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ARTICLE

Termites and ungulates affect arbuscular mycorrhizal richness and infectivity in a semiarid savanna

Renee H. Petipas and Alison K. Brody

Abstract: In savanna ecosystems, mound-building termites and ungulate herbivores profoundly affect the abundance and diversity of aboveground organisms. Yet, surprisingly little is known about how these two groups interact to impact belowground communities. Using the Kenya Long-term Exclosure Experiment (KLEE), where ungulate herbivores have been excluded for over 15 years, we examined how the presence of termites and ungulate herbivore exclusion affected species richness, community composition, and infectivity of arbuscular mycorrhizal fungi (AMF). We also measured plant richness and soil nutrients to examine how the effects of termites and ungulate exclusion may indirectly impact AMF communities. AMF richness and infectivity and plant richness were significantly lower on termite mounds than in off-mound areas. AMF infectivity and plant richness were significantly higher in off-mound areas, especially where herbivores had access. Our results revealed a strong suppressive effect of termites on AMF communities that was not enhanced or ameliorated by the presence of ungulate herbivores. Herbivores, by contrast, enhanced the relationship between plants and their fungal symbionts but only in the absence of the suppressive effects of termites. Our results underscore the importance of multiple drivers affecting the patterns of both above- and below-ground communities.

Key words: arbuscular mycorrhizal fungi (AMF), community ecology, Kenya Long-term Exclosure Experiment (KLEE), aboveground–belowground interactions, semiarid savanna, species richness, community composition.

Résumé : Dans les écosystèmes de la savane, les termites qui construisent des termitières hors-terre et les herbivores ongulés affectent profondément l'abondance et la diversité des organismes de surface. De manière surprenante, on en connaît peu sur la façon par laquelle ces deux groupes interagissent pour affecter les communautés souterraines. Grâce à l'expérience KLEE (« Kenya Long-Term Exclosure Experiment »), où les herbivores ongulés ont été exclus pendant plus de 15 ans, nous avons examiné si la présence des termites et l'exclusion des herbivores ongulés affectaient la richesse en espèces, la composition de la communauté et l'infectiosité des champignons mycorhiziens à arbuscules (CMA). Nous avons aussi mesuré la richesse des plantes et des nutriments du sol afin d'examiner comment les effets des termites et de l'exclusion des ongulés peuvent affecter indirectement les communautés de CMA. La richesse et l'infectiosité des CMA et la richesse des plantes étaient significativement plus faibles dans les termitières comparativement aux zones hors-termitières. L'infectiosité des CMA et la richesse des plantes étaient significativement plus élevées dans les zones hors-termitières, notamment là où les ongulés avaient un accès. Nos résultats ont révélé un fort effet suppresseur des termites sur les communautés de CMA, qui n'était pas accru ou amélioré par la présence d'ongulés herbivores. Les herbivores, en revanche, accroissaient la relation entre les plantes et leurs symbiotes fongiques mais seulement en absence des effets suppresseurs des termites. Nos résultats soulignent l'importance des multiples éléments moteurs qui affectent les patrons des communautés de surface et souterraines. [Traduit par la Rédaction]

Mots-clés : champignons mycorhiziens à arbuscules (CMA), écologie des communautés, « Kenya Long-Term Exclosure Experiment » (KLEE), interactions surface–souterrain, savane semi-aride, richesse en espèces, composition de la communauté.

Introduction

Ground-dwelling termites and ungulate herbivores drive patterns of plant species abundance and diversity in East African savannas (e.g., Moe et al. 2009; Brody et al. 2010; Sileshi et al. 2010). Although the significance of these two groups in shaping aboveground communities seems clear (Okullo and Moe 2012*a*, 2012*b*), we know little of how they interact to shape belowground communities. Here, we tested how termites and vertebrate herbivores affect a common plant endosymbiont, arbuscular mycorrhizal fungi (AMF).

There are a number of reasons to expect that both ground-dwelling termites and ungulate herbivores impact AMF communities. In our study area, soil nutrients are higher and plant diversity is lower on termite mounds (Brody et al. 2010). These differences in edaphic conditions and plant community composition may affect belowground communities. AMF tend to be suppressed under elevated levels of nutrients, such as nitrogen and, especially, phosphorus (Treseder 2004), and AMF diversity and plant diversity are closely linked (e.g., van der Heijden et al. 1998; Kivlin and Hawkes 2011).

Likewise, ungulate herbivores may impact AMF via their effects on available nutrients and plant diversity. In addition, they may impact carbon allocation of plants to AMF. Ungulates may increase available nitrogen (Hobbs 1996) and, although AMF tend to be less sensitive to nitrogen than to other nutrients, in some cases they decline when nitrogen availability increases (Treseder 2004). Ungulate herbivores may also reduce or eliminate competitive

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dominants, thus increasing plant diversity (Grime 1973) and, as a consequence, increasing AMF diversity. Leaf damage can reduce AMF colonization through a reduction in carbon allocation to roots, although this effect is highly variable and may depend largely on the system studied (see Gehring and Whitham 1994 and Barto and Rillig 2010 for reviews). Thus, there are myriad ways in which termites and vertebrate herbivores can individually affect AMF.

Given the ability of both termites and ungulate herbivores to shape aboveground communities, there is a strong potential for interactive effects, which, to our knowledge, have not been previously examined. Ungulate herbivores preferentially feed in open areas (Riginos and Grace 2008) and termite mounds, being treeless and slightly raised, are prime grazing locations (Mobaek et al. 2005; Brody et al. 2010). Herbivore preference for on-mound grazing areas could affect mycorrhizal communities in several ways. Herbivore damage to grasses growing on termite mounds may increase levels of stress to plants, encouraging increased AMF colonization (Bennett and Bever 2007) despite higher nutrient conditions. Grazing by ungulate herbivores may amplify the plant community heterogeneity driven by termites (Okullo and Moe 2012*b*) and, thus, could enhance AMF diversity differences between on-mound and off-mound areas. Alternatively, the increase in urine and dung deposition occurring as a result of herbivore preference for these areas could decrease colonization because of further enhanced nutrient conditions.

Here, we examined the effects of termite mounds and ungulate herbivores on species richness, community composition, and infectivity of the AMF community in an East African savanna. In this ecosystem, termite mounds and large herds of wild and domestic herbivores are dominant features of the landscape. Using the Kenya Long-term Exclosure Experiment (KLEE; Young et al. 1998), we asked (*i*) how do islands of fertility created by termites along with the exclusion of ungulate herbivores affect patterns of mycorrhizal species richness, community composition, and infectivity? In addition, because fungal diversity is likely to be linked to both nutrient conditions and plant diversity, we asked (*ii*) are the effects of termites and ungulate herbivores associated with differences in soil nutrients and (or) plant richness and community composition?

Materials and methods

Study site

We studied the AMF community at the Mpala Research Centre (MRC), located on the Laikipia plateau (37°E, 0°N: 1800 m a.s.l.) in central Kenya. The study site is a semiarid grassland with an overstory dominated by *Acacia drepanolobium* Harms ex B.Y.Sjöstedt and a diverse herbaceous understory (ca. 100 species) dominated by five common grasses and twenty common forbs (Young et al. 1998). There are over ten large herbivore species commonly grazing on the Laikipia plateau (Young et al. 1998), including Grant's gazelle (*Nanger granti* Brooke), Thomson's gazelle (*Eudorcas thomsonii* Günther), African buffalo (*Syncerus caffer* Sparrman), hartebeest (*Alcelaphus buselaphus* Pallas), oryx (*Oryx beisa* Rüppell), plains zebra (*Equus quagga* Boddaert), Grevy's zebra (*Equus grevyi* Oustalet), African elephant (*Loxodonta africana* Blumenbach), giraffe (*Giraffa camelopardalis* Linnaeus), and one species of domesticated cattle (*Bos taurus indicus* Linnaeus). The low-lying, lenticular-shaped mounds of *Odontotermes* termites (Order Blattoidea: *Odontotermes* sp., an undescribed species) occur evenly spaced (~50 m) across the "black cotton" vertisol soils of our study site (Pringle et al. 2010). Mounds are approximately 0.5 m high and 10–20 m wide (Brody et al. 2010). These termites build subterranean nests that significantly alter the physical and chemical characteristics of soils (Darlington 1985). *Odontotermes* mounds are approximately 80% higher in nitrogen and phosphorus and 12% lower in clay content than surrounding soil (Fox-Dobbs et al. 2010; A.K. Brody and T.M. Palmer, unpublished data).

Grass root and soil collection

To examine the effects of termites and herbivores on AMF richness, community composition, and infectivity, we used the Kenya Long-term Exclosure Experiment (KLEE; Young et al. 1998). The exclosures were established in 1995 as a randomized block design consisting of 4-ha treatment plots within each of three geographic blocks. Ungulates are excluded from plots by high voltage wire, delivering up to 7000 V, effective against even the largest ungulate herbivores (Young et al. 1998). We utilized three replicate plots that exclude all but the smallest ungulate herbivore (steinbuck (*Raphicerus campestris* Thunberg) <60 cm tall at the shoulder) and three replicate plots that allow grazing by all native ungulate herbivores and domestic cattle (referred to as O and MWC, respectively, in Young et al. 1998) referred to here as fenced (F) or open (O).

We sampled the roots and immediate soil environment of the dominant C4 grass species, *Pennisetum stramineum* Peter, on and off termite mounds in fenced and open plots. Because the identity of plant host can influence AMF community composition (Bever et al. 1996), and plant communities differ noticeably among the different treatment areas, we only sampled the rhizosphere of *P. stramineum* because it is one of a few grasses that is common throughout. We defined on-mound simply as the center of a termite mound and off-mound as the distance equal to twice the diameter of the termite mound measured from the mound edge (e.g., if the mound was ~10 m across, we measured 20 m from the mound edge into the surrounding area). The edge of each termite mound was delineated by clear changes in topography and a transition from only grasses to grasses beneath a woody canopy (Brody et al. 2010). To characterize species richness, community composition, and infectivity we collected rhizosphere samples from under three haphazardly selected *P. stramineum* plants. Soils collected from under these plants were homogenized within each on-mound and off-mound area; thus, the design included homogenized samples from three mounds (on, off) in two herbivory treatments (F, O), replicated 3 times, for a total of 36 sampling areas. To standardize the sampling of roots and soil, we used a 10 cm × 10 cm template to cut out a block of soil with a *P. stramineum* situated directly in the middle. We sampled to a depth of 15 cm, which captured most of the root material. Soils were collected in late April 2010 and stored at the University of Vermont until use in infectivity assays (hereafter referred to as raw soils) or used to start trap pot cultures. All soils were stored at 4 °C. In early June 2010, we set up 36 trap pot cultures, one for each sampling area, to assess AMF species richness, community composition, and infectivity. For soil nutrient analysis, we used a single sample of air-dried soil from on and off one termite mound in each replicate herbivory treatment.

AMF spore richness and community composition

AMF species richness and community composition were based on the identification of spores produced in greenhouse trap pot cultures started from field soils (Morton et al. 1993). Trap pot cultures are often used in AMF diversity analyses to overcome a suite of limitations in assessing diversity in field-collected soils (Bever et al. 1996; Stutz et al. 2000). Unfortunately, due to importation restrictions, we were unable to grow *P. stramineum* plants for trap pot cultures or infectivity assays. Instead, pots were seeded with a sterilized highly mycotrophic C4 host plant, sorghum-Sudan grass (*Sorghum bicolor* (L.) Moench. Sorghum) has been used extensively as a trap pot host plant (Bever et al. 1996; Eom et al. 2000) because it encourages sporulation of many AMF species (Morton et al. 1993), recreating a community similar to that of the starting inoculum (Bever et al. 1996; Eom et al. 2000). Trap pot cultures were started in a greenhouse, at the University of Vermont, using a mixture (1:1 *v*/*v*) of Kenyan field soil and autoclaved (1 h at 121 °C) sand. Plants were grown under a 12 h day – 12 h night photoperiod with temperatures ranging from 20 to 24 °C during the day and 17 to 19.5 °C during the night. Soil moisture was checked twice daily and plants were watered as needed. Plants were

fertilized with a low phosphorus fertilizer (17:4:17 *v*/*v*/*v*) when they showed signs of nutrient stress. Ninety days after germination, pots were allowed to dry out for one week, and belowground contents were transferred to sealable plastic bags and stored at 4 °C until spores could be extracted for identification. Spores were isolated from homogenized 50 mL samples of soil and roots using wet sieving and decanting (Gerdemann and Nicolson 1963). Spores were transferred in reverse osmosis water to gridded Petri dishes, where we randomly chose 10 grids out of 36 to identify spores. To confirm identification, we mounted 50–100 spores of each morphotype on slides with polyvinyl-lacto-glycerol (PVLG) and stained with Melzers reagent in PVLG (recipes can be found at http://invam.wvu.edu/methods/recipes). Criteria for morphological identification of spores were obtained during several visits to the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM), in West Virginia and via their web-based resources (http://invam.caf.wvu.edu/index.html). Data were rarefied to control for the increased likelihood of species detection that can occur with uneven sampling effort and (or) differences in species abundance (Magurran 2004). To rarefy species richness, presence–absence data were summed across grids to get an overall estimate of the frequency of occurrence within a sample. Although this method is likelyto underestimate common species (Magurran 2004), it provides a conservative estimate of how frequently a species occurs.

Plant species richness

To examine the relationship between plant diversity and fungal diversity as mediated by termites and ungulate herbivores, we quantified plant species richness and community composition. In July 2010, we measured plant diversity by censusing one transect per mound. The identity and abundance (measured as counts) of grasses and herbaceous vegetation was determined within 1 m^2 quadrats placed every 2 m along the transect, and then summed over on-mound and off-mound areas to get a total abundance for each area. The exact number of quadrats was proportional to the size of the mound and a corresponding number of quadrats were examined in off-mound areas.

AMF infectivity

To examine infectivity of mycorrhizal inoculum from the different sampling locations, we used a mean infection percentage (MIP) assay, which is an assessment of how quickly a highly mycotrophic species becomes colonized by AMF (Moorman and Reeves 1979). We performed assays using both raw soils and trap pot soils in December of 2010. Although both provide an estimate of infectivity, raw soils indicate the infectivity of propagules that were active in the soil at the time of sampling, whereas trap pot soils provide a measure of "optimal" infectivity under growth conditions that favor colonization and sporulation by all AMF in the sampled community. For the MIP assay, we used corn (*Zea mays* L.) as the host plant because it is highly mycotrophic and compatible with many AMF species (Moorman and Reeves 1979). Seeds were surface sterilized in 70% ethanol for 10 min, rinsed thoroughly and planted, one seed per pot, in 115 mL deepots (Stuewe and Sons Inc., Tangent, Oregon, USA). Seeds were sown onto a 1:10 ratio (*v*/*v*) of inoculum and a mixture (1:1 *v*/*v*) of autoclaved sand and calcined clay (Industrial Materials Corp., Deerfield, Illinois, USA). Five replicates per treatment (inoculum source: raw, trap soil; termite mound: on, off; herbivory treatment: fenced, open) were grown in a growth chamber (Percival Scientific Model I-37LXX, Perry, Iowa, USA) under a 12 h day – 12 h night photoperiod with the temperature at 24 °C during the day and 20 °C at night. After a period of 30 days, assay plants were removed from pots and cleared with 10% potassium hydroxide (KOH), acidified in 1% hydrochloric acid, and stained with 0.05% trypan blue in lactoglycerol (protocol modified from Phillips and Hayman 1970). Infectivity was estimated using the magnified intersection method (McGonigle et al. 1990). For each plant, we examined at least 50 intersections using eyepiece crosshairs (×200 magnification) at each intersection, we assessed the presence of arbuscules, hyphae, and vesicles. Results are reported here as total colonization, equivalent to the proportion of roots colonized with AMF fungal structures (arbuscules, hyphae, and vesicles).

Soil characteristics

To examine differences in edaphic conditions attributable to the activities of termites and ungulate herbivores, we analyzed on-mound and off-mound soil samples for each herbivory treatment. Soils were tested for pH, available phosphorus, potassium, calcium, magnesium, sulfur, boron, copper, iron, manganese, sodium, aluminum, zinc, organic matter, cation exchange capacity, ammonium, and nitrate. Organic matter was measured, after oven drying, using loss on ignition (LOI) at 375 °C. Available phosphorus was extracted by Modified Morgan P (MM-P) method and measured colorimetrically. All other nutrients were extracted using MM-P and measured by optical emission spectroscopy (ICP-OES). Effective cation exchange capacity (ECEC) was calculated by summation of exchangeable cations: Ca, K, Mg, and Na. Nitrogen was extracted using 1 mol·L^{-1} potassium chloride and analyzed with an automated colorimetric analyzer (Lachat QuikChem 8000, Loveland, Colorado, USA). All chemical analyses were done at the University of Maine, except nitrogen (NH_4^+ and NO_3), which was analyzed at the University of Vermont.

Data Analysis

We used Ecosim (version 8.0) to generate rarefied species richness values for plant and AMF communities for each sampling area (Gotelli and Entsminger 2011). A nested mixed effects model (JMP 8.0.2, SAS Institute Inc. 2009) was used to analyze AMF and plant species richness, using both rarefied and unrarefied richness values, with geographic block ("location") and "mound" as random factors. Termite mound (on, off) and herbivory treatment (F, O) were treated as fixed effects and mound was nested within treatment. Model coefficients were fit using restricted maximum likelihood (REML).

To assess AMF and plant community composition, we used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). PERMANOVA was designed specifically to deal with nonparametric ecological community data that rarely fit the assumptions of parametric multivariate methods (Anderson 2001). PERMANOVA partitions variance and generates a pseudo-*F* statistic based on any metric or semimetric distance matrix. *P* values are estimated based on permutations. We used PERMANOVA to describe how AMF and plant community composition were affected by experimental manipulations. We performed a two-way PERMANOVA using the Jaccard index of dissimilarity for AMF species presence–absence data and for plant species abundance data (Oksanen et al. 2011). To control for the split-plot experimental design, we included mound nested within treatment as a factor. To control for the block effect, we restricted the randomizations within geographic location. PERMANOVA was performed using the ADONIS function in the vegan package (Oksanen et al. 2011) of R (version 2.13.1; R Core Team 2011) with 1000 permutations (R code S1[1]). Data were visualized using two-dimensional nonmetric multidimensional scaling (NMDS). NMDS is a robust, nonparametric ordination technique (Minchin 1987) that allows a visual exploration of multidimensional response variables in two-dimensional space. NMDS was performed using Jaccard dissimilarities with the metaMDS function in R (version 2.13.1).

To examine the infectivity of AMF among treatments (i.e., MIP assay), we used a three-way ANOVA, testing for effects of termite mound (on, off), herbivory (F, O), and inoculum source (raw or trap

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2013-0223.

pot cultures). Data from the MIP assay were expressed as proportions and were arcsine square root transformed before analysis. We first included all possible interactions in the model and then removed those that were statistically not significant ($P > 0.05$). The final model included termite mound, herbivory treatment, inoculum source, and the interaction of herbivory treatment and termite mound. Three-way ANOVA was performed in JMP (8.0.2, SAS Institute Inc. 2009).

To examine differences in soil conditions among treatments, we used a two-way ANOVA (JMP 8.0.2, SAS Institute Inc. 2009), testing for effects of termite mound (on, off) and herbivory (F, O). To explore the relationship between AMF community composition and environmental variables, we ordinated the subset of samples that had associated soil nutrient data and used the R function "envfit" to conduct permutation tests to assess the significance of these correlations and function "envplot" to plot corresponding vectors onto AMF community ordination. NMDS was performed using Jaccard dissimilarities; however, for this ordination (unlike previous ordinations) we did not specify that the data should be treated as binary and, thus, used summed presence–absence data to estimate the frequency of occurrence within a sample. As noted above, this approach provides a conservative estimate of how frequently a species occurs but potentially underestimates common species (Magurran 2004).

Results

AMF diversity and community composition

We identified 14 AMF species (Table 1). Richness within each treatment ranged from four to eleven species, with some species being rare or absent from particular areas. Specifically, *Funneliformis constrictum* was never observed in any off-mound areas and *Acaulospora trappei* was only found in off-mound open areas. *Entrophospora infrequens* was rarely found in samples collected on termite mounds (~20% samples surveyed). Others, such as *Glomus aggregatum* and *Glomus microaggregatum* were common and found in nearly all of the samples. AMF species richness was consistently higher off rather than on mounds. When differences in abundance were accounted for via rarefaction, AMF richness was marginally higher for off-mound areas ($F = 3.72$, $P = 0.06$). We found the highest AMF diversity in open, off-mound areas, which had 27% more species than on-mound areas; however, this difference was not statistically significant. Overall, the presence of herbivores did not affect AMF species richness (Table 2; Fig. 1). PERMANOVA results suggest that the presence of termites strongly influences AMF community composition. There was no overall impact of ungulate herbivores on community composition and no significant interaction (Table A1; Fig. 2).

Plant diversity and community composition

Plant species richness was 57% lower on-mound compared with off-mound in open areas, and 43% lower on-mound than off-mound in fenced areas. Overall, open areas also had higher plant richness than fenced areas. Again, the differences in treatment means were largely driven by higher diversity in open, off-mound areas (Table 2; Fig. 1). Rarefied species richness showed the same trends, except there was only a marginally significant interaction between herbivory and termite mound ($F = 3.76$, $P = 0.06$), indicating that differences in richness in off-mound open areas may be partly driven by species abundance. Plant community composition was significantly impacted by termites, ungulate herbivores, and the interactive effects of termites and herbivores (Table A1). The NMDS plot shows a clear separation between the treatment groups (Fig. 2).

AMF infectivity

Mean infection percentages (MIP) from both field-collected and trap pot cultured soils ranged from 21% to 81% colonization (Table A2). Overall, the infectivity of AMF from off-mound areas was significantly greater than from on-mound sites, regardless of whether the fungi were grown in trap pot cultures or collected from the field. However, infectivity of fungi from trap pot cultures was consistently higher than that from the raw field soils. There was no overall effect of excluding herbivores on infectivity but a significant herbivory-by-termite mound interaction, where soils with highest infectivity were collected from open, off-mound areas (Table 3; Fig. 3).

Table 1. List of arbuscular mycorrhizal fungal species and percentage occurrence among all samples (nine per treatment) isolated from trap pot-cultures established with field soil collected from on and off termite mounds in fenced and open areas.

	Fenced		Open	
AMF Species	On	Off	On	Off
Glomus unknown	88.9	22.2	100	88.9
C. luteum	77.8	77.8	33.3	100
F. mosseae	88.9	100	88.9	88.9
*G. sinuosum**	44.4	66.7	22.2	77.8
E. infrequens	0	55.6	22.2	77.8
F. geosporum?	66.7	33.3	44.4	77.8
D. eburnea	55.6	77.8	77.8	88.9
G. aggregatum†	100	100	100	88.9
G. microaggregatum	100	100	100	100
R. intraradices	22.2	77.8	33.3	66.7
F. constrictum	44.4	0	66.7	0
D. trimurales?	22.2	22.2	22.2	33.3
A. trappei	0	0	0	11.1
P. occultum	77.8	88.9	77.8	100

Note: Question marks indicate a tentative diagnosis. *G*, *Glomus*; *C*, *Claroideoglomus*; *F*, *Funneliformis*; *E*, *Entrophospora*; *D*, *Diversispora*; *R*, *Rhizophagus*; *A*, *Archaeospora*; *P*, *Paraglomus*. AMF, arbuscular mycorrhizal fungal.

*Alternatively called *Sclerocystis sinuosum*.

†Alternatively called *Rhizophagus aggregatus*.

Table 2. Summary of nested mixed effects models testing the impact of ungulate herbivores (fenced, open) and termites (on, off) on arbuscular mycorrhizal fungal (AMF) and plant richness.

	Source	Num df	Den df	*F* value	*P* value
AMF	Herbivores (H)	1	4	3.32	0.14
	Termites (T)	1	26	5.5	0.03
	H × T	1	26	2.91	0.10
Plant	Herbivores (H)	1	4	11.85	0.03
	Termites (T)	1	26	21.29	0.0001
	H × T	1	26	4.25	0.05

Fig. 1. Arbuscular mycorrhizal fungal (AMF) species richness assessed from trap pot cultures created from field collected soil and plant species richness from on termite mounds and paired off-mound areas in fenced and open treatments. Columns represent treatment means and bars represent standard deviations. Levels not connected by the same letter are significantly different.

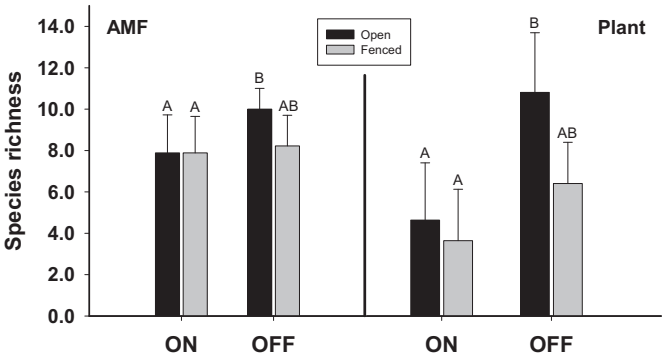


Fig. 2. Nonmetric multidimensional scaling (NMDS) ordination of arbuscular mycorrhizal fungal (AMF) and plant communities from on termite mounds and paired off-mound areas in fenced and open treatments. The AMF NMDS had a stress of 0.17 and the plant NMDS had a stress of 0.18. Jaccard dissimilarities were calculated for each plot and the NMDS ordination is a representation of dissimilarities in two-dimensions. Permutational multivariate analysis of variance (PERMANOVA) suggest that on and off AMF communities are significantly different, whereas plant communities are significantly affected by both herbivores and termites.

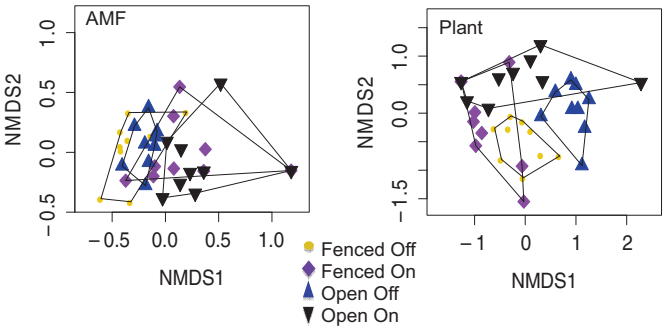
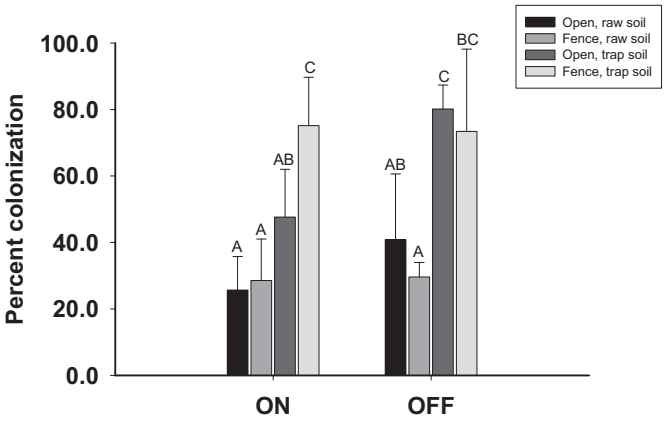


Table 3. Summary of three-way analysis of variance (ANOVA) testing the effects of ungulate herbivores (fenced, open), termites (on, off), and inoculum source (raw, trap) on infectivity of arbuscular mycorrhizal fungi.

Source	df	*F* value	*P* value
Herbivores (H)	1	0.65	0.43
Termites (T)	1	4.24	0.05
Inoculum Source	1	81.2	0.0001
H × T	1	8.5	0.009
Error	27		

Fig. 3. Mean infection percentages (MIP) of assay plants colonized by fungi from on and off termite mounds in fenced and open areas. Corn plants were grown in soils collected directly from the field (raw) or soils cultured in trap pots in the greenhouse (trap). Infection was measured as percent colonization (the proportion of intersections that contain arbuscules, hyphae, and (or) vesicles) for a sample of root material. Columns represent treatment means and bars represent standard deviation. Levels not connected by the same letter are significantly different.



Soil characteristics

We found pronounced differences in soil nutrients between on-mound and off-mound areas. Soil pH, phosphorus, nitrate, calcium, boron, and cation exchange capacity were higher on termite mounds than off termite mounds. In contrast, magnesium and manganese concentrations were higher off mound (Table 4). Nutrient conditions did not differ between fenced and open areas, nor did we find significant interactions between fencing and termite mounds. NMDS with vector overlay indicate that soil pH (P = 0.022), boron (P = 0.029), calcium (P = 0.048), cation exchange capacity (P = 0.049), manganese (P = 0.022), and magnesium (P = 0.045) were all significantly correlated with AMF community composition (Fig. 4) and phosphorus was marginally significant. Interestingly, neither nitrogen (P = 0.361) nor plant richness (P = 0.249) were significantly correlated with AMF community composition. Vectors for pH, boron, calcium, and cation exchange capacity aligned with on-mound communities, whereas vectors for manganese and magnesium aligned with off-mound communities.

Discussion

The activities of ground-dwelling termites had striking effects on arbuscular mycorrhizal communities and these effects outweighed those of vertebrate herbivores. AMF species richness and infectivity were significantly higher and AMF communities were significantly different in off- versus on-mound soils. Several factors could contribute to these differences. First, termites affect both physical and chemical properties of soils in ways that may reduce plant reliance on AMF. Mound soils provide a more hospitable environment for plant growth because of their higher levels of phosphorus, nitrogen, micronutrients, and enhanced water-holding capacities (Jouquet et al. 2011 and see Table 4). Thus, mounds reduce plant reliance on AMF for nutrient acquisition. In addition, mounds are dominated by very few plant species. Higher nutrient conditions may promote the dominance of a few strong competitor plant species (Grime 1973) or the lower species richness could be a result of the activities of termites themselves. Regardless, lower plant diversity may contribute to lower AMF diversity and infectivity (Barni and Siniscalco 2000; Kivlin and Hawkes 2011). However, our AMF community ordination results indicate a stronger role for nutrient conditions (primarily soil pH, calcium, cation exchange capacity, magnesium, and manganese) rather than plant diversity in structuring fungal diversity. Phosphorus was only marginally correlated with AMF community composition. Although phosphorus can depress AMF colonization (Treseder 2004), it appears that AMF diversity is only affected at very high levels of phosphorus (Gosling et al. 2013). In other systems, reduced AMF colonization, spore number, and spore viability on termite mounds have been attributed to either high nutrient conditions (Diaye et al. 2003; Duponnois et al. 2005) or inhibitory chemicals excreted by termites (Harinikumar and Bagyaraj 1994). In general, we found overall low spore diversity, a finding consistent with previous work done in arid to semiarid environments (~6–12 species; Stutz et al. 2000; Kamareh et al. 2011; Sánchez-Castro et al. 2012).

It should be emphasized that although we found notable differences in spore diversity between on-mound and off-mound areas, we would have gathered a more complete picture by also considering molecular diversity of AMF within plant roots. Spore morphology can be an incomplete estimate of AMF diversity because sporulation can be influenced by local biotic and abiotic conditions (Sanders 2004; Landis et al. 2004). We removed some of this bias by encouraging sporulation under common greenhouse conditions. Because sporulation rates may not be even among AMF species, we took a conservative approach by only using species richness and presence–absence in community analysis. Thus, we are not speculating about the importance (abundance) of a particular species within the system based on sporulation alone. Although sorghum encourages the sporulation of many AMF species (Morton et al. 1993), it might not encourage sporulation of all species, especially those with high fidelity to their original host.

Table 4. Nutrient conditions from soils collected in fenced and open areas, on termite mounds and in corresponding off-mound areas.

	Fenced		Open			
	Off	On	Off	On	*F* value	*P* value
pH	6.17 (0.27)	7.36 (0.11)	6.31 (0.13)	7.50 (0.16)	135.11	<0.0001 ON
P	1.19 (0.08)	4.26 (2.61)	1.41 (0.15)	2.31 (0.20)	6.86	0.0307 ON
Mg	982.83 (53.08)	614.00 (10.33)	968.50 (19.87)	699.17 (224.16)	22.81	0.0014 OFF
Ca	4365.50 (554.32)	8256.67 (781.54)	4207.17 (236.08)	7860.0 (1798.77)	40.56	0.0002 ON
B	0.25 (0.04)	0.85 (0.19)	0.28 (0.03)	0.81 (0.17)	56.20	<0.0001 ON
Mn	73.28 (23.04)	45.83 (14.70)	70.75 (13.11)	34.93 (7.81)	12.25	0.0081 OFF
ECEC	33.68 (3.02)	49.42 (4.48)	32.97 (0.85)	48.96 (5.43)	13.88	<0.0001 ON
NO_3^-	1.33 (0.59)	17.97 (4.18)	1.0 (0.06)	14.67 (19.76)	6.81	0.0311 ON

Note: P, Phosphorus; Mg, Magnesium; Ca, Calcium; B, Boron; Mn, Manganese; ECEC, effective cation exchange capacity; NO_3^-, nitrate. Effective cation exchange capacity was estimated by summation of exchangeable cations: Ca, K, Mg, and Na. Available phosphorus was extracted by Modified Morgan P (MM-P) method and measured colorimetrically. Means and standard deviations (±) are presented. *P* values are listed in the last column along with the higher main effect; only significant results are shown.

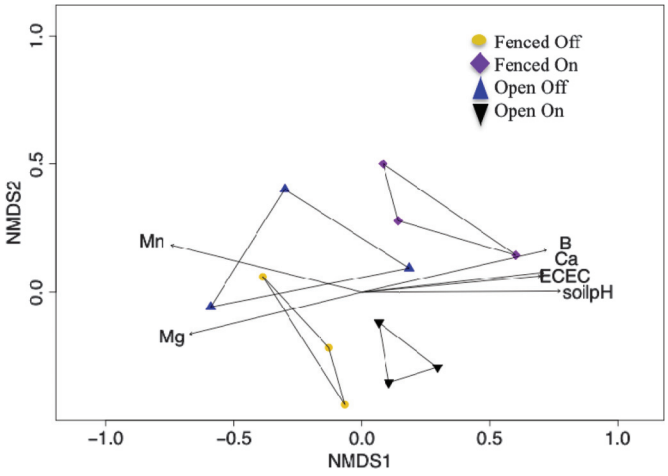


Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination of a subset of AMF communities from on termite mounds and paired off-mound areas in fenced and open treatments. The stress value of this NMDS is 0.16. Envfit was used to overlay environmental variables. Soil pH, boron (B), calcium (Ca), effective cation exchange capacity (ECEC), manganese (Mn), and magnesium (Mg) are all significantly correlated ($P < 0.05$) and phosphorus was marginally significantly ($P = 0.057$) correlated with AMF community composition. The direction of the vectors indicates the direction of the environmental gradient.

Here, herbivore exclusion impacted AMF infectivity but not AMF richness or community composition. Although we found a trend toward higher richness and distinct communities in open areas, those differences were not significant. We cannot rule out the possibility of a type II error because of the small sample sizes implicit in the KLEE design (only three replicates per herbivory treatment). Nonetheless, AMF from soils collected from open, off-mound areas had significantly higher levels of infectivity than where herbivores were excluded. Our results are consistent with previous research that showed a 37% increase in colonization of roots when plants were grown in soils from open areas compared with fenced areas (Gehring et al. 2002). Although the underlying mechanism driving these effects is unknown, plants growing under stressful conditions may impact the propensity of AMF to sporulate (Gehring et al. 2002) or small changes in AMF diversity may produce detectable changes in infectivity. In general, the links between AMF and herbivory have been equivocal. Herbivory may increase (Eom et al. 2001; Gehring et al. 2002; Wearn and Gange 2007; Murray et al. 2010; Ruotsalainen and Eskelinen 2011; Ba et al. 2012) or decrease (Gehring and Whitham 1994; Eom et al. 2001; Gange et al. 2002; Barto and Rillig 2010; Barber et al. 2012) AMF colonization and diversity.

How do the effects of termites and herbivores interact? Despite preferential grazing on termite mounds (Brody et al. 2010), AMF communities seemed to be largely unaffected by the exclusion of ungulate herbivores. We found no change in on-mound AMF richness or infectivity of field-collected soils with fencing. Termites are especially good at maintaining homeostasis in their mound environment (Darlington 1985) and have earned the title "ecosystem engineers" for precisely this reason (Jouquet et al. 2006). Termites manipulate the belowground environment to keep it amenable to growing the fungi that are critical in processing plant material. Hence, the unique conditions that lead to the termite mound effect are maintained even when surrounding conditions change. Our results indicate that the mound environment is almost entirely attributable to the activities of termites themselves, rather than the product of termites and ungulate herbivores.

Our work adds to the growing body of knowledge of how important drivers of aboveground patterns (Keesing 1998; Brody et al. 2010; Fox-Dobbs et al. 2010; Pringle et al. 2010; Sileshi et al. 2010) can also affect those below ground. In particular, although long-term exclusion of large herbivores did little to impact mycorrhizal communities on termite mounds, off-mound communities became less infective and slightly less diverse. Taken together, our results suggest that the patterns of AMF diversity as well as their propensity to infect hosts are driven by multiple factors including the effects of termites and large, vertebrate herbivores.

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References

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. **26**(1): 32–46. doi:10.1111/j.1442-9993.2001.01070.pp.x.

Ba, L., Ning, J., Wang, D., Facelli, E., Facelli, J.M., Yang, Y., and Zhang, L. 2012. The relationship between the diversity of arbuscular mycorrhizal fungi and grazing in a meadow steppe. Plant Soil, **352**(1–2): 143–156. doi:10.1007/s11104-011-0985-6.

Barber, N.A., Adler, L.S., Theis, N., Hazzard, R.V., and Kiers, E.T. 2012. Herbivory reduces plant interactions with above-and belowground antagonists and mutualists. Ecology, **93**(7): 1560–1570. doi:10.1890/11-1691.1. PMID:22919903.

Barni, E., and Siniscalco, C. 2000. Vegetation dynamics and arbuscular mycorrhiza in old-field successions of the western Italian Alps. Mycorrhiza, **10**(2): 63–72. doi:10.1007/s005720000059.

Barto, E.K., and Rillig, M.C. 2010. Does herbivory really suppress mycorrhiza? A meta-analysis. J. Ecol. **98**(4): 745–753. doi:10.1111/j.1365-2745.2010.01658.x.

Bennett, A.E., and Bever, J.D. 2007. Mycorrhizal species differentially alter plant growth and response to herbivory. Ecology, **88**: 210–218. doi:10.1890/0012-9658(2007)88[210:MSDAPG]2.0.CO;2. PMID:17489469.

Bever, J.D., Morton, J.B., Antonovics, J., and Schultz, P.A. 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. J. Ecol. **84**(1): 71–82. doi:10.2307/2261701.

Brody, A.K., Palmer, T.M., Fox-Dobbs, K., and Doak, D.F. 2010. Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*. Ecology, **91**(2): 399–407. doi:10.1890/09-0004.1. PMID:20392005.

Darlington, J. 1985. Lenticular soil mounds in the Kenya highlands. Oecologia, **66**(1): 116–121. doi:10.1007/BF00378562.

Diaye, D.N., Duponnois, R., Brauman, A., and Lepage, M. 2003. Impact of a soil feeding termite, *Cubitermes nikoloensis*, on the symbiotic microflora associated with a fallow leguminous plant *Crotalaria ochroleuca*. Biol. Fertil. Soils, **37**(5): 313–318.

Duponnois, R., Paugy, M., Thioulouse, J., Masse, D., and Lepage, M. 2005. Functional diversity of soil microbial community, rock phosphate dissolution and growth of *Acacia seyal* as influenced by grass-, litter- and soil-feeding termite nest structure amendments. Geoderma, **124**(3–4): 349–361. doi:10.1016/j.geoderma.2004.05.012.

Eom, A.-H., Hartnett, D.C., and Wilson, G.W.T. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia, **122**(3): 435–444. doi:10.1007/s004420050050.

Eom, A.-H., Wilson, G.W.T., and Hartnett, D.C. 2001. Effects of ungulate grazers on arbuscular mycorrhizal symbiosis and fungal community structure in tallgrass prairie. Mycologia, **93**(2): 233–242. doi:10.2307/3761643.

Fox-Dobbs, K., Doak, D.F., Brody, A.K., and Palmer, T.M. 2010. Termites create spatial structure and govern ecosystem function by affecting N_2 fixation in an East African savanna. Ecology, **91**(5): 1296–1307. doi:10.1890/09-0653.1. PMID:20503863.

Gange, A.C., Bower, E., and Brown, V.K. 2002. Differential effects of insect herbivory on arbuscular mycorrhizal colonization. Oecologia, **131**(1): 103–112. doi:10.1007/s00442-001-0863-7.

Gehring, C.A., and Whitham, T.G. 1994. Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. Trends Ecol. Evol. **9**(7): 251–255. doi:10.1016/0169-5347(94)90290-9.

Gehring, C.A., Wolf, J.E., and Theimer, T.C. 2002. Terrestrial vertebrates promote arbuscular mycorrhizal fungal diversity and inoculum potential in a rain forest soil. Ecol. Lett. **5**(4): 540–548. doi:10.1046/j.1461-0248.2002.00353.x.

Gerdemann, J.W., and Nicolson, T.H. 1963. Spores of mycorrhizal Endogone species extracted from soil by wet sieving and decanting. Trans. Br. Mycol. Soc. **46**(2): 235–244. doi:10.1016/S0007-1536(63)80079-0.

Gosling, P., Mead, A., Proctor, M., Hammond, J.P., and Bending, G.D. 2013. Contrasting arbuscular mycorrhizal communities colonizing different host plants show a similar response to a soil phosphorus concentration gradient. New Phytol. **198**(2): 546–556. doi:10.1111/nph.12169. PMID:23421495.

Gotelli, N.J., and Entsminger, G.L. 2011. Ecosim: Null models software for ecology. Acquired Intelligence Inc. & Kesey-Bear, Jericho, Vt.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature, **242**: 344–347. doi:10.1038/242344a0.

Harinikumar, K.M., and Bagyaraj, D.J. 1994. Potential of earthworms, ants, millipedes, and termites for dissemination of vesicular-arbuscular mycorrhizal fungi in soil. Biol. Fertil. Soils, **18**(2): 115–118. doi:10.1007/BF00336456.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. **60**(4): 695–713. doi:10.2307/3802368.

SAS Institute Inc. 2009. JMP. Version 8.0.2. SAS Institute Inc., Cary, N.C.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P., and Lepage, M. 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. Appl. Soil Ecol. **32**(2): 153–164. doi:10.1016/j.apsoil.2005.07.004.

Jouquet, P., Traore, S., Choosai, C., Hartmann, C., and Bignell, D. 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil Biol. **47**(4): 215–222. doi:10.1016/j.ejsobi.2011.05.005.

Kamareh, T.F., Shirvany, A., Matinizadeh, M., Etemad, V., and Khoshnevis, M. 2011. Arbuscular mycorrhizal fungi in endemic and native tree species, wild pear (*Pyrus glabra*) and maple (*Acer cinerascens*). Afr. J. Agric. Res. **6**(18): 4308–4317.

Keesing, F. 1998. Impacts of ungulates on the demography and diversity of small mammals in central Kenya. Oecologia, **116**(3): 381–389. doi:10.1007/s004420050601.

Kivlin, S.N., and Hawkes, C.V. 2011. Differentiating between effects of invasion and diversity: impacts of aboveground plant communities on belowground fungal communities. New Phytol. **189**(2): 526–535. doi:10.1111/j.1469-8137.2010.03494.x. PMID:20958304.

Landis, F.C., Gargas, A., and Givnish, T.J. 2004. Relationships among arbuscular mycorrhizal fungi, vascular plants and environmental conditions in oak savannas. New Phytol. **164**(3): 493–504. doi:10.1111/j.1469-8137.2004.01202.x.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Publishing, Malden, Massachusetts.

McGonigle, T.P., Miller, M.H., Evans, D.G., Fairchild, G.L., and Swan, J.A. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phytol. **115**(3): 495–501. doi:10.1111/j.1469-8137.1990.tb00476.x.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio **69**(1–3): 89–107. doi:10.1007/BF00038690.

Mobaek, R., Narmo, A.K., and Moe, S.R. 2005. Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. J. Zool. **267**: 97–102. doi:10.1017/S0952836905007272.

Moe, S.R., Mobaek, R., and Narmo, A.K. 2009. Mound building termites contribute to savanna vegetation heterogeneity. Plant Ecol. **202**(1): 31–40. doi:10.1007/s11258-009-9575-6.

Moorman, T., and Reeves, F.B. 1979. Role of endomycorrhizae in revegetation practices in the semi-arid west. II. Bioassay to determine the effect of land disturbance on endomycorrhizal populations. Am. J. Bot. **66**(1): 14–18. doi:10.2307/2442619.

Morton, J.B., Bentivenga, S., and Wheeler, W. 1993. Germ-plasm in the International Collection of Arbuscular and Vesicular-arbuscular Mycorrhizal Fungi (INVAM) and procedures for culture development, documentation, and storage. Mycotaxon, **48**: 491–528.

Murray, T.R., Frank, D.A., and Gehring, C.A. 2010. Ungulate and topographic control of arbuscular mycorrhizal fungal spore community composition in a temperate grassland. Ecology, **91**(3): 815–827. doi:10.1890/09-0209.1. PMID:20426339.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., and Wagner, H. 2011. Vegan: Community Ecology Package. R package version 2.0.2. http://CRAN.R-project.org/package=vegan.

Okullo, P., and Moe, S.R. 2012*a*. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation. J. Ecol. **100**(1): 232–241. doi:10.1111/j.1365-2745.2011.01889.x.

Okullo, P., and Moe, S.R. 2012*b*. Large herbivores maintain termite-caused differences in herbaceous species diversity patterns. Ecology, **93**(9): 2095–2103. doi:10.1890/11-2011.1. PMID:23094381.

Phillips, J.M., and Hayman, D.S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. **55**: 158–161. doi:10.1016/S0007-1536(70)80110-3.

Pringle, R.M., Doak, D.F., Brody, A.K., Jocque, R., and Palmer, T.M. 2010. Spatial pattern enhances ecosystem functioning in an African savanna. PloS Biol. **8**(5): 1–12. doi:10.1371/journal.pbio.1000377.

R Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Riginos, C., and Grace, J.B. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology, **89**(8): 2228–2238. doi:10.1890/07-1250.1.

Ruotsalainen, A.L., and Eskelinen, A. 2011. Root fungal symbionts interact with mammalian herbivory, soil nutrient availability and specific habitat conditions. Oecologia, **166**(3): 807–817. doi:10.1007/s00442-011-1928-x. PMID:21301877.

Sánchez-Castro, I., Ferrol, N., Cornejo, P., and Barea, J.M. 2012. Temporal dynamics of arbuscular mycorrhizal fungi colonizing roots of representative shrub species in a semi-arid Mediterranean ecosystem. Mycorrhiza, **22**(6): 449–460. doi:10.1007/s00572-011-0421-z. PMID:22124663.

Sanders, I.R. 2004. Plant and arbuscular mycorrhizal fungal diversity – are we looking at the relevant levels of diversity and are we using the right techniques? New Phytol. **164**(3): 415–418. doi:10.1111/j.1469-8137.2004.01208.x.

Sileshi, G.W., Arshad, M.A., Konaté, S., and Nkunika, P.O.Y. 2010. Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. J. Veg. Sci. **21**(5): 923–937. doi:10.1111/j.1654-1103.2010.01197.x.

Stutz, J.C., Copeman, R., Martin, C.A., and Morton, J.B. 2000. Patterns of species composition and distribution of arbuscular mycorrhizal fungi in arid regions of southwestern North America and Namibia, Africa. Can. J. Bot. **78**(2): 237–245. doi:10.1139/b99-183.

Treseder, K.K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol. **164**(2): 347–355. doi:10.1111/j.1469-8137.2004.01159.x.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., and Sanders, I.R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature, **396**: 69–72. doi:10.1038/23932.

Wearn, J.A., and Gange, A.C. 2007. Above-ground herbivory causes rapid and sustained changes in mycorrhizal colonization of grasses. Oecologia, **153**(4): 959–971. doi:10.1007/s00442-007-0789-9. PMID:17594116.

Young, T.P., Okello, B., Kinyua, D., and Palmer, T.M. 1998. KLEE: a long-term, large-scale herbivore exclusion experiment in Laikipia, Kenya. Afr. J. Range Forage Sci. **14**: 94–102.

Appendix A

Table A1. Summary of two-way permutational multivariate analysis of variance (PERMANOVA) exploring how ungulate herbivores (H) and termites (T) impact arbuscular mycorrhizal fungal (AMF) and plant community composition.

	Source	df	*F* value	R^2	*P* value
AMF	Herbivores (H)	1	1.33	0.03	0.24
	Termites (T)	1	8.24	0.19	0.001
	H × T	1	1.80	0.04	0.12
	Residuals	32			
	Total	35			
Plant	Herbivores (H)	1	4.25	0.09	0.001
	Termites (T)	1	8.08	0.17	0.001
	H × T	1	2.66	0.06	0.01
	Residuals	32			
	Total	35			

Table A2. Average hyphal colonization in corn colonized by arbuscular mycorrhizal fungi from on and off termite mounds in fenced (F) and open areas.

Herbivory treatment	Termite mound	Inoculum source	Sample size	Mean hyphal colonization (%)	Standard deviation (%)
F	OFF	R	5	30	4
F	OFF	T	2	73	25
F	ON	R	4	29	12
F	ON	T	4	81	4
Open	OFF	R	4	41	20
Open	OFF	T	4	79	8
Open	ON	R	3	21	3
Open	ON	T	2	44	1

Note: Assays were conducted using both field soil (R) and trap pot soil (T).