

Termites create spatial structure and govern ecosystem function by affecting N₂ fixation in an East African savanna

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Abstract. The mechanisms by which even the clearest of keystone or dominant species exert community-wide effects are only partially understood in most ecosystems. This is especially true when a species or guild influences community-wide interactions via changes in the abiotic landscape. Using stable isotope analyses, we show that subterranean termites in an East African savanna strongly influence a key ecosystem process: atmospheric nitrogen fixation by a monodominant tree species and its bacterial symbionts. Specifically, we applied the ¹⁵N natural abundance method in combination with other biogeochemical analyses to assess levels of nitrogen fixation by *Acacia drepanolobium* and its effects on co-occurring grasses and forbs in areas near and far from mounds and where ungulates were or were not excluded. We find that termites exert far stronger effects than do herbivores on nitrogen fixation. The percentage of nitrogen derived from fixation in *Acacia drepanolobium* trees is higher (55–80%) away from mounds vs. near mounds (40–50%). Mound soils have higher levels of plant available nitrogen, and *Acacia drepanolobium* may preferentially utilize soil-based nitrogen sources in lieu of fixed nitrogen when these sources are readily available near termite mounds. At the scale of the landscape, our models predict that termite/soil derived nitrogen sources influence >50% of the *Acacia drepanolobium* trees in our system. Further, the spatial extent of these effects combine with the spacing of termite mounds to create highly regular patterning in nitrogen fixation rates, resulting in marked habitat heterogeneity in an otherwise uniform landscape. In summary, we show that termite-associated effects on nitrogen processes are not only stronger than those of more apparent large herbivores in the same system, but also occur in a highly regular spatial pattern, potentially adding to their importance as drivers of community and ecosystem structure.

Key words: Kenya; nitrogen fixation; savanna; spatial structure; stable isotopes; termites.

INTRODUCTION

Spatial structure in biotic processes has long been thought to be important in regulating community interactions and ecosystem processes (Levin 1992, Reitkerk and van de Koppel 2008). However, the mechanisms by which even the clearest of keystone and dominant species exert community-wide effects are often only partially understood. This is especially true of effects created via indirect interactions, such as when one species or guild influences the interactions of others by way of changes in the abiotic landscape. Here, we examine the relative importance of termites and ungulates, two groups that have been repeatedly claimed to have special importance for savanna ecosystems, in creating and maintaining spatial structure in a semiarid East African savanna. Both termites and ungulates have been identified as keystones (Whitford 1996, Sinclair

2003), strong interactors and, in the case of termites, ecosystem engineers (Decaens et al. 2001) in savannas. While many ecologists may quibble about these exact labels, our goal was to understand these species' roles in controlling a key ecosystem process, biological nitrogen (N) fixation. In particular, although the importance of termites in biogeochemical cycling and, in some cases, the creation of heterogeneous habitat, is well recognized (e.g., Arshad 1981, Jouquet et al. 2005, Moe et al. 2009; see review in Jones 1990), the range of mechanisms by which they exert their effects have remained unclear, as has the spatial extent and patterning of their influences.

Grassland communities make up 40% of terrestrial land cover (Bailey 1996), and >15% the African continent (Mayaux et al. 2004). Although grasslands are often species rich, many are also dominated by only a handful of plant species and a few guilds of animal species. Termites and ungulates are integral components of African savannas, particularly with respect to nutrient cycling (Jones 1990, McNaughton et al. 1997, Augustine et al. 2003). The relative impacts of these very different organisms on landscape-scale processes are

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difficult to quantify, but fungus-growing termites and large herbivores can consume equivalent quantities of plant material in semiarid Kenyan grassland (Lepage 1981). Past observational and experimental research has documented substantial effects of both termites and mammalian herbivores on N cycling (Jones 1990, McNaughton et al. 1997, Craine et al. 2009), and on species diversity, individual plant growth, and other community and ecosystem characteristics (Palmer 2003, Goheen et al. 2004). However, past studies have examined the effects of either termites or herbivores, but not their relative importance nor the possibility of synergistic interactions of these two guilds. Wildfires are another important component of grassland ecology; fires can control or influence nearly every aspect of African savanna ecosystem dynamics (Archibald et al. 2005, Zavala and Holdo 2005, Okello et al. 2008, Fuhlendorf et al. 2009). For example, fires may be a primary source of nitrogen removal from savannas, determine when and where herbivores graze, and dictate species composition of plant communities.

We tested for the effects of both mammalian herbivores and of termites on ecosystem N processes in clay-rich vertisol soil ("black cotton") savannas in north-central Kenya. Ungulate herbivores and termites are known to redistribute organic N across the landscape, and generate "hotspots" of soil organic N (McNaughton et al. 1997, Jouquet et al. 2005). The scales of these hotspots are different, but both can be relatively small (at the level of latrines and individual mounds, respectively), although previous research has also established that large mammal herbivory may sometimes generate isotopic variability in vegetation across broad spatial scales (e.g., Cook 2001, Craine et al. 2009). Using isotopic analyses, coupled with large-scale experiments and spatial modeling, we examined how termites and ungulates drive biogeochemical patterns of N availability and acquisition. Despite the potential importance of fires in grassland systems, we do not consider their effects in this study, since our study area is located in a region with a multi-decadal legacy of fire suppression. The black cotton savanna studied here is uniquely suited for investigating spatial biogeochemical patterns because (1) it is nearly flat, with very little abiotic structuring over large areas (Fig. 1) and (2) the vegetation is largely comprised of a small suite of C₄ grasses and a single overstory tree, *Acacia drepanolobium* (Fabaceae; hereafter, *Acacia*), a N₂-fixing legume (Young et al. 1998). *Acacia* dominates the black cotton savanna in both numbers and biomass, and is far and away the most common N₂ fixer in this ecosystem.

Legumes acquire atmospheric N₂ by supporting nitrogen-fixing bacterial symbionts, a costly process that can be rapidly adjusted in response to changing soil N availability (Allos and Bartholomew 1959). It can also be an important input of N into N-limited ecosystems (Vitousek et al. 1987). Therefore, we focused on the influences of termites and ungulates on N acquisition by

Acacia. The widespread success of *Acacia* trees growing in arid and semi-arid regions of Africa has been attributed to their prowess as N₂ fixers (Högberg 1986). Although levels of fixation vary amongst species and across topoedaphic and climatic gradients (Schulze et al. 1991, Raddad et al. 2005), the potential for *Acacia* trees to obtain large fractions of N from fixation allows them to thrive in N-poor soils (Högberg 1986). Nitrogen isotope ($\delta^{15}\text{N}$) values measured in plant tissues provide insight into relative contributions of N sources (e.g., fixed N₂ vs. soil N), if the sources are isotopically discreet. We applied the ¹⁵N natural abundance method in combination with other plant and soil biogeochemical analyses to assess spatial patterning of N₂ fixation by *Acacia* and its effects on co-occurring grasses and forbs in areas near and far from mounds and where ungulates were or were not excluded. Using spatially explicit isotopic analyses and simple statistical models, our results demonstrate that termites create strong spatial structuring in a key ecosystem process: atmospheric N₂ fixation by the dominant tree species. Given the community-wide and landscape scale effects of this biogeochemical process, we suggest it may be the most significant influence of termites in this widespread savanna community.

MATERIALS AND METHODS

Study system.—We collected samples for this study during three field seasons at the Mpala Research Centre (0°20' N, 36°53' E, 1800 m elevation) on the Laikipia Plateau, in Kenya. The vegetation in our study area is wooded grassland (Fig. 1A): *Acacia drepanolobium* accounts for >97% of the overstory, while five C₄ grasses constitute ~90% of the understory (Young et al. 1998, Riginos and Young 2007). *Acacia* species are often the dominant trees on East African volcanic plateaus in semi-arid or arid regions (Högberg 1986). Black cotton vertisols are biogeochemically and structurally challenging environments for plant growth. Vertisols shrink and swell with alternate drying and wetting, exerting substantial shearing forces on fine roots (Duchaufour 1977). They are prone to water-logging (and the resulting denitrification), leaching, and have high wilting points, since water is held tightly within the small pore spaces of the abundant heavy clays (Brady and Weil 2002). In addition, although they are rich in exchangeable cations, they are often low in plant accessible N and P. While most woody plants in our black cotton study area have deep taproots for water procurement, the lateral roots of these plants are generally within the top 50cm of soil (including *Acacia* and *Aerva lantana*; K. Fox-Dobbs, *personal observation*).

Odontotermes (termite) mounds occupy ~20% of the landscape in our study area (T. M. Palmer, *unpublished data*), and appear to play a central role in structuring black cotton savanna communities. *Odontotermes* mounds are highly over-dispersed to >100 m (D. F. Doak and R. M. Pringle, *unpublished analysis*), low

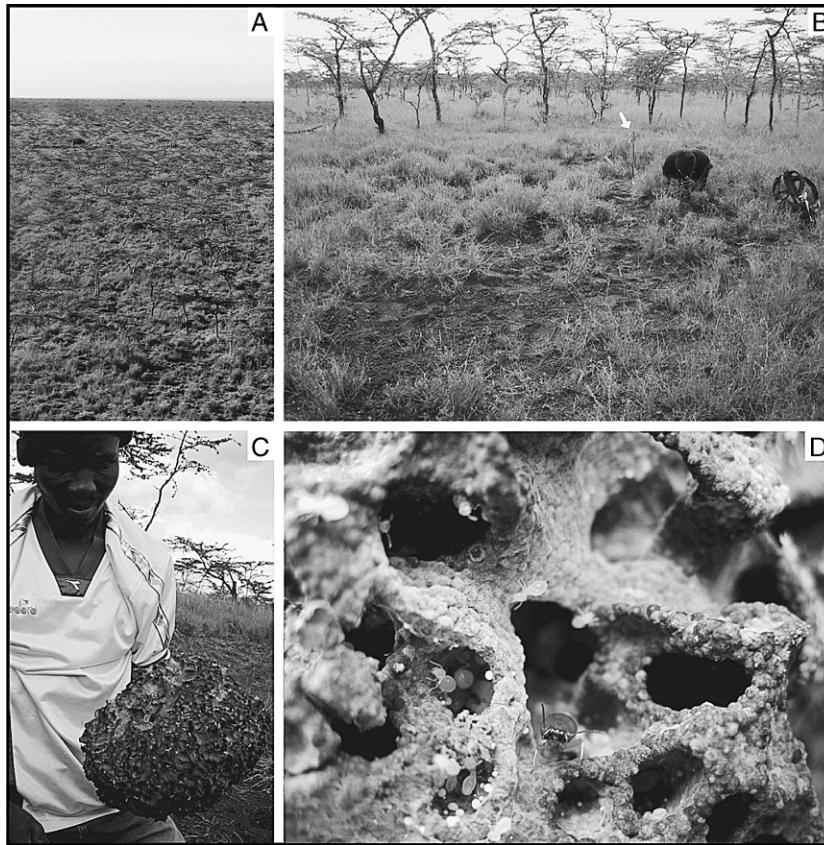


FIG. 1. Photographs of the study area in Kenya, and termite (*Odontotermes* spp.) mound and fungal comb. (A) Oblique aerial view of black cotton savanna shows the lack of topography and the *Acacia drepanolobium* dominated canopy. (B) Ground view of a termite mound; this mound is ~ 10 m in diameter, and the flag (shown by the white arrow) indicates the mound center. (C) One of many fungal combs (termitaria) that underlie a mound. (D) Close-up view of the fungal comb showing the fungal fruiting bodies (small spheres) and the unpigmented worker termites. Photos taken by (A) K. Chapman, (B) K. Fox-Dobbs, and (C, D) K. Rudolph.

lying, generally ~ 10 m in diameter, and no more than 0.5 m high (Darlington and Bagine 1999). All but the very centers of mounds support the same trees, shrubs, and grass genera as non-mound areas (Fig. 1B). The immediately obvious mound centers support lower densities of trees and shrubs than matrix habitat and feature a significantly higher abundance (4.8 \times) of the palatable grass *Pennisetum stramineum* and significantly lower abundance (3.4 \times) of the unpalatable grass *P. mezianum* relative to matrix areas (A. K. Brody, unpublished data).

Odontotermes spp. in black cotton savannas appear to import coarse particles (sand) in the construction of their mounds, improving water infiltration, reducing water-logging, and lowering wilting point in these heavy clay soils (Brady and Weil 2002; T. M. Palmer, personal observation). By binding soil particles together with saliva and fecal material, termites create soil aggregates (e.g., Arshad 1981), which increase pore space within the soil profile. Coupled with their construction of tunnels, flight vents and nest chambers, these modifications strongly increase water infiltration and aeration within

soils (Brady and Weil 2002). This in turn may reduce potential for N loss via denitrification during extreme saturation and drying cycles that are common in black cotton (off mound) soils. In addition to causing physical disturbance, termites contribute to nutrient loading of soils through the concentration of organic material into mound areas (Fig. 1C, D) and by incorporation of saliva and fecal material into mound structures (Arshad 1981, Holt and Lepage 2000, Jouquet et al. 2005). Their physical modification of mound soils supports soil microbial activity, which ultimately facilitates breakdown of organic material into plant available nutrient compounds (Abbadie and Lepage 1989).

Our study was conducted within and close to the Kenya Long-term Exclusion Experiment (KLEE) ungulate exclosures. This large-scale experiment, established in 1995, includes three blocks of 200-ha plots that allow different combinations of cattle, small to medium-sized wild ungulates, and megaherbivore browsing and grazing (Young et al. 1998). Research in KLEE has shown that herbivory significantly influences vegetation. For example, *Acacia* growth rates are lower and

mortality higher when herbivores are present (J. MacLean, *unpublished analysis*). Wildfires are a natural phenomenon in East African savannas, but fires have been suppressed on the Laikipia plateau for at least the past 50 years, and likely much longer.

Plant collection, preparation, and analyses.—In January 2007 (a dry season that was relatively wet; 20.6 mm rainfall) we collected paired sets of leaf samples from *Acacia*, *Aerva lanata* (hereafter referred to as *Aerva*), and *Pennisetum* spp. (grass) from “on mound” and “off mound” locations at 19 sites. *Aerva* is one of the most widespread forbs on the site, and was used to obtain isotopic values for a non-fixing, C₃ plant. The on-mound grass samples were collected on the mound, while the on-mound *Aerva* and *Acacia* samples were collected from plants on the mounds when possible, but mostly at the edge of mounds (generally 5–10 m from mound centers). The off-mound samples were collected >30 m from the center of a mound. The mounds were located in either the “zero” (ungulates absent) or “MWC” (all ungulates present) plots of KLEE or within 0.5 km of KLEE but outside the treatment blocks (and thus equivalent to the MWC plots). In sum, we collected 38 samples each of *Acacia*, *Aerva*, and grass. Each sample was a composite, comprised of three to five of the newest fully unfurled leaves from three to five plants within a 3–5 m radius area.

To examine the degree to which proximity to mounds affects N₂ fixation, in June–July 2007 (wet season; total 232.6 mm rainfall) we collected *Acacia* leaf samples from 5–10 trees along transects that extended up to 40 m away from the centers of each of 23 mounds. These mounds were not within the KLEE plots (i.e., native ungulates and cattle were present), and were haphazardly chosen within an approximately 2.0 × 1.6 km area. Each sample was comprised of five newest fully unfurled leaves from single *Acacia* trees that were 2–4 m in height; we sampled a total of 160 trees. We also recorded tree size, measured as maximum height, and the latitude and longitude of each mound. Immediately after collection we dried all plant samples in an oven at 60°C until they reached a constant weight. We later ground the samples into a coarse powder with a mortar and pestle, and weighed 3–5 mg into tin boats for isotopic and elemental analyses (conducted at the University of California Santa Cruz Stable Isotope Laboratory using a Costech 4010 elemental analyzer [Costech, Valencia, California, USA] interfaced with a Thermo Finnigan Delta^{PLUS} XP continuous flow stable isotope ratio mass spectrometer [Thermo-Finnigan, Waltham, Massachusetts, USA]). The δ¹³C and δ¹⁵N values of replicate plant samples were on average within 0.3‰ and 0.2‰ of each other, respectively.

Soil sample collection, preparation, and analyses.—In addition to the plant samples, we collected a limited number of soil samples (January–February 2008; total 22.4 mm rainfall) at different depths and distances from six termite mounds to assess availability of soil N and P,

and to isotopically characterize soil N. For the shallow (2–10 cm depth) soil sampling we selected four mounds that were also part of the *Acacia* transect sampling, and collected soil from three locations; 6–8 m (the mound edge), 14–18 m, and 28–38 m from the mound center (total sample *N* = 12). These distances correspond to our plant sampling locations; since neither *Acacia* nor *Aerva* usually grow directly on mound centers, the 6–8 m soil samples correspond to the “on mound” plant samples, while the 28–38 m samples are comparable to the “off mound” plants. We also collected deeper (30 cm) replicate soil samples near (~3 m) and far (~30 m) from two mounds that were not part of the *Acacia* transect sampling (total *N* = 10, isotopic and elemental analyses only).

Samples were placed in a drying oven at 60°C immediately after field collection, and dried to a constant mass. Subsequently, we homogenized the samples with a mortar and pestle. We weighed out subsamples for extractable NO₃⁻ (5 g), PO₄³⁻ (2.5 g), and isotopic (δ¹⁵N) and elemental (%C and %N) analyses (25 mg). NO₃⁻ and PO₄³⁻ analyses were done at the University of Wyoming Soil Testing Laboratory. For NO₃⁻ analysis, soil samples were extracted in a 1 mol/L KCl solution, and cadmium reduction was used as the detection method. The pH of a subset of samples was ~7.0. PO₄³⁻ analysis was done with the Olsen method (sodium bicarbonate extraction with Molybdenum blue detection). Isotopic and elemental analyses were conducted at the University of Wyoming Stable Isotope Facility (using a Costech 4010 elemental analyzer interfaced with a Thermo Finnigan Delta^{PLUS} XP continuous flow stable isotope ratio mass spectrometer). We used two-ANOVA models to investigate how soil parameters varied among termite mounds, and with distance from the mounds.

Investigating the effects of termites and herbivores on plant biogeochemistry.—We used nested ANOVA models to investigate the relative effects of termite mound proximity and herbivore enclosure treatment on δ¹³C, δ¹⁵N, and %N of the paired samples of *Acacia*, grass, and *Aerva* leaves collected near and far from mounds and inside and outside the KLEE ungulate enclosures (data in Appendix A). For each species and dependent variable, we ran a separate ANOVA with three predictor variables: herbivore treatment (no herbivores vs. herbivores present), mound identity nested within treatment, and on/off mound.

To better characterize the spatial pattern of mound effects on *Acacia* leaf N, we analyzed the leaf samples collected from individual *Acacia* on transects running away from mounds outside of the KLEE enclosures (data in Appendix B). To find the best predictive models for both log(δ¹⁵N_{acacia} + 1) and %N, we ran a total of 59 different GLMs for each variable, using different, biologically plausible combinations of independent variables, and then used Akaike’s information criterion

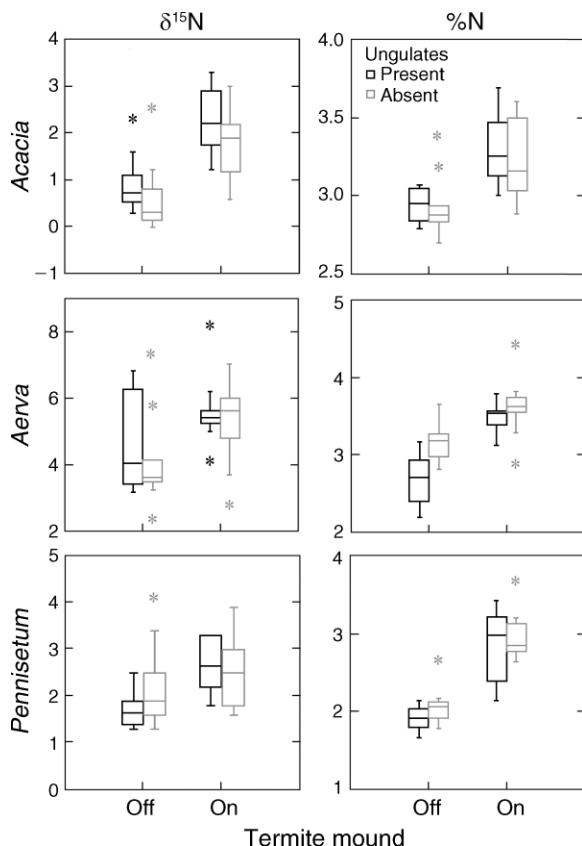


FIG. 2. Box plots for paired on/off termite mound $\delta^{15}\text{N}$ and dry mass N percentage (%N) values for *Acacia*, *Aerva*, and *Pennisetum* spp. (C_4 grasses), with ungulates present (from Kenya Long-term Exclusion Experiment [KLEE] all-ungulates-present [MWC] plots and nearby sites) and absent (from KLEE zero [no-ungulates] plots). Box plots consist of quartiles (central box includes the two middle quartiles, separated by the median), and asterisks denote values outside of the interquartile range.

(AIC) weights to determine support for different models and explanatory factors (Burnham and Anderson 2002).

Construction of *Acacia* $\delta^{15}\text{N}$ and N_2 fixation landscapes.—Although the simple statistical tests just described show that proximity to termite mounds strongly influences $\delta^{15}\text{N}_{\text{acacia}}$ values (see *Results*), these tests do not directly assess the community-wide importance of these effects. To begin to address this larger issue, we constructed maps of both average $\delta^{15}\text{N}_{\text{acacia}}$ values and the estimated proportion of *Acacia* leaf N derived from fixation for a 300×550 m section of black cotton savanna (see white boxed area in Fig. 5A). We began by mapping all mound centers within this section of savanna, which borders the KLEE experiment, using GPS points and satellite imagery. We used these locations to calculate the minimum distance to a mound center of each point on a 1×1 m grid. We then used the best GLM model fit to our transect data to estimate the average $\delta^{15}\text{N}_{\text{acacia}}$ value for *Acacia* at each grid point, and used these results to create an “isotope,” or spatial

map of estimated values. Since our estimated of $\delta^{15}\text{N}_{\text{acacia}}$ values from the transect data are also based upon distance to nearest mound, this extrapolation is appropriate. This mapping shows how mounds produce a highly over-dispersed pattern in mean $\delta^{15}\text{N}_{\text{acacia}}$ values.

Using the ^{15}N natural abundance method, we next estimated the proportion of *Acacia* leaf N derived from fixation, pN_{fix} , at different distances from termite mounds, in order to create spatial maps of *Acacia* fixation patterns. These calculations are complicated by the potential for an accumulated isotopic signal of atmospheric N_2 in soil N pools in areas with high fixation, resulting in lower plant $\delta^{15}\text{N}$ values, even for non-fixing plants (Fig. 2). To account for this effect, we began by using the paired data from the on/off-mound samples of *Acacia* and *Aerva*. Because termite mounds are long-lived (Darlington 1982), we assume that the vegetation and soil N pools in our study landscape are at an ecological steady-state. We began with a simple mixing model equation for $\delta^{15}\text{N}_{\text{acacia}}$ as a function of proportion N_2 fixation:

$$\delta^{15}\text{N}_{\text{acacia}} = pN_{\text{fix}}(\delta^{15}\text{N}_{\text{atm}} + \Delta^{15}\text{N}_{\text{assim-atm}}) + (1 - pN_{\text{fix}})(\delta^{15}\text{N}_{\text{soil}} + \Delta^{15}\text{N}_{\text{assim-soil}}) \quad (1)$$

where pN_{fix} is the proportion of *Acacia* leaf N that is from fixation, $\Delta^{15}\text{N}_{\text{assim}}$ is the isotopic spacing from source (atm, atmospheric N_2 ; soil, plant-available soil N) to leaf tissue; $\Delta^{15}\text{N}_{\text{assim}}$ is an approximation of the actual isotopic differences between the sources and leaf tissue but is appropriate because the values differ by $<10\%$ (Taylor 1974). Values for $\delta^{15}\text{N}_{\text{atm}}$ and $\delta^{15}\text{N}_{\text{soil}}$ are the $\delta^{15}\text{N}$ values for atmospheric N_2 and soil-derived plant available N, respectively. To solve for pN_{fix} , we simplified Eq. 1 by assuming that $\delta^{15}\text{N}_{\text{soil}} + \Delta^{15}\text{N}_{\text{assim-soil}} = \textit{Aerva}$ $\delta^{15}\text{N}$ values ($\delta^{15}\text{N}_{\text{aerva}}$). By definition, $\delta^{15}\text{N}_{\text{atm}} = 0\%$, allowing us to rearrange this equation to predict pN_{fix} :

$$pN_{\text{fix}} = (\delta^{15}\text{N}_{\text{acacia}} - \delta^{15}\text{N}_{\text{aerva}}) / (\Delta^{15}\text{N}_{\text{assim-atm}} - \delta^{15}\text{N}_{\text{aerva}}) \quad (2)$$

If we assume a value for $\Delta^{15}\text{N}_{\text{assim-atm}}$, we can use this equation to estimate pN_{fix} values ($pN_{\text{fix-est}}$) for each pair of *Acacia* and *Aerva* samples. We made these predictions for two values of $\Delta^{15}\text{N}_{\text{assim-atm}}$: 0‰ and -2‰. Although the *Acacia* in our study area do not have $\delta^{15}\text{N}$ values below -1‰, we extended our $\Delta^{15}\text{N}_{\text{assim-atm}}$ range to -2‰ in order to cover the plausible range of $\delta^{15}\text{N}_{\text{assim-atm}}$ values for leguminous trees (Shearer and Kohl 1986, Stock et al. 1995). Our final step was to predict $pN_{\text{fix-est}}$ values from $\delta^{15}\text{N}_{\text{acacia}}$ values, which our transect data allow us to tie to distance from mound centers and for which we had already created spatial maps. To do so, we fit simple linear regressions between the $pN_{\text{fix-est}}$ and $\delta^{15}\text{N}_{\text{acacia}}$ values of our paired samples: these explain 84% and 46% of the variance in $pN_{\text{fix-est}}$ for assumed values of $\Delta^{15}\text{N}_{\text{assim-atm}} = 0\%$ and -2%,

respectively. We then used these regression parameters to convert our map of $\delta^{15}\text{N}_{\text{acacia}}$ into maps of mean $\rho\text{N}_{\text{fix-est}}$ values.

The approach we took to estimating fixation rates and their spatial pattern uses the ^{15}N natural abundance method. There is a large literature addressing the assets and liabilities of this approach to estimating N₂ fixation by legumes (Shearer and Kohl 1986, Boddey et al. 2000, Spriggs et al. 2003), which includes examples of studies where this method worked (Raddad et al. 2005), and where it was not effective (Gehring and Vlek 2004). Choice of a non-fixing reference plant, and the assumption that the $\delta^{15}\text{N}$ value of that species reflects a purely soil-derived N source, are the most contentious parts of the ^{15}N natural abundance method. A range of factors must be considered, including phylogeny, rooting depth, and mycorrhizal status. Acquisition of N via associations with mycorrhizal fungi vs. direct root uptake of soil N can influence foliar $\delta^{15}\text{N}$ values. Several studies have shown that mycorrhizal plants generally have lower $\delta^{15}\text{N}$ values than co-occurring non-mycorrhizal plants, although this difference can be strongly influenced by the type of mycorrhizal association (e.g., ericoid vs. arbuscular; Handley et al. 1993, Michelsen et al. 1998, Spriggs et al. 2003).

Our use of *Aerva* as a non-N₂-fixing reference plant is justified for five reasons: (1) there are no abundant non-fixing leguminous trees in our study system (the most obvious choice for reference plant), (2) *Acacia* and *Aerva* have similar lateral rooting depths (the majority of roots within the top ~50 cm of soil), (3) there is no evidence that *Aerva* forms strong associations with mycorrhizal fungal symbionts (D. F. Doak and K. Fox-Dobbs, *personal observation*), and thus *Aerva* is likely to be directly dependent upon soil N sources, (4) *Aerva* is the most abundant woody forb in the study area (Young et al. 1998), and the only woody forb we were able to reliably pair with *Acacia* for our spatially explicit modeling, and (5) *Aerva* $\delta^{15}\text{N}$ values are high compared to $\delta^{15}\text{N}$ values of other non-fixing grasses, forbs and shrubs in the study area (K. Fox-Dobbs, *unpublished data*), indicating that any bias in our estimates of *Acacia* N₂ fixation will result in underestimation. Specifically, we isotopically surveyed a suite of other co-occurring non-fixing plants in the study area, and on average found >6‰ variation in $\delta^{15}\text{N}$ values among species at a given sampling location. In general, grasses had the lowest $\delta^{15}\text{N}$ values at each site, while *Aerva* and *Cadaba farinosa* had the highest values.

RESULTS

Soil biogeochemical analyses.—To put our *Acacia* fixation estimates into a meaningful ecosystem context, it was important to document the spatial variation in basic nutrient variables (data in Appendix C; Fig. 3). For shallow soils (2–10 cm depth) mound identity (ID) had no significant effect (two-way ANOVA; $P > 0.05$, no mound ID \times distance interaction) on NO_3^-

concentrations, %N, $\delta^{15}\text{N}$ values, or C/N ratios. There was more plant-available N (as NO_3^-) in shallow soils near vs. away from termite mounds (two-way ANOVA; $F_{1,11} = 9.12$, $P = 0.04$), but $\delta^{15}\text{N}$ values did not vary with distance from mounds (two-way ANOVA; $F_{1,11} = 0.10$, $P = 0.76$). While not significant, the total nitrogen content (%N range = 0.28–0.10%, two-way ANOVA; $F_{1,11} = 3.22$, $P = 0.15$), the quality of soil organic material (C/N ratio range = 12.4–10.0, two-way ANOVA; $F_{1,11} = 5.29$, $P = 0.08$), and plant-available P (PO_4^{3-} concentration range = 3.0–0.8 ppm, sample too small for statistical analysis) were generally higher in shallow soils near vs. far from mounds. The $\delta^{15}\text{N}$ and %N values for the deeper soil samples (30 cm depth) did not change significantly among mounds or with distance from termite mounds (two-way ANOVA; $P > 0.05$ for both effects and interaction), and were within the range of shallow soil values (mean values = 5.3‰ and 0.14 ppm, respectively). Since the shallow and deep samples were not collected from the same mounds, we did not directly compare the N data sets. In general, it does not appear that black cotton soil $\delta^{15}\text{N}$ values change with depth, while soil %N values are slightly lower at depth.

Effects of termites and herbivores on plant biogeochemistry.—Analysis of our paired plant samples from on and off mounds and exposed or protected from mammalian herbivores showed that (1) $\delta^{13}\text{C}$ values were not significantly influenced by any predictor and (2) N biogeochemistry of leaves was far more strongly influenced by proximity to termite mounds than by the presence of herbivores (Fig. 2). Both $\delta^{15}\text{N}$ and %N were higher close to mounds than far away for all plant groups (Table 1). For *Acacia*, exclusion of ungulates resulted in slightly lower $\delta^{15}\text{N}$ values; the opposite was true for grass, and *Aerva* showed no significant effect of ungulate treatment (Table 1). The percentage of variance in $\delta^{15}\text{N}$ values explained by proximity to termites was 9.9, 7.6, and 1.4 times higher than that explained by the presence or absence of ungulates for *Acacia*, grasses, and *Aerva*, respectively.

While no single explanatory model for $\log(\delta^{15}\text{N}_{\text{acacia}} + 1)$ of the *Acacia* transect data had an AIC weight over 0.17 (Table 2), the nine models with weights > 0.05 all included distance from mound, in combination with other factors, and the summed AIC weight for a distance effect > 0.99 . For %N, all six models with AIC weights > 0.05 included distance from mound (Table 2), and the summed AIC weight for a distance effect = 0.844. The best models for each variable predict gradual falloff of both $\delta^{15}\text{N}_{\text{acacia}}$ and, with far more noise, %N values, as distance from mound centers increases (Fig. 4). Strikingly, these effects occur well beyond the typical radius of discernable mound effects above ground (~5–10 m).

Acacia $\delta^{15}\text{N}$ value and N₂ fixation landscapes.—Both *Acacia* $\delta^{15}\text{N}$ values and N₂ fixation rates are predicted to vary strongly and regularly across our sample landscape, which has a typical density and arrangement of termite mounds (Fig. 5B–D). These maps show that termite

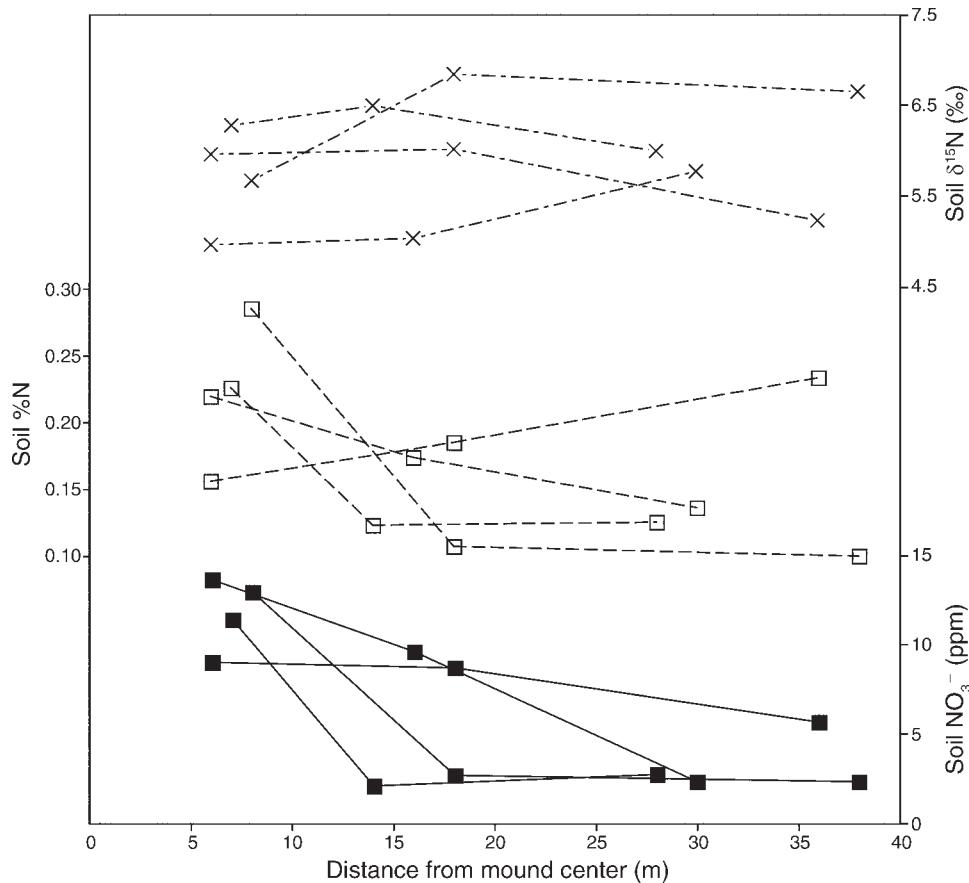


FIG. 3. Nitrogen isotope values ($\delta^{15}\text{N}$; crosses and dot-dashed lines), nitrogen percent (%N; open boxes and dashed lines), and nitrate (NO_3^- ; solid boxes and solid lines) concentrations for shallow soil samples (2–10 cm depth) along transects away from four termite mounds in the study area.

effects create striking differences in fixation activity, ranging from less than 50% on mounds to more than 80% off mounds, assuming the more likely $\Delta^{15}\text{N}_{\text{assim-atm}}$ of 0‰. While a $\Delta^{15}\text{N}_{\text{assim-atm}}$ of -2‰ yields smaller differences between on and off mound fixation rates (less than 40% on and greater than 55% off) the resulting spatial structure patterning in fixation activity is very similar (Fig. 5D), with termite mounds showing significantly lower fixation activity than do matrix areas. Regardless of the $\Delta^{15}\text{N}_{\text{assim-atm}}$ value assumed, the resulting maps show the strong effect of termites in driving a regular patterning in landscape level fixation rates and the hyperdispersion of these termite-driven effects across large areas (Fig. 5A). Last, at the scale of the landscape, our models predict that 73% or 51% of total N in *Acacia* is derived from atmospheric fixation, given estimates of $\Delta^{15}\text{N}_{\text{assim-atm}}$ of 0‰ or -2‰ , respectively. However, if no termite mounds were present, the total N from fixation would rise to 89% or 58%

DISCUSSION

Here, we document both the strong, indirect effects of termites on the interactions between *Acacia* trees and

their N_2 -fixing-symbionts and the relatively minor role that ungulates play in comparison to termites with the regulation of plant N sources. In addition, we show that the over-dispersion of termite mounds leads to effects on *Acacia* that create spatial patterning in an otherwise homogeneous community, with strong, indirect effects on other plants species, as shown by their isotopic and %N values. By estimating termite mound effects on *Acacia* N_2 fixation and mapping the spatial patterns created by these interactions, we demonstrate not only that termites have profound effects on a key ecosystem process, but that these effects create a striking landscape-scale spatial structure driven entirely by biotic interactions. The effect of termites on *Acacia* N_2 fixation attenuates far from the obvious edges of the visible mounds, which demonstrates that spatial patterning created by biotic interactions can be cryptic even while it is strong and consistent.

Although spatial patterning is widely suggested to be a key feature in the maintenance of species diversity and community structure (Karieva 1990, Tilman and Karieva 1997, Tews et al. 2004), there are still relatively few study systems in which the mechanisms driving such

TABLE 1. Results of nested ANOVAs on nitrogen percentage and δ¹⁵N values of leaf tissues for the factors of presence or absence of ungulates (ungulate), near or far proximity to termite mounds (mound), and mound identity (ID, nested within ungulate treatment).

Dependent variable	r ²	Ungulates		Mound		ID		Error
		SS	P	SS	P	SS	P	
δ ¹⁵ N								
<i>Acacia</i>	0.82	1.5273	0.0472	15.1945	<0.0001	11.6815	0.0714	6.0587
<i>Aerva</i>	0.79	1.4590	0.2101	11.0637	0.0021	47.3495	0.0090	15.5496
Grass	0.79	1.8202	0.0187	2.5485	0.0068	13.7786	0.0135	4.9026
%N								
<i>Acacia</i>	0.76	0.0076	0.6304	0.9078	<0.0001	0.8654	0.1633	0.5699
<i>Aerva</i>	0.81	0.7526	0.0077	3.7604	<0.0001	1.9213	0.2668	1.5071
Grass	0.93	0.1742	0.0710	8.1306	<0.0001	2.8582	0.0053	0.8512

effects, especially when they are created by biotic forces, are well-understood or documented (van der Valk and Warner 2009). One of the surprising results of our work was the relative simplicity of the mechanisms generating spatial pattern, which seems to derive entirely from shifts in *Acacia* fixation rates due to termite activity. We had expected that the abundant large herbivores in this system would react to and hence modify the effects of termite mounds, but find little evidence for such interactions. We also chose a system with unusually little abiotic structure, allowing us to better estimate biotically driven effects. While communities with more topographic, climatic, or other abiotic heterogeneity may show more variable biotic structuring, we suggest that the interaction of the different forces may result in even stronger (though more complicated) effects of key biological processes in pattern generation.

The effects we find in this system illustrate that N₂ fixation by *Acacia* is not a static process, and suggest

that *Acacia* preferentially utilizes soil-based N sources when these sources are readily available near termite mounds. In fact, termite/soil derived N sources influence >50% of the *Acacia* trees in our system. Counter-intuitively, termite mounds are nutrient “hotspots,” yet suppress a major N input into the system, atmospheric N₂ fixation by *Acacia*. Indeed, the presence of termite mounds decreases *Acacia* N₂ fixation by at least 5% over 50–90% of the landscape (Δ¹⁵N_{assim-atm} of 0‰ or –2‰, respectively). This reduction in support of bacterial symbionts represents a potentially important gain in energy efficiency: *Acacia* grow faster and have higher reproduction when growing adjacent to termite mounds (Brody et al. 2010; T. M. Palmer, unpublished data). Estimates of %N derived from N₂ fixation by *Acacia* species (using the ¹⁵N natural abundance method) in other regions of Africa are variable, but encompass the fixation levels we report here. For example, fixed N accounts for 51% of the N in invading *Acacia* trees in

TABLE 2. Best-supported models for nitrogen percent (%N) and δ¹⁵N values for *Acacia* transect data.

Explanatory factors in model										
Mound ID	Latitude	Longitude	Longitude ²	Ant	Distance	Height	Diameter	NP	ΔAIC	AIC weight
Models for δ ¹⁵ N										
	X		X		X			5	0.000	0.170
	X		X	X	X			6	0.367	0.142
	X		X		X		X	6	1.240	0.092
	X	X	X		X		X	6	1.240	0.092
	X		X	X	X		X	7	1.396	0.085
	X		X		X	X		6	1.520	0.080
	X		X	X	X	X		7	1.587	0.077
	X	X	X		X			6	1.996	0.063
	X	X	X	X	X			7	2.359	0.052
Models for %N										
	X				X			25	0.000	0.254
	X				X		X	26	0.938	0.159
	X			X	X			26	1.029	0.152
	X			X	X		X	27	1.787	0.104
	X				X	X		26	1.844	0.101
	X			X	X	X		27	2.736	0.065

Notes: In all, 59 models were fit for each dependent variable, using different combinations of eight explanatory variables: mound identity, relative latitude, longitude, (longitude)², species of ant symbiont, distance from nearest termite mound, tree height, and tree diameter. The number of fitted parameters (NP), relative AIC value (ΔAIC, the difference in AIC values of each model and that of the best model), and AIC weight (the probability that a model is the best predictive model of those tested) are shown for all models with AIC weights ≥0.05.

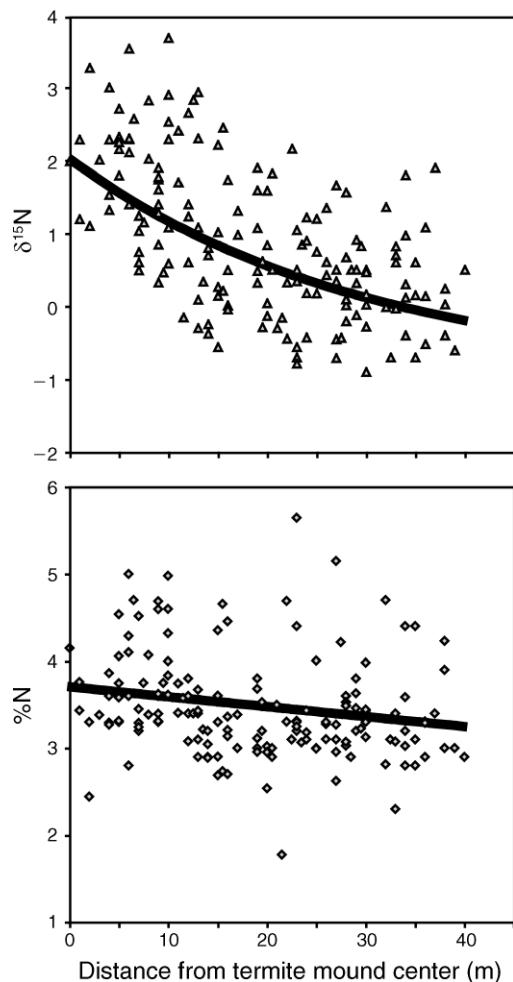


FIG. 4. Scatter plots of *Acacia* $\delta^{15}\text{N}$ and dry mass N percentage (%N) values along $\sim 45\text{-m}$ transects away from termite mound centers ($N = 23$ mounds). Lines show best-fit model predictions (not including positional variables): $\%N = 3.6864 - 0.0114(\text{distance from mound center})$; $\log(\delta^{15}\text{N} + 1) = 1.103838 - 0.033626(\text{distance from mound center})$. Fitting of the $\delta^{15}\text{N}$ estimates was conducted on a log scale to meet linearity assumptions.

South Africa (Stock et al. 1995), between $<5\%$ to $>70\%$ of N in *Acacia* trees along an aridity gradient in Namibia (Schulze et al. 1991), and up to 61% of N in an *Acacia* species from Sudan (Raddad et al. 2005).

Odontotermes mounds (Fig. 1B–D) are underlain by a substantial amount of organic material in the form of numerous large fungal combs (termitaria), termite feces, and termite body tissues (Boutton et al. 1983, Palmer 2003). While mound-derived organic N is largely unavailable to plants, the physical and hydrological modification of mound soils by termites (Jones 1990) creates a microenvironment that enhances microbial conversion of organic N to mineral forms of N (Fig. 3; Jouquet et al. 2005). Our modest data sets of static soil biogeochemical measurements allow us to investigate some basic patterns of soil N related to mound

proximity. Specifically, the N content of soils is higher near mounds, and mineral N (as NO_3^-) in soils decreases significantly with distance from termite mounds. Because our measurements are not dynamic we cannot know whether higher mound NO_3^- concentrations reflect enhanced mineralization of a somewhat larger organic N pool, or reduced N loss via leaching and denitrification. Studies of soils associated with termite structures (mounds and sheeting) have reported both higher and lower levels of denitrification (Lensi et al. 1992, Ndiaye et al. 2004), and this is a subject that warrants further investigation in our study area. Soil N transformations are associated with (sometimes large) isotopic fractionations (Evans 2007), which ultimately determine the $\delta^{15}\text{N}$ values of plant available N. For example, denitrification can strongly influence the $\delta^{15}\text{N}$ values of soil N since the N_2O and N_2 volatilized during this transformation are depleted in ^{15}N (Evans 2007), resulting in a soil N pool that is ^{15}N enriched. We used the spatial variability in *Aerva* $\delta^{15}\text{N}$ values to account for potential differences in mineral N $\delta^{15}\text{N}$ values that result from varying rates and magnitudes of N transformations in soils near and far from termite mounds.

We found minimal variation in soil $\delta^{15}\text{N}$ values, both laterally and vertically, suggesting that black cotton vertisols are not strongly stratified with regards to organic N, and that organic N pools are isotopically similar on and off mounds. We might expect mound soil $\delta^{15}\text{N}$ values to be significantly higher than off mound $\delta^{15}\text{N}$ values because organic N sources on mounds include consumer (termite and fungus) tissues that could be enriched in ^{15}N relative to plant material (Högberg 1997). The lack of ^{15}N enrichment in mound soils may demonstrate that termite mounds are relatively 'closed systems' with respect to organic N. In other words, once N enters the mound as plant tissue it may cycle through various organic forms (fungal and termite tissues, or residual vegetative material), but will not be rapidly exported out of the mound. Potential export mechanisms include loss via soil transformations and termite removal via predation by termitivores such as aardvarks and aardwolves. Finally, we consider how mycorrhizal fungal symbionts could influence our isotopic results and subsequently our interpretations of N_2 fixation via the ^{15}N natural abundance method. Reliance upon root fungal derived N generally correlates with lower foliar $\delta^{15}\text{N}$ values (e.g., Spriggs et al. 2003). The relatively high $\delta^{15}\text{N}$ values of *Aerva* suggest that our reference plant does not have strong mycorrhizal associations. Arbuscular mycorrhizae have been associated with other *Acacia* species, but at this time we do not have evidence for presence of any mycorrhizae on/in *Acacia* roots. Regardless, the use of fungal symbiont derived N by *Acacia* should result in an underestimate of N derived from fixation (Högberg 1990; Handley et al. 1993), meaning that our estimates are conservative.

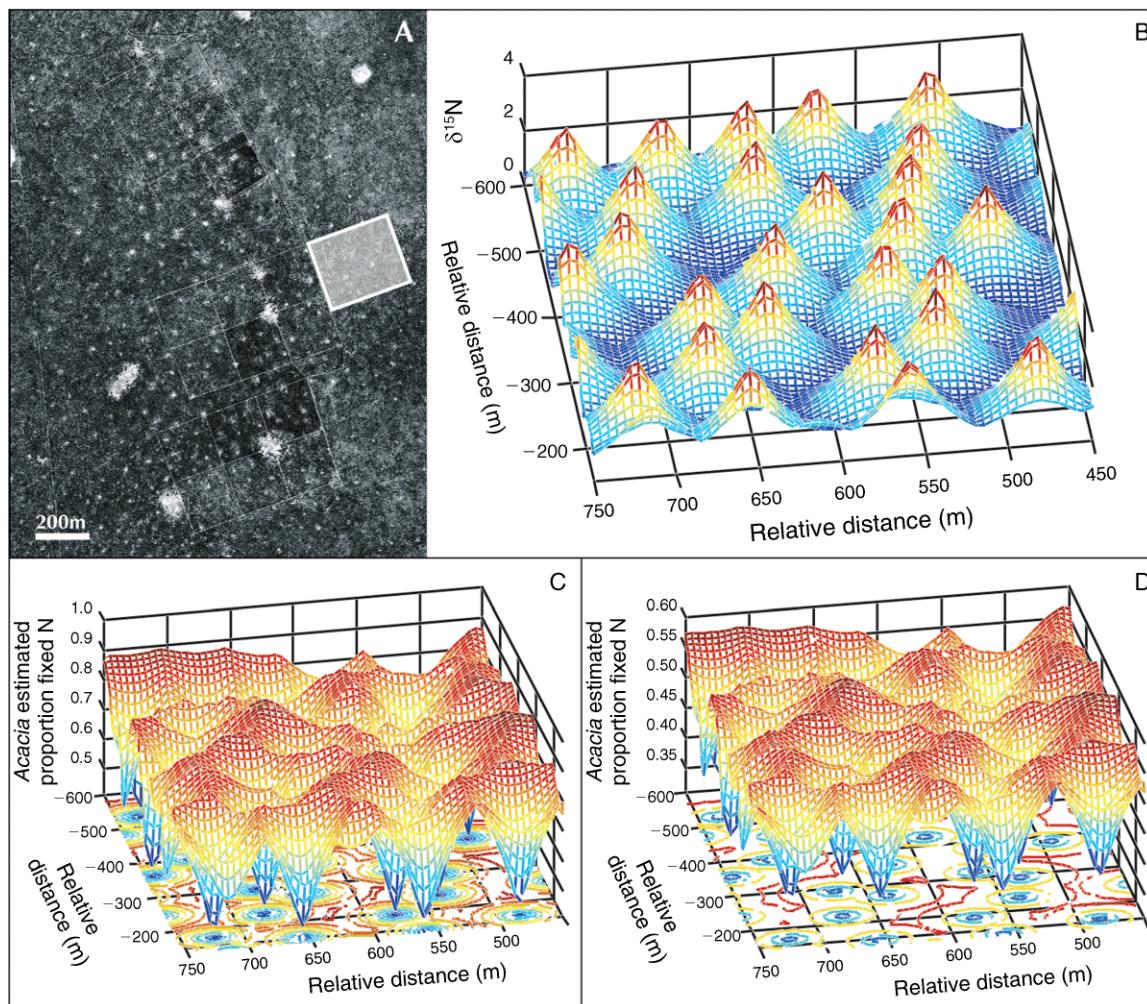


FIG. 5. The mapped region of black cotton savanna used to generate an *Acacia* leaf $\delta^{15}\text{N}$ isoscape and estimated *Acacia* N₂ fixation landscapes. (A) Normalized difference vegetation index (NDVI) satellite image (provided by T. P. Young) of study area at the Mpala Research Center that shows KLEE plots (faint white lines), over-dispersed termite mound distribution (white dots), and mapped region selected for *Acacia* $\delta^{15}\text{N}$ isoscape (white box). (B) *Acacia* $\delta^{15}\text{N}$ isoscape for the region shown in panel A (area shown is less than that mapped to improve clarity of presentation). Surface values derived from the best-fit model for *Acacia* $\delta^{15}\text{N}$, using averages of relative latitude and longitude for the mapped region: $\log(\delta^{15}\text{N} + 1) = 1.2608 - 0.0347(\text{distance from mound center}) + 0.000255(\text{relative latitude}) - 6.0308 \times 10^{-7}(\text{relative longitude})^2$. (C) The fixation landscape assuming that $\Delta^{15}\text{N}_{\text{assim-atm}} = 0\text{‰}$ (the estimated proportion of *Acacia* leaf N that is from fixation, $p\text{N}_{\text{fix-est}} = 0.945 - 0.150\delta^{15}\text{N}$). (D) The fixation landscape assuming that $\Delta^{15}\text{N}_{\text{assim-atm}} = -2\text{‰}$ ($p\text{N}_{\text{fix-est}} = 0.603744 - 0.068759\delta^{15}\text{N}$).

N₂-fixing *Acacia* species are common dominants in arid woodland savannas where soil N is readily lost by leaching, denitrification, and volatilization during episodic precipitation and sporadic wildfire events (Högberg 1986, Cook 2006). Invading leguminous trees are known to alter the N cycle of ecosystems they invade (Vitousek et al. 1987), and isotopic evidence for this quickly shows up in the $\delta^{15}\text{N}$ values of local plants and soils (Yelenik et al. 2004). For example, the invasion of N₂-fixing *Acacia* trees into fynbos and strandveld ecosystems in South Africa rapidly influenced N cycling and was reflected in the dilution of soil $\delta^{15}\text{N}$ values (Stock et al. 1995). Similar to invaded vs. non-invaded systems, the off-mound non-*Acacia* plant $\delta^{15}\text{N}$ values in

our study record the contribution of ¹⁴N-enriched *Acacia* leaf litter to soil N pools and show the community-wide effects of these termite-driven patterns in *Acacia* biogeochemistry. The pattern is magnified by the high foliar N content of *Acacia* relative to grasses, the subcanopy dominant in our system, and the sheer abundance of *Acacia*.

Marrying the ¹⁵N natural abundance approach with spatial mapping of termite effects provided our most interesting results. Although spatial configurations of isotopic variability (isoscapes) are routinely used to study animal migration and movement histories (Bowen et al. 2005), our *Acacia* N₂ fixation isoscapes represent a novel application of this technique; we illuminate not

just a pattern, but also a key ecological process at the scale relevant for both individual and community dynamics, which is therefore likely to be of key importance in governing ecological functioning in this system. As our results show, this combination of methods can allow us to understand the magnitude of, and mechanisms for, species effects on their surrounding communities and suggest how cryptic effects may be critical in shaping natural ecosystems.

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APPENDIX A

On/off termite mound plant sample list and biogeochemical data (*Ecological Archives* E091-090-A1).

APPENDIX B

Acacia drepanolobium transect sample list and biogeochemical data (*Ecological Archives* E091-090-A2).

APPENDIX C

Soil sample biogeochemical data (*Ecological Archives* E091-090-A3).