maize production by smallholders in SSA is largely rainfed (Prassana et al., 2021) which makes it susceptible to termite damage (Govorushko, 2019). In western Kenya, farmers reported damage of their crops and trees by termites (Adoyo et al., 1997) while in Zimbabwe, Mutsamba et al. (2016) observed a high prevalence of Macrotermitinae termites in maize under conservation agriculture.

Different termite species have been identified in Kenya (Anyango et al., 2020; Ayuke et al., 2011; Kagezi et al., 2011; Makonde et al., 2013; Vesala et al., 2017). However, there are limited studies on the influence of land use, soil properties and seasons on their diversity. Land use change through agricultural intensification can affect termite diversity and the ecosystem services that they provide. Soil macrofauna in Zambia varied across land use systems whereby termite abundance was higher in miombo woodland relative to maize monoculture and maize intercropped with trees (Sileshi and Mafongoya, 2006). Black and Okwakol (1997) posits that land use change from natural vegetation to agricultural land can affect termite diversity which can consequently affect nutrient cycling, energy flow, gas fluxes and vegetation diversity. In Cameroon, agricultural land that was converted from a tropical forest had a lower number of soil-feeding termite species which the authors argued could negatively affect crop yields (Eggleton et al., 2002). Similarly, anthropogenic disturbance in a West African savannah resulted in reduced population densities of termite species relative to a protected national park (Hausberger and Korb, 2016).

In addition to the influence of land use change on termites, soil properties and climatic variables can also affect their diversity (Eggleton, 2000; Bourguignon et al., 2015; Davies et al., 2015). Soil that has finer particles is preferred by termites (Jouquet et al., 2002) and soil properties influence their interactions with micro- and macro-aggregates (Jouquet et al., 2016) and also affect occurrence of different species (Sanabria et al., 2016). Temperature and moisture variations across seasons also affect termite diversity (Davies et al., 2015) —warming and rainfall influences the distribution and architecture of mounds (Korb and Linsenmair, 1998; Shanbhag et al., 2017). Knowledge on the influence of land use change on termite diversity in Kenyan maize agro-ecosystems and natural systems is crucial since it will form a basis for understanding their ecological role and potential economic impact which will consequently inform sustainable crop production that taps into the ecosystem services that they provide. Such information will also be important in designing species-specific integrated termite management programmes that are ecologically sustainable. We therefore tested the hypotheses that i) land use change affects termite diversity and ii) termite diversity is affected by soil and climatic variables.

2. Materials and methods

2.1. Study sites

The study was conducted in Kithimani, Matuu, and Ndalani locations of Machakos County and Kangaru, Kamiu and Ena of Embu County, Kenya (Figure 1). Study sites in Machakos and Embu were at an average altitude of 1240 and 1600 m above sea level, respectively. The rainfall pattern in both counties is bimodal, with the first rainy season (long rains) starting from March to June while the second (short rains) starts in mid-October and ends in December. In each location, three macrohabitats comprising of maize monocrop farms, maize intercropped with beans and natural vegetation were sampled. Three replicates of each macrohabitat in each County were sampled. The replicates were 20km apart from each other. In both Counties, natural vegetation comprised of grass, *Lantana camara* and *Acacia* species. The maize monocrop and maize-bean intercrop macrohabitats had been converted from adjacent natural vegetation and had been under cultivation for 20 years.

2.2. Termite sampling and identification

Three 100 × 2 m belt transects separated by 100m were laid out at each macrohabitat as described by Jones et al. (2003). Twenty 5 × 2 m sections from each transect were sampled (one-person hour) from different microhabitats that included dead wood, soil, mounds, leaf litter, sheeting and runways. From each section, termites were also collected from twelve (12 cm × 12 cm, 10 cm deep) pits. Sampling across all sites was done during dry and wet seasons for two consecutive years (dry

Figure 1. Study sites at Kithimani, Matuu, and Ndalani locations of Machakos County and Kangaru, Kamiu and Ena of Embu County, Kenya.

season one -July to September 2018, dry season two – Jan to March 2019, wet season one – Oct to Dec 2018 and wet season two – March to May 2019). During each season, samples were collected at monthly intervals and stored in 80% ethanol. Collections of soldier and/or worker castes were identified to species levels using taxonomic guides (Webb, 1961; Sands, 1998) and through reference collections of National Museums of Kenya. For soil physico-chemical analysis, samples were collected from each point in the macrohabitats and a composite 500g sample was used for analysis. Soil samples were air dried at 23–55 °C before analyses at the Kenya Agricultural and Livestock Research Organization, National Agricultural Research Laboratories. Soil texture was determined using the hydrometer method (Klute, 1986) while the Mehlich double acid method was used to assess Phosphorus, Sodium, Potassium, Calcium, Magnesium and Manganese (Mehlich et al., 1962). Nitrogen content was analyzed using the Kjeldahl digestion method (Bremner and Mulvaney 1982) and soil pH was determined in a 1:1 (w/v) water extract as described by Mehlich et al. (1962). For analyses of Copper, Iron and Zinc, 0.1 M HCL in 1:10 (w/v) ratio was used for extraction before Atomic Absorption Spectrophotometer readings were taken (Mehlich et al., 1962). Carbon was determined colorimetrically following Anderson and Ingram (1993).

The average rainfall and minimum temperature data were obtained from the Kenya Meteorological Department.

2.3. Data analysis

We checked the termite species abundance data for normality and log (x+1) transformed where necessary. The data from the two dry seasons (dry season one -July to September 2018, dry season two – Jan to March 2019) was pooled and the average was used for subsequent analyses. The same was done for the two wet seasons (wet season one – Oct to Dec 2018 and wet season two – March to May 2019). To assess the influence of season (dry and wet) and macrohabitats (maize monocrop, maize intercropped with beans and natural vegetation) on termite species and diversity indices in Embu and Machakos Counties, we performed a two-way analysis of variance with subsequent Tukey honestly significant difference post hoc tests. We also conducted simple main effects tests for significant season × macrohabitat interactions. Species richness, Pielou's evenness, Shannon-Weaver and Simpson diversity indices were analyzed using vegan package version 2.5–7 in R statistical software (Oksanen et al., 2020). To assess the contribution of α (diversity within fields) and β diversity (diversity between fields in different sites) to the total termite diversity (γ = α+β), we carried out additive diversity partitioning (Lande,

1996) using the *adipart* function (Crist et al., 2003) in R package vegan version 2.5–7 (Oksanen et al., 2020). This function considers that mean alpha (α) and beta (β) diversities add up to gamma (γ) diversity. The six sites were Kangaru, Kamiu, Ena (Embu County), Matuu, Mamba and Kambi ya mawe (Machakos County). The additive partitioning of diversity was based on species richness, Shannon-Weaver and Simpson indices. Permutation analyses was used to determine the expected diversity.

Non-metric multidimensional scaling (nMDS; Clarke and Ainsworth, 1993) using Jaccard index was used to present the spatial patterns of termite species populations in Embu and Machakos Counties and the differences were analyzed using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) with soil type as a fixed factor, followed by permutational multivariate analysis of dispersion (PERMDISP) (Anderson, 2006). We evaluated the most influential species and their contribution to site dissimilarities using similarity percentage analysis (SIMPER). The vegan functions *simper, metaMDS, adonis* and *betadisper* in R version 2.5–7 were used in the analyses (Oksanen et al., 2020). We determined relationships between climate and soil variables through Canonical correspondence analysis (CCA) in vegan package (Oksanen et al., 2020).

3. Results

Across the two Counties, seven termite species were recorded with Machakos County having the highest number—seven due to the presence of *Trinervitermes gratiosus*. In Embu County, season significantly influenced the abundance of *Macrotermes subhyalinus*, *Macrotermes herus*, and *Coptotermes formosanus*. *Odontotermes badius* was the only species whose abundance was influenced by the interaction of season and macrohabitat (Table 1; Figures 2 and 3). A test of simple main effects showed that interaction between dry season and natural vegetation was significant ($P = 0.01$).

In Machakos County, the abundance of one species (*Cubitermes ugandensis*) was affected by season × macrohabitat interaction. Specifically, there was a significant interaction of both seasons with maize monocrop ($P < 0.001$). The number of *M. herus*, and *O. longignathus*, was affected by season. Abundance of *T. gratiosus*, and *C. formosanus*, was influenced by both season and macrohabitat. *Trinervitermes gratiosus* which was only recorded in Machakos County occurred in greater numbers in the natural vegetation macrohabitat. In Embu and Machakos Counties, *C. formosanus* occurred in greater numbers during the wet season (Table 1; Figures 2 and 3). Machakos County had the highest

Table 1. Two-way analysis of variance of season, macrohabitat and their interaction on termite species in Embu and Machakos Counties.

	Season		Macrohabitat		Season X macrohabitat	
	F	P	F	P	F	P
Embu						
Macrotermes subhyalinus	9.0	0.011*	0.1	0.895	0.3	0.723
Macrotermes herus	12.0	0.005**	2.3	0.139	1.0	0.397
Odontotermes badius	16.3	0.002**	1.0	0.397	4.3	0.038*
Cubitermes ugandensis	2.0	0.183	0.5	0.619	0.5	0.619
Odontotermes longignathus	3.2	0.099	0.2	0.821	0.2	0.821
Coptotermes formosanus	36.0	<0.001***	3.3	0.074	2.3	0.148
Machakos						
Macrotermes subhyalinus	4.5	0.055	0.7	0.537	0.1	0.911
Macrotermes herus	5.6	0.036*	0.1	0.946	0.4	0.686
Trinervitermes gratiosus	17.3	0.001**	8.6	0.004**	2.8	0.102
Odontotermes badius	0.9	0.361	1.3	0.308	0.3	0.746
Cubitermes ugandensis	196.0	<0.001***	19	<0.001***	7.0	<0.001***
Odontotermes longignathus	8.0	0.015*	0.9	0.441	0.1	0.883
Coptotermes formosanus	14.3	0.003**	8.1	0.006**	1.9	0.198

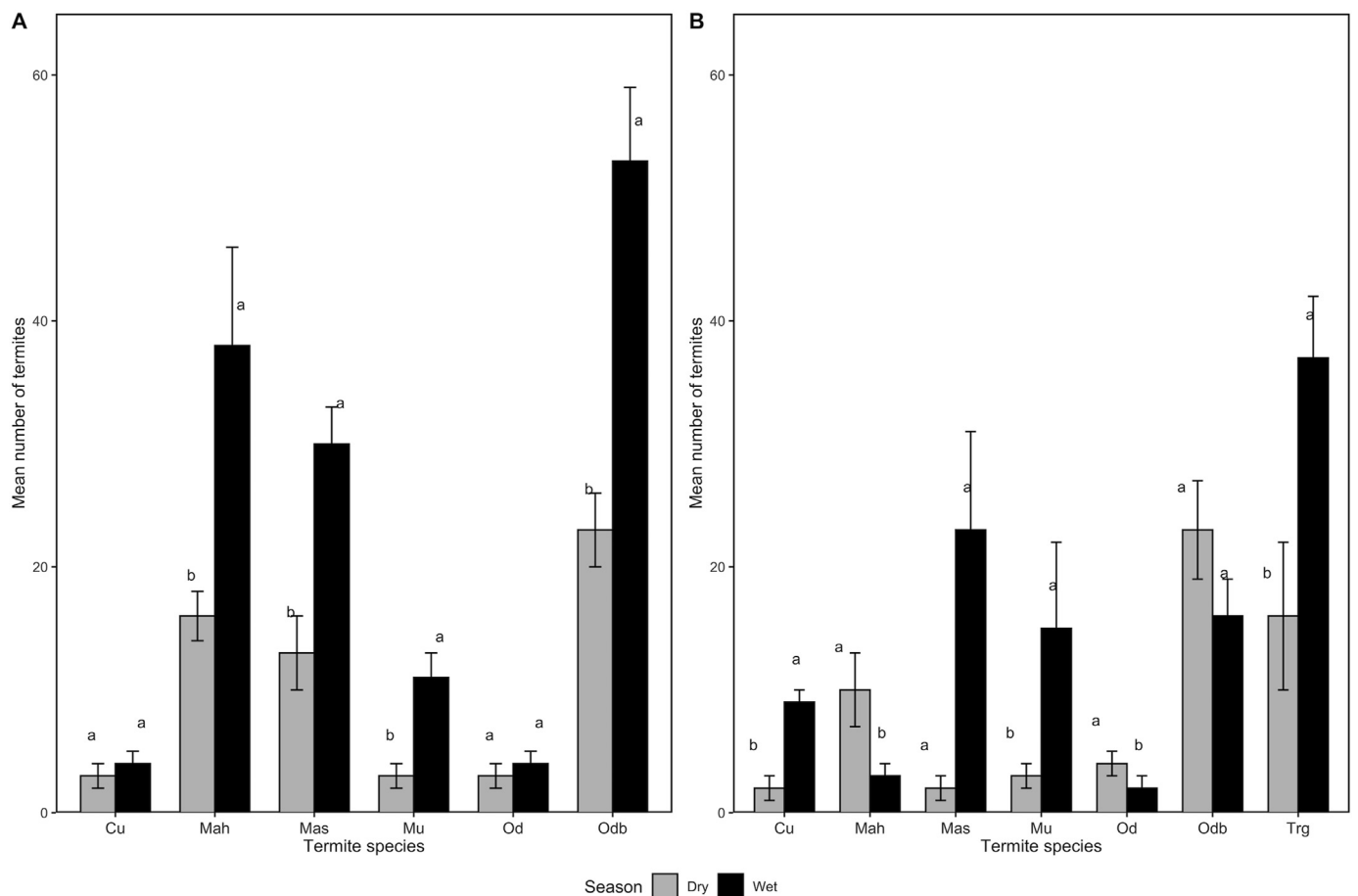*** = P < 0.001, ** = P < 0.01, * = P < 0.05.

Figure 2. Abundance (mean ± standard error) of termite species during dry and wet season in A) Embu and B) Machakos Counties. Different letters indicate significant differences in abundance of termite species. Mas- *Macrotermes subhyalinus,* Mah-*Macrotermes herus,* Trg- *Trinervitermes gratiosus,* Odb- *Odontotermes badius,* Cu-*Cubitermes ugandensis,* Od- *Odontotermes longignathus* and Mu- *Coptotermes formosanus.*

number of termite species; however, the species richness did not vary across macrohabitats within each of the two Counties. However, Pielou'evenness was significantly lower, in the maize-beans intercrop relative to natural vegetation in Embu County (Table 2). In Machakos County, the Simpson diversity index was greater during the wet season (see Table 3).

Additive diversity partitioning was conducted for species richness, Shannon-Weaver and Simpson indices in Kangaru, Kamiu, Ena (Embu County), Matuu, Mamba and Kambi ya mawe (Machakos County) sites. From the diversity partitioning of richness, 98.3% of the total diversity was contributed by α component which was significantly lower than expected ($P = 0.0001$). On the other hand, contribution of β diversity was higher than expected by chance ($P = 0.0001$). Within fields, α Simpson diversity was greater (99.1%) than β diversity but lower than expected ($P = 0.0001$; Figure 4).

In the NMDS analysis, there was distinct differentiation of termite species in Machakos and Embu County (Figure 5; PERMANOVA, $R^2 = 0.4$, $F = 12.7$, $P = 0.001$; PERMDISP, $F = 9.91$, $P = 0.006$) with an average dissimilarity of 50.5%. The most influential species contributing to the dissimilarity were *M. herus, T. gratiosus,* and *O. badius.*

Soil from Embu and Machakos showed significant variations in pH, P, Ca, Mg, Mn, Zn, sand and clay (Table 4). From the CCA analysis of soil properties and termite species, the first and second axes accounted for 79.9% of the variance. *Trinervitermes gratiosus* was negatively associated with Mn but positively correlated to pH and sand. *Macrotermes subhyalinus* and *M. herus* showed a positive association with P and silt while *C. formosanus* was positively correlated to Ca and Mg. There was a positive correlation between *O. badius* and Cu (Figure 6).

The minimum temperature and rainfall during the study period is provided in Table 5. Minimum temperature (°C) in Embu County during both seasons ranged from 12.7 ± 0.2 to 15.6 ± 0.68 while rainfall (mm) was 30.2 ± 8.17 to 117.8 ± 49.67. The lowest minimum temperature and rainfall in Machakos County was 11.5 ± 0.78 and 5.6 ± 5.07, respectively. Based on the CCA analysis of climatic variables and termite species, 23.1% and 1.4% of the variance was explained by the first and second axis, respectively. *Trinervitermes gratiosus* showed a negative correlation with rainfall and minimum temperature while *M. subhyalinus* and *M. herus* were positively associated with rainfall (Figure 7).

4. Discussion

Several factors including anthropogenic disturbances resulting from land use change affect termite diversity (Muvengwi et al., 2017; Netshifhefhe et al., 2019). In this study, seven termite species were observed across the two Counties with Machakos County having the highest number—seven due to the presence of *T. gratiosus*. Presence of *T. gratiosus* in Machakos County may have been due to region-specific factors. Termite species observed in this study have been reported in Kenya and the number is within that observed in other studies (Anyango et al., 2020; Ayuke et al., 2011; Kagezi et al., 2011; Makonde et al., 2013; Vesala et al., 2017). Additive diversity partitioning of species richness and Simpson diversity showed that α component contributed 98.3% and 99.1% of the total diversity, respectively; an indication that most species were similar within fields in the two Counties. The low beta diversity within each county may be an indication of lack of significant differences in microhabitats which resulted in homogenization of the termite communities (Liu et al., 2019).
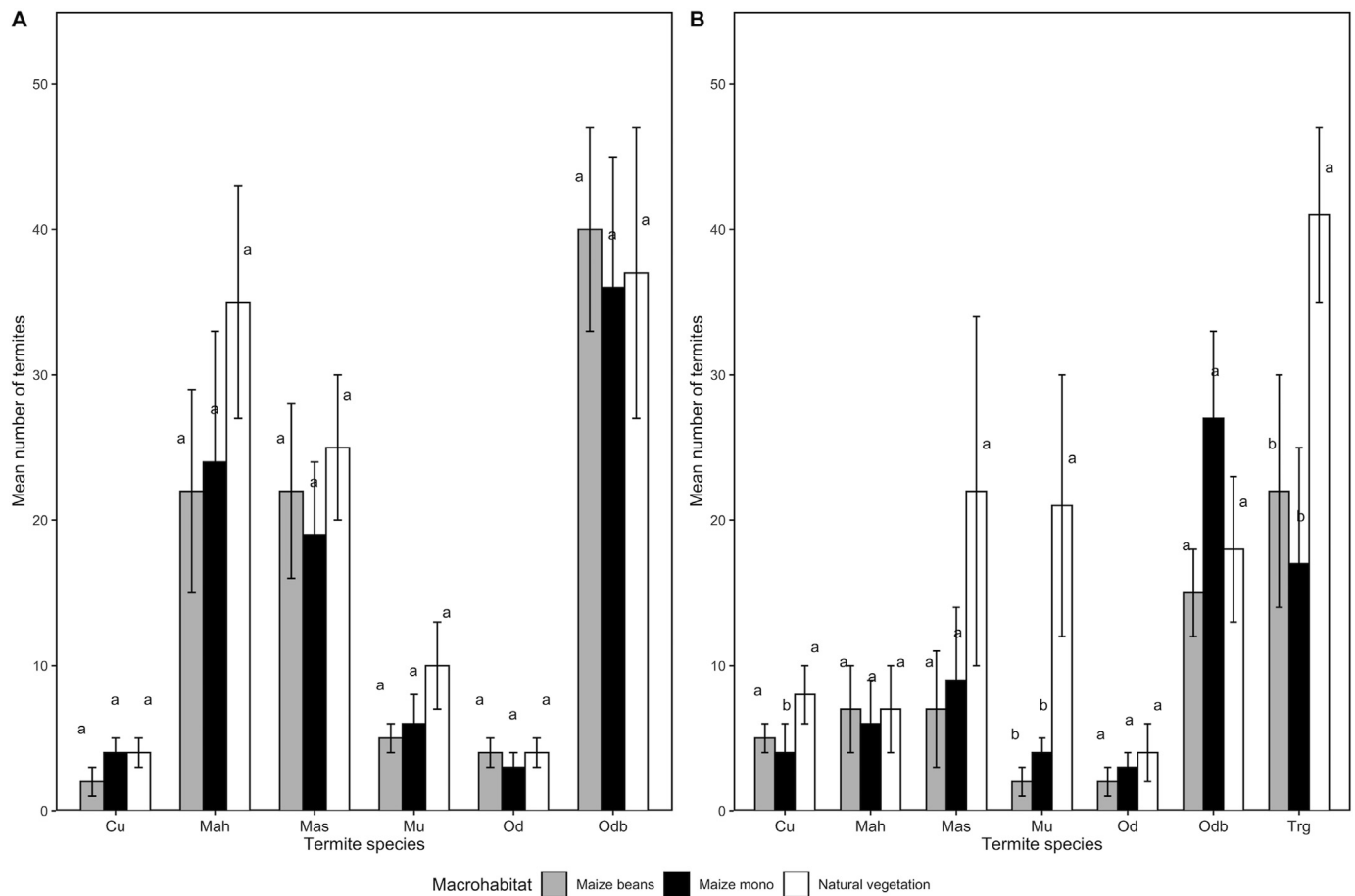
Figure 3. Abundance (mean ± standard error) of termite species in maize-beans intercrop, maize monocrop and natural vegetation macrohabitats in A) Embu and B) Machakos Counties. Different letters indicate significant differences in abundance of termite species. Mas- *Macrotermes subhyalinus,* Mah-*Macrotermes herus,* Trg-*Trinervitermes gratiosus,* Odb- *Odontotermes badius,* Cu- *Cubitermes ugandensis,* Od- *Odontotermes longignathus* and Mu- *Coptotermes formosanus.*

Table 2. Species richness, Pielou's evenness, Shannon-Weaver and Simpson diversity indices of three macrohabitats in Embu and Machakos Counties during wet and dry seasons.

County	Index	Maize-beans intercrop		Maize monocrop		Natural vegetation	
		Mean	SE	Mean	SE	Mean	SE
Embu	Shannon-Weaver	1.32a	0.04	1.37a	0.05	1.45a	0.02
	Simpson diversity	0.67a	0.02	0.69a	0.02	0.73a	0.01
	Species richness	5.83a	0.17	5.83a	0.17	5.83a	0.17
	Pielou's evenness	0.75b	0.01	0.78ab	0.02	0.83a	0.02
Machakos	Shannon-Weaver	1.37a	0.06	1.2a	0.10	1.42a	0.08
	Simpson diversity	0.68a	0.02	0.61a	0.04	0.68a	0.03
	Species richness	6.33a	0.33	5.67a	0.42	6.67a	0.33
	Pielou's evenness	0.74a	0.02	0.69a	0.04	0.75a	0.03

Different letters across the row indicate significant differences. SE-Standard error.

Population densities of three termite species significantly varied between macrohabitats in Machakos County but there were no differences in termite species abundance in Embu County. In addition, there were no significant differences in species richness between macrohabitats within each County. Contrary to the observations made in this study, loss of termite species due to agricultural activities has been reported in several studies. For instance, in Uganda 40% reduction in termite species richness was observed after a forest was cleared and the numbers reduced further when banana was cultivated (Okwakol, 2000). An agricultural field in Zimbabwe had lower termite species richness compared to a woodland and grazing area (Muvengwi et al., 2017). Application of fertilizers, liming and tillage— which led

to termite habitat changes —were farming practices that contributed to low number of termite species in Colombia. Furthermore, cultivation of annual crops such as maize was considered as the most unfavorable land use type for termite species (Sanabria et al., 2016). Supporting the observations of low termite abundance in Embu County, Kagezi et al. (2011) reported that there was no difference in populations of termite species between forested land and agricultural fields in Kenya. This was attributed to the study site altitude and the fact that moderate levels of disturbance did not affect species abundance. This is further corroborated by Muvengwi et al. (2017) in Zimbabwe where there were no differences in species richness between farmland and woodland habitats.

Table 3. Two-way analysis of variance of season, macrohabitat and their interaction on species richness, Pielou's evenness, Shannon-Weaver and Simpson diversity indices in Embu and Machakos Counties.

County		Season		Macrohabitat		Season X macrohabitat	
		F value	P value	F value	P value	F value	P value
Embu	Shannon-Weaver	0.19	0.67	2.89	0.09	0.25	0.79
	Simpson diversity	0.46	0.51	3.59	0.06	0.41	0.67
	Species richness	3.00	0.10	0.10	1.00	0.10	1.00
	Pielou's evenness	3.61	0.08	5.53	0.02*	0.39	0.69
Machakos	Shannon-Weaver	3.27	0.10	2.68	0.11	2.40	0.13
	Simpson diversity	5.07	0.04*	1.93	0.19	1.70	0.22
	Species richness	0.31	0.59	2.15	0.16	2.15	0.16
	Pielou's evenness	4.31	0.06	1.24	0.32	1.60	0.24

* = P < 0.05.

In Embu, *O. badius* which occurred in greater numbers during the wet season was influenced by season × macrohabitat interaction. Similar interaction in Machakos affected the abundance of *C. ugandensis* which was lower in the maize monocrop. Natural vegetation had a higher number of the species although it was not significantly different from maize-beans intercrop. *Odontotermes* spp. whose foraging activity increases during the wet season (Sattar and Naeem, 2013) causes considerable damage in maize and a study in Kenya demonstrated that they were associated with lodging in the crop (Anyango et al., 2019). Corroborating the observations made in this study, Okwakol (2000) observed a reduction in abundance of *Cubitermes* spp. and *Trinervitermes* spp. after clearance of a forest and subsequent banana cultivation which was attributed to mound destruction. Similarly, in West Africa, *Cubitermes* spp. occurred in lower numbers in agricultural plots due to high levels of disturbance (Eggleton et al., 2002). This species improves soil quality and fertility (Donovan et al., 2001), influences availability of nutrients to plants and the indirect contribution of symbiotic microorganisms to nutrient acquisition (Diaye et al., 2003). Reduced densities of *Cubitermes* spp. may therefore negatively affect crop yields (Eggleton et al., 2002).

In addition, there was a significant influence of habitat on *T. gratiosus* and *C. formosanus* in Machakos with both species occurring in higher numbers in natural vegetation. Occurrence of *Coptotermes* spp. in natural vegetation consisting of *Acacia* spp. has been previously reported (Intachat and Kirton 1997; Kirton et al., 1999). On the other hand, *Trinervitermes* has also been observed in undisturbed land in other studies (Hausberger and Korb 2016; Schyra and Korb, 2019). Compared to other termite species, *Trinervitermes* spp. is highly susceptible to disturbances because it is specialized in how it feeds and nests (Schyra and Korb, 2019). *Coptotermes* is among the invasive termite species (Evans, 2021) with potential ecological consequences. They colonize dead or living trees (Lee et al., 2015) in large colonies causing considerable damage to trees (Evans, 2021).

NMDS analysis clearly differentiated termite species in Machakos and Embu County probably due to regional differences. As per our hypothesis, soil properties affected termite species whereby *T. gratiosus* was negatively associated with Mn but positively correlated to pH and sand. *M. subhyalinus* and *M. herus* showed a positive association with P and silt while *C. formosanus* was positively correlated to Ca and Mg. Soil properties influence termite abundance and diversity (Dosso et al., 2010) and mound properties (Jouquet et al., 2015). *Trinervitermes* spp. is adapted to a wide range of soil types (Brossard et al., 2007) and can tolerate pH levels above 4 as observed in the current study (Mugerwa et al., 2011). Mills et al. (2009) observed that clay content in the top soil around
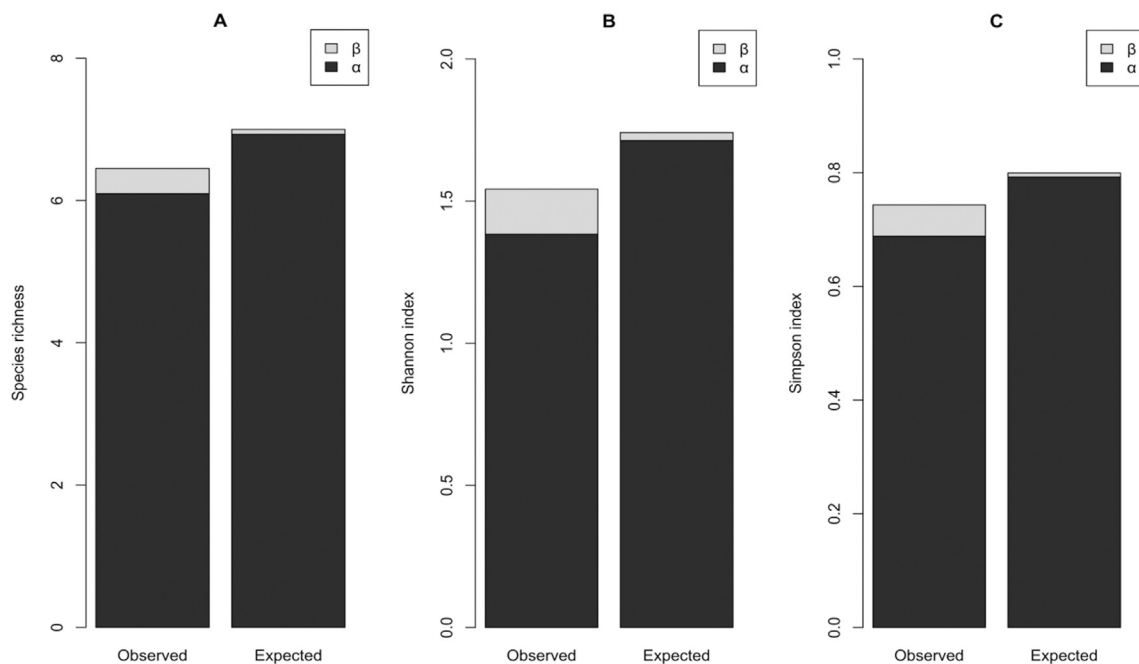

Figure 4. Additive partitioning of A) species richness B) Shannon-Weaver diversity and C) Simpson diversity for fields in Kangaru, Kamiu, Ena (Embu County), Matuu, Mamba and Kambi ya mawe (Machakos County) sites. Total diversity (γ) is partitioned into (α) and beta (β) components.
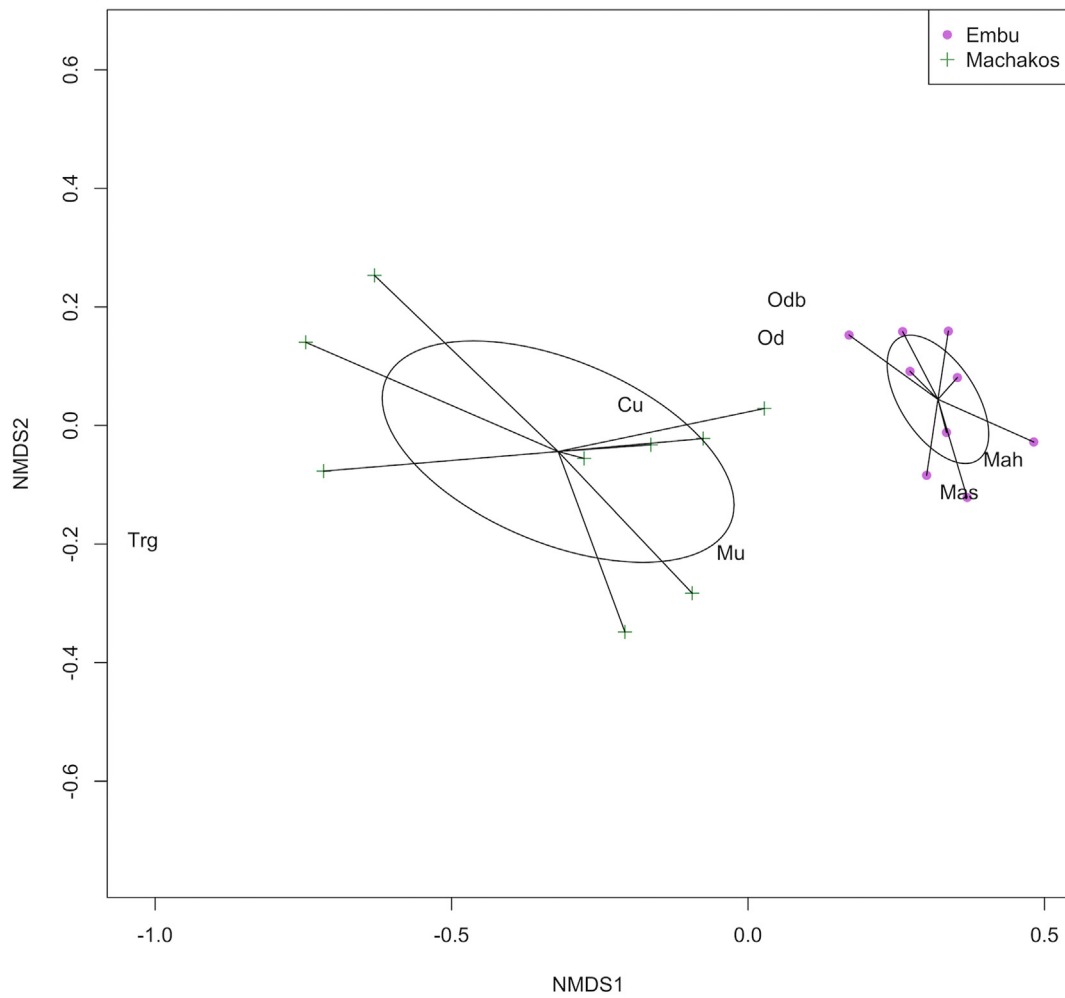
Figure 5. Non-metric multidimensional scaling (nMDS) ordination of maize-beans intercrop, maize monocrop and natural vegetation macrohabitats in Kangaru, Kamiu, Ena (Embu County), Matuu, Mamba and Kambi ya mawe (Machakos County) sites based on distribution of termite species (PERMANOVA: P = 0.001, NMDS; Stress = 0.06). Mas- *Macrotermes subhyalinus,* Mah-*Macrotermes herus,* Trg- *Trinervitermes gratiosus,* Odb- *Odontotermes badius,* Cu- *Cubitermes ugandensis*, Od- *Odontotermes longignathus* and Mu- *Coptotermes formosanus*.

Table 4. Physical and chemical properties of soil collected from Embu and Machakos Counties.

Soil property	Embu		Machakos		P value
	Mean	SE	Mean	SE	
pH	4.79a	0.07	7.26b	0.28	<0.001***
Total Nitrogen %	0.21a	0.07	0.17a	0.06	0.648
Total organic Carbon %	1.52a	0.18	1.2a	0.23	0.297
Phosphorous ppm	20.11a	1.42	15.44b	1.26	0.026*
Potassium meq%	0.44a	0.07	0.56a	0.11	0.362
Calcium meq%	0.84a	0.25	15.73b	5.83	0.021*
Magnesium meq%	0.83a	0.13	2.29b	0.63	0.039*
Manganese meq%	0.93a	0.08	0.33b	0.1	<0.001***
Copper ppm	0.5a	0.3	0.5a	0.11	0.99
Iron ppm	17.58a	2.97	17.58a	3.5	1
Zinc ppm	12.09a	3.26	1.54b	0.16	0.005**
Sodium meq%	0.47a	0.05	0.66a	0.12	0.151
Sand	47.11b	0.48	72a	4.18	<0.001***
Clay	47.33b	1	23.11a	3.7	<0.001***
Silt	5.56a	0.73	5.11a	0.75	0.68

Means with the same letter across the row are not significantly different. *** = P < 0.001, ** = P < 0.01, * = P < 0.05. SE-Standard error.
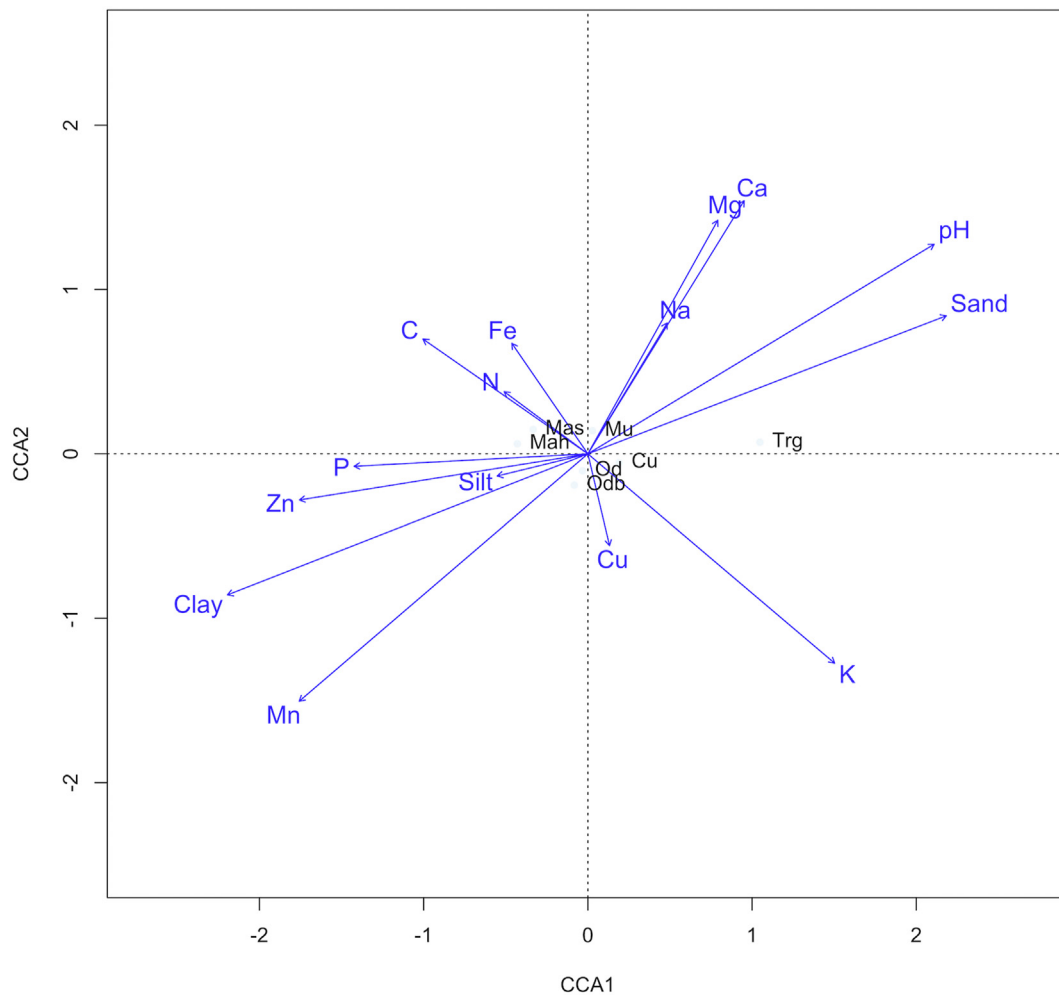
Figure 6. Canonical correspondence analysis of seven termite species in Embu and Machakos Counties using soil physico-chemical properties (pH, N, C, P, K, Ca, Mg, Mn, Cu, Fe, Zn, Na, sand, clay and silt) marked by arrows. The first and second axes explain 79.8% and 0.07%, of the variance, respectively. Mas- *Macrotermes subhyalinus,* Mah-*Macrotermes herus,* Trg- *Trinervitermes gratiosus,* Odb- *Odontotermes badius,* Cu- *Cubitermes ugandensis,* Od- *Odontotermes longignathus* and Mu- *Coptotermes formosanus.*

Trinervitermes spp. nests was much lower compared to *Macrotermes* mounds. Soil physical characteristics coupled with environmental conditions affects the survival and body hydration levels in termites (Jin et al., 2020). Contrary to the findings in this study, *Macrotermes* spp. did not show a significant correlation with silt in Ghana (Usher, 1975). The positive association of *Macrotermes* with P may be related to phosphorus adsorption dynamics during mound construction (Seymour et al., 2014). Similarly, for the mound outer casing, *Coptotermes* spp. uses clay which is rich in inorganic ions such as Ca and Mg (Wang and Henderson, 2014).

In Embu County, season significantly influenced the abundance of *M. subhyalinus*, *M. herus*, and *C. formosanus* with all the species occurring in greater numbers during the wet season. From the CCA analysis of climatic variables, there was a negative correlation between *T. gratiosus*, minimum temperature and rainfall while *M. subhyalinus* and *M. herus* were positively associated with rainfall. However, the variance explained by the first two axes was low. Woon et al. (2019) demonstrated that moisture which determines the rate of desiccation also influences distribution of termite species which may affect ecological roles that they perform. In addition, temperature also influences dispersal of termites and their foraging behavior; species have different thermal tolerance levels (Smith and Rust, 1994; Woon et al., 2019). Cao and Su (2016) observed that *Reticulitermes* spp. was found in areas with lower temperatures compared to *Coptotermes* spp. and the authors argued that

temperature preferences of termite species can be used in prediction of invasion patterns to new regions. In the tropics, average and very high temperature have direct and indirect relationships with termite species richness (Cerezer et al., 2020). For *Trinervitermes* spp., temperature is important in providing ideal conditions in the nest that allow decomposition of plant material and survival of termites (Aiki et al., 2019).

Table 5. Minimum temperature and rainfall during dry and wet seasons in Embu and Machakos Counties.

County	Season	Minimum temperature (°C)	Rainfall (mm)
Embu	Dry season one	12.7 ± 0.2	36.3 ± 9.51
	Dry season two	14 ± 0.2	30.2 ± 8.17
	Wet season one	14.9 ± 0.28	86.9 ± 17.91
	Wet season two	15.6 ± 0.68	117.8 ± 49.67
Machakos	Dry season one	11.5 ± 0.78	5.6 ± 5.07
	Dry season two	14 ± 0.21	9.7 ± 3.81
	Wet season one	14.7 ± 0.09	124.5 ± 54.16
	Wet season two	15 ± 0.47	26.7 ± 13.61

Dry season one - July to September 2018, Dry season two – Jan to March 2019, Wet season one – Oct to Dec 2018 and Wet season two – March to May 2019.
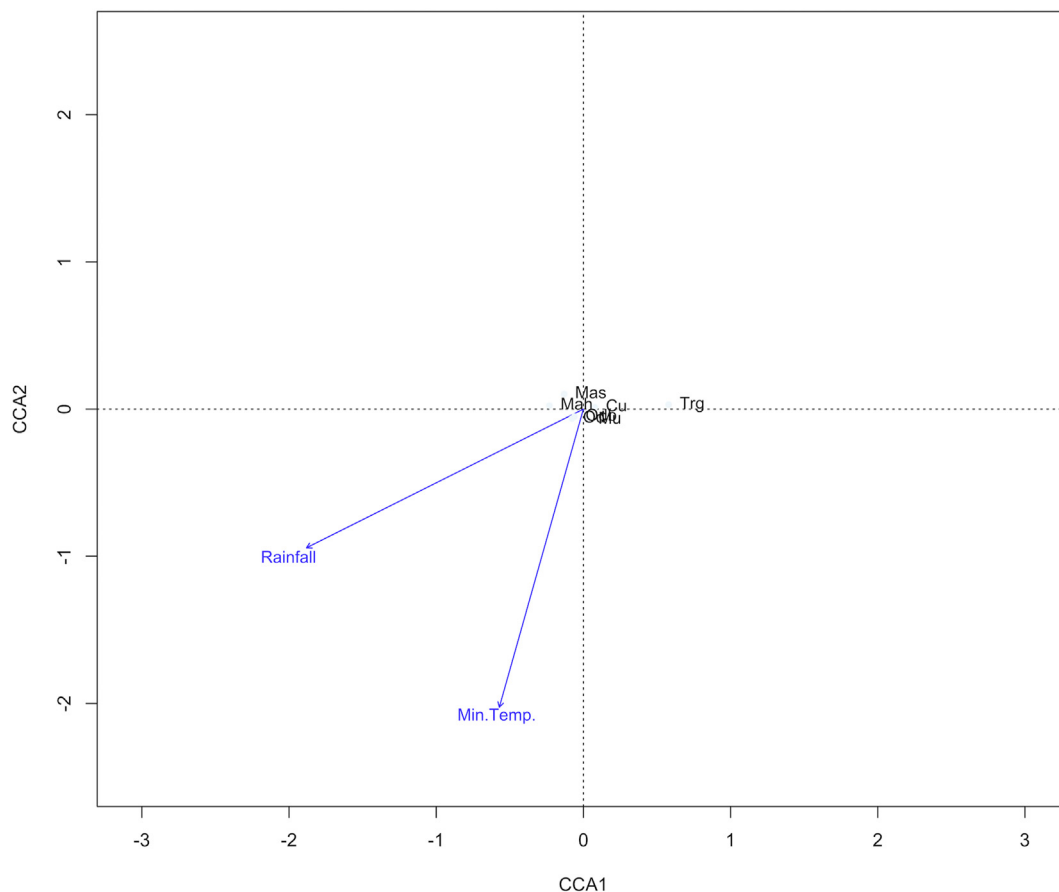
Figure 7. Canonical correspondence analysis of seven termite species in Embu and Machakos Counties using minimum temperature and rainfall marked by arrows. The first and second axes explain 24.5% of the observed variance. Odb- *Odontotermes badius,* Od- *Odontotermes longignathus* and Mu- *Coptotermes formosanus* (over-lapping labels), Mas- *Macrotermes subhyalinus,* Mah-*Macrotermes herus,* Cu- *Cubitermes ugandensis*, Trg- *Trinervitermes gratiosus.*

Foraging activity of fungus-cultivating termites increases during the wet season (Schuurman, 2006) and in some species, such as *M. gilvus,* flight is positively correlated with rainfall (Neoh and Lee, 2009). This could be a possible explanation of the high population densities of *Macrotermes* spp. that were observed in this study during the wet season which corrobo-rates findings by Dangerfield and Schuurman (2000). Similarly, Korb and Linsenmair (2001) reported that the activity of *M. bellicosus* increased during the rainy season in a savanna in Cote d'Ivoire. In Botswana, occurrence of termite species was linked to seasons with *M. subhyalinus* preferring the wet season (Séré et al., 2018). *Macrotermes* spp. prefer to construct their mounds in areas of high moisture levels due to the fact that they need to provide optimal humidity conditions for their symbiotic *Termitomyces* fungi (Bardunias et al., 2020; Aanen and Eggleton, 2005). *Coptotermes* spp. occurrence is also largely dependent on rainfall (Lee et al., 2017).

In this study, habitat type, edaphic and climatic variables influenced abundance of certain termite species. However, influence of other factors such as predator-prey interactions (Sanabria et al., 2016) and compe-tence cannot be ruled out and requires further investigations. Land use change can result in shifts of termite species which contribute to both beneficial ecosystem functions and also cause damage to plants. As put forward by Jouquet et al. (2020) benefits and risks attributed to termites are mutually exclusive and there is therefore need to design programmes that can achieve an ecological balance between the two extreme-s.Cropping practices in maize farming systems in Kenya should therefore have minimal detrimental effects on the soil engineers. Control strategies of termite species that attack maize should also consider non-target ef-fects on beneficial termites. There should also be continuous monitoring to assess the long-term impact of land use change on termites.

Declarations

Author contribution statement

Nahashon Kanyi: Conceived and designed the experiments; Per-formed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Hannah Karuri, Benson Mwangi and Johnson Nyasani: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

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Data availability statement

Data will be made available on request.

Declaration of interests statementt

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

References

Aanen, D.K., Eggleton, P., 2005. Fungus-growing termites originated in African rain forest. Curr. Biol. 15, 851–855.

Adoyo, F., Mukalama, J.B., Enyola, M., 1997. Using tithonia concoctions for termite control in Busia district, Kenya. ILEIA Newsletter 13, 24–25.

Aiki, I.P., Pirk, C.W.W., Yusuf, A.A., 2019. Thermal regulatory mechanisms of termites from two different savannah ecosystems. J. Therm. Biol. 85, 102–418.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253.

Anderson, J.M., Ingram, J.S.I., 1993. Tropical Soil Biology and Fertility: A Handbook of Methods. CAB International, Wallingford, Oxon, England, p. 221.

Anyango, J.J., Bautze, D., Fiaboe, K.K., Lagat, Z.O., Muriuki, A.W., Stöckli, S., Onyambu, G.K., Musyoka, M.W., Karanja, E.N., Adamtey, N., 2019. Termite-induced injuries to maize and baby corn under organic and conventional farming systems in the Central Highlands of Kenya. Insects 10, 367.

Anyango, J.J., Bautze, D., Fiaboe, K.K., Lagat, Z.O., Muriuki, A.W., Stöckli, S., Riedel, J., Onyambu, G.K., Musyoka, M.W., Karanja, E.N., Adamtey, N., 2020. The impact of conventional and organic farming on soil biodiversity conservation: a case study on termites in the long-term farming systems comparison trials in Kenya. BMC Ecol. 20, 1–14.

Ayuke, F.O., Pulleman, M.M., Vanlauwe, B., de Goede, R.G., Six, J., Csuzdi, C., Brussaard, L., 2011. Agricultural management affects earthworm and termite diversity across humid to semi-arid tropical zones. Agric. Ecosyst. Environ. 140, 148–154.

Baker, C.C., Castillo Vardaro, J.A., Doak, D.F., Pansu, J., Puissant, J., Pringle, R.M., Tarnita, C.E., 2020. Spatial patterning of soil microbial communities created by fungus-farming termites. Mol. Ecol. 29, 4487–4501.

Bardunias, P.M., Calovi, D.S., Carey, N., Soar, R., Turner, J.S., Nagpal, R., Werfel, J., 2020. The extension of internal humidity levels beyond the soil surface facilitates mound expansion in Macrotermes. Proc. Royal Soc. B 287 (1930), 20200894.

Black, H.I.J., Okwakol, M.J.N., 1997. Agricultural intensification, soil biodiversity and agro-ecosystem function in the tropics: the role of termites. Appl. Soil Ecol. 6, 37–53.

Bourguignon, T., Drouet, T., Šobotník, J., Hanus, R., Roisin, Y., 2015. Influence of soil properties on soldier less termite distribution. PLoS One 23, 10–11.

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-total. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, 2nd Edn. Number 9 (Part 2), Agronomy. Am. Soc. of Agron. Inc, Soil Sci. Soc. of Am, Inc. Madison, Wisconsin, USA, pp. 595–622.

Brossard, M., López-Hernández, D., Lepage, M., Leprun, J.C., 2007. Nutrient storage in soils and nests of mound-building Trinervitermes termites in Central Burkina Faso: consequences for soil fertility. Biol. Fertil. Soils 43, 437–447.

Cao, R., Su, N.Y., 2016. Temperature preferences of four subterranean termite species (Isoptera: Rhinotermitidae) and temperature-dependent survivorship and wood-consumption rate. Ann. Entomol. Soc. Am. 109, 64–71.

Cerezer, F.O., de Azevedo, R.A., Nascimento, M.A.S., Franklin, E., de Morais, J.W., de Sales Dambros, C., 2020. Latitudinal gradient of termite diversity indicates higher diversification and narrower thermal niches in the tropics. Global Ecol. Biogeogr. 29, 1967–1977.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. 92, 205.

Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S., 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. Am. Nat. 162, 734–743.

Dangerfield, J.M., Schuurman, G., 2000. Foraging by fungus-growing termites (Isoptera: termitidae, Macrotermitinae) in the Okavango delta, Botswana. J. Trop. Ecol. 16, 717–731.

Davies, A.B., Eggleton, P., van Rensburg, B.J., Parr, C.L., 2015. Seasonal activity patterns of African savanna termites vary across a rainfall gradient. Insectes Soc. 62, 157–165.

Diaye, D.N., Duponnois, R., Brauman, A., Lepage, M., 2003. Impact of a soil feeding termite, *Cubitermes niokoloensis*, on the symbiotic microflora associated with a fallow leguminous plant *Crotalaria ochroleuca*. Biol. Fertil. Soils 37, 313–318.

Donovan, S.E., Eggleton, P., Dubbin, W.E., Batchelder, M., Dibog, L., 2001. The effect of a soil-feeding termite, *Cubitermes fungifaber* (Isoptera: termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests. Pedobiologia 45, 1–11.

Dosso, K., Konaté, S., Aidara, D., Linsenmair, K.E., 2010. Termite diversity and abundance across fire-induced habitat variability in a tropical moist savanna (Lamto, Central Côte d'Ivoire). J. Trop. Ecol. 26, 323–334.

Eggleton, P., 2000. Global Patterns of Termite Diversity. Kluwer Academic Publishers, Dordrecht Netherlands, pp. 25–51.

Eggleton, P., Bignell, D.E., Hauser, S., Dibog, L., Norgrove, L., Madong, B., 2002. Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. Agric. Ecosyst. Environ. 90, 189–202.

Evans, T.A., 2021. Predicting ecological impacts of invasive termites. Curr. Opin. Insect. Sci. 46, 88–94.

FAOSTAT, 2021. Crop Production Statistics. Available from. http://www.fao.org/faostat/en/#compare. (Accessed 27 July 2021).

Fox-Dobbs, K., Doak, D.F., Brody, A.K., Palmer, T.M., 2010. Termites create spatial structure and govern ecosystem function by affecting N2 fixation in an East African savanna. J. Ecol. 91, 1296–1307.

Govorushko, S., 2019. Economic and ecological importance of termites: a global review. Entomol. Sci. 22, 21–35.

Haggar, J., Nelson, V., Lamboll, R., Roddenberg, J., 2020. Understanding and informing decisions on sustainable agri- cultural intensification in sub-Saharan Africa. Int. J. Sustain. Agric.

Hausberger, B., Korb, J., 2016. The impact of anthropogenic disturbance on assembly patterns of termite communities. Biotropica 48, 356–364.

Intachat, J., Kirton, L.G., 1997. Observations on insects associated with Acacia mangium in Peninsular Malaysia. J. Trop. For. Sci. 9, 561–564.

Jin, Z., Chen, J., Wen, X., Wang, C., 2020. Effects of clay materials and moisture levels on habitat preference and survivorship of Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Blattodea: Rhinotermitidae). PeerJ 8, e10243.

Jones, D.T., Susilo, F.X., Bignell, D.E., Hardiwinoto, S., Gillison, A.N., Eggleton, P., 2003. Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. J. Appl. Ecol. 40, 380–391.

Jouquet, P., Lepage, M., Velde, B., 2002. Termite soil preferences and particle selections: strategies related to ecological requirements. Insectes Soc. 49, 1–7.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., Bignell, D., 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil Biol. 47, 215–222.

Jouquet, P., Guilleux, N., Shanbhag, R.R., Subramanian, S., 2015. Influence of soil type on the properties of termite mound nests in Southern India. J. Appl. Ecol. 96, 282–287.

Jouquet, P., Bottinelli, N., Shanbhag, R.R., Bourguignon, T., Traoré, S., Abbasi, S.A., 2016. Termites: the neglected soil engineers of tropical soils. J. Soil Sci. 181, 157–165.

Jouquet, P., Traoré, S., Harit, A., Choosai, C., Cheik, S., Bottinelli, N., 2020. Moving beyond the distinction between the bright and dark sides of termites to achieve sustainable development goals. Curr. Opin. Insect. Sci. 40, 71–76.

Jungerius, P.D., Van Den Ancker, J.A.M., Mücher, H.J., 1999. The contribution of termites to the microgranular structure of soils on the Uasin Gishu Plateau, Kenya. Catena 34, 349–363.

Kagezi, G.H., Kaib, M., Nyeko, P., Bakuneeta, C., Schädler, M., Brandl, R., 2011. Decomposition of tissue baits and termite density along a gradient of human land-use intensification in Western Kenya. Afr. J. Ecol. 49, 267–276.

Kaiser, D., Lepage, M., Konaté, S., Linsenmair, K.E., 2017. Ecosystem services of termites (Blattoidea: termitoidae) in the traditional soil restoration and cropping system Zaï in northern Burkina Faso (West Africa). Agric. Ecosyst. Environ. 236, 198–211.

Kirton, L.G., Brown, V.K., Azmi, M., 1999. The pest status of the termite *Coptotermes curvignathus* in *Acacia mangium* plantations: incidence, mode of attack and inherent predisposing factors. J. Trop. For. Sci. 822–831.

Klute, A., 1986. Water retention: laboratory methods. Methods Soil Anal.: Phys. Mineralog. Methods 5, 635–662.

Korb, J., Linsenmair, K.E., 1998. The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. Insectes Soc. 45, 51–65.

Korb, J., Linsenmair, K.E., 2001. Resource availability and distribution patterns, indicators of competition between *Macrotermes bellicosus* and other macro-detritivores in the Comoé National Park, Côte d'Ivoire. Afr. J. Ecol. 39, 257–265.

Kuyah, S., Sileshi, G.W., Nkurunziza, L., Chirinda, N., Ndayisaba, P.C., Dimobe, K., Öborn, I., 2021. Innovative agronomic practices for sustainable intensification in sub-Saharan Africa. A review. Agron. Sustain. Dev. 41, 1–21.

Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76, 5–13.

Lee, T.R., Cameron, S.L., Evans, T.A., Ho, S.Y., Lo, N., 2015. The origins and radiation of Australian Coptotermes termites: from rainforest to desert dwellers. Mol. Phylogenet. Evol. 82, 234–244.

Lee, T.R., Evans, T.A., Cameron, S.L., Hochuli, D.F., Ho, S.Y., Lo, N., 2017. Ecological diversification of the Australian Coptotermes termites and the evolution of mound building. J. Biogeogr. 44, 1405–1417.

Liu, S., Lin, X., Behm, J.E., Yuan, H., Stiblik, P., Šobotník, J., Gan, J., Xia, S., Yang, X., 2019. Comparative responses of termite functional and taxonomic diversity to land-use change Ecol. Entomol 44, 762–770.

Makonde, H.M., Boga, H.I., Osiemo, Z., Mwirichia, R., Stielow, J.B., Goeker, M., Klenk, H.P., 2013. Diversity of Termitomyces associated with fungus-farming termites assessed by cultural and culture-independent methods. PLoS One 8, 56464.

Mehlich, A., Pinkerton, A., Robertson, W., Kepton, R., 1962. Mass Analysis Methods for Soil Fertility Evaluation. Cyclostyled Paper. National Agric. Laboratories, Nairobi.

Mills, A.J., Milewski, A., Fey, M.V., Groengroeft, A., Petersen, A., 2009. Fungus culturing, nutrient mining and geophagy: a geochemical investigation of Macrotermes and Trinervitermes mounds in southern Africa. J. Zool. 278, 24–35.

Mugerwa, S., Nyangito, M., Mpairwe, D., Nderitu, J., 2011. Effect of biotic and abiotic factors on composition and foraging intensity of subterranean termites. Afr. J. Environ. Sci. Technol. 5, 579–588.

Mutsamba, E.F., Nyagumbo, I., Mafongoya, P., 2016. Termite prevalence and crop lodging under conservation agriculture in sub-humid Zimbabwe. J. Crop Prot. 82, 60–64.

Muvengwi, J., Mbiba, M., Ndagurwa, H.G., Nyamadzawo, G., Nhokovedzo, P., 2017. Termite diversity along a land use intensification gradient in a semi-arid savanna. J. Insect Conserv. 21, 801–812.

Neoh, K.B., Lee, C.Y., 2009. Flight activity of two sympatric termite species, *Macrotermes gilvus* and *Macrotermes carbonarius* (Termitidae: Macrotermitinae). Environ. Entomol. 38, 1697–1706.

Netshifhefhe, S.R., Kunjeku, E.C., Duncan, F.D., 2019. Effects of different land use patterns on seasonal termite species diversity within the Vhembe district of the Limpopo province, South Africa. Int. J. Trop. Insect Sci. 1–15.

Nyantakyi-Frimpong, H., 2020. What lies beneath: climate change, land expropriation, and zaï agroecological innovations by smallholder farmers in Northern Ghana. Land Use Pol. 92, 104–469.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. Vegan: Community Ecology Package. R Package Version 2, pp. 5–7.

Okwakol, M.J., 2000. Changes in termite (Isoptera) communities due to the clearance and cultivation of tropical forest in Uganda. Afr. J. Ecol. 38, 1–7.

Prassana, B.M., Cairns, J.E., Zaidi, P.H., Beyene, Y., Makumbi, D., Gowda, M., Magorokosho, C., Zaman-Allah, M., Olsen, M., Das, A., Worku, M., 2021. Beat the stress: breeding for climate resilience in maize for the tropical rain fed environments. Theor. Appl. Genet. 1–24.

Pringle, R.M., Doak, D.F., Brody, A.K., Jocqué, R., Palmer, T.M., 2010. Spatial pattern enhances ecosystem functioning in an African savanna. PLoS Biol. 8, 1000377.

Roose, E., Kabore, V., Guenat, C., 1999. Zaï practice: a West African traditional rehabilitation system for semiarid degraded lands, a case study in Burkina Faso. Arid Land Res. Manag. 13, 343–355.

Sanabria, C., Dubs, F., Lavelle, P., Fonte, S.J., Barot, S., 2016. Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos. Eur. J. Soil Biol. 74, 81–92.

Sands, W.A., 1998. The Identification of Worker Castes of Termite Gen- Era from Soils of Africa and Middle East. CAB International, Wallingford.

Sattar, A., Naeem, M., 2013. Impact of environmental factors on the population dynamics, density and foraging activities of *Odontotermes lokanandi* and *Microtermes obesi* in Islamabad. SpringerPlus 2, 1–7.

Schuurman, G., 2006. Foraging and distribution patterns in a termite assemblage dominated by fungus-growing species in semi-arid northern Botswana. J. Trop. Ecol. 22, 277–287.

Schyra, J., Korb, J., 2019. Termite communities along a disturbance gradient in a West African savanna. Insects 10, 17.

Séré, A., Bougma, A., Ouilly, J.T., Traoré, M., Sangaré, H., Lykke, A.M., Ouédraogo, A., Gnankiné, O., Bassolé, I.H.N., 2018. Traditional knowledge regarding edible insects in Burkina Faso. J. Ethnobiol. Ethnomed. 14, 1–11.

Seymour, C.L., Milewski, A.V., Mills, A.J., Joseph, G.S., Cumming, G.S., Cumming, D.H.M., Mahlangu, Z., 2014. Do the large termite mounds of Macrotermes concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas? Soil Biol. Biochem. 68, 95–105.

Shanbhag, R.R., Kabbaj, M., Sundararaj, R., Jouquet, P., 2017. Rainfall and soil properties influence termite mound abundance and height: a case study with *Odontotermes obesus* (Macrotermitinae) mounds in the Indian Western Ghats forests. Appl. Soil Ecol. 111, 33–38.

Sileshi, G., Mafongoya, P.L., 2006. Variation in macrofaunal communities under contrasting land use systems in eastern Zambia. Appl. Soil Ecol. 33, 49–60.

Smith, J.L., Rust, M.K., 1994. Temperature preferences of the western subterranean termite, *Reticulitermes hesperus* Banks. J. Arid Environ. 28, 313–323.

Usher, M.B., 1975. Studies on a wood-feeding termite community in Ghana, West Africa. Biotropica 217–233.

Vesala, R., Niskanen, T., Liimatainen, K., Boga, H., Pellikka, P., Rikkinen, J., 2017. Diversity of fungus-growing termites (Macrotermes) and their fungal symbionts (Termitomyces) in the semiarid Tsavo Ecosystem, Kenya. Biotropica 49, 402–412.

Wang, C., Henderson, G., 2014. Clay preference and particle transport behavior of Formosan subterranean termites (Isoptera: Rhinotermitidae): a laboratory study. J. Insect Sci. 21, 785–795.

Webb, G.C., 1961. Keys to the Genera of the African Termites. Ibadan University Press, Ibadan.

Woon, J.S., Boyle, M.J.W., Ewers, R.M., Chung, A., Eggleton, P., 2019. Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. Insectes Soc. 66, 57–64.

Zabel, F., Delzeit, R., Schneider, J.M., Seppelt, R., Mauser, W., Václavík, T., 2019. Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. Nat. Commun. 10, 1–10.