

SAVANNA TREE DENSITY, HERBIVORES, AND THE HERBACEOUS COMMUNITY: BOTTOM-UP VS. TOP-DOWN EFFECTS

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Abstract. Herbivores choose their habitats both to maximize forage intake and to minimize their risk of predation. For African savanna herbivores, the available habitats range in woody cover from open areas with few trees to dense, almost-closed woodlands. This variation in woody cover or density can have a number of consequences for herbaceous species composition, cover, and productivity, as well as for ease of predator detection and avoidance. Here, we consider two alternative possibilities: first, that tree density affects the herbaceous vegetation, with concomitant “bottom-up” effects on herbivore habitat preferences; or, second, that tree density affects predator visibility, mediating “top-down” effects of predators on herbivore habitat preferences. We sampled sites spanning a 10-fold range of tree densities in an *Acacia drepanolobium*-dominated savanna in Laikipia, Kenya, for variation in (1) herbaceous cover, composition, and species richness; (2) wild and domestic herbivore use; and (3) degree of visibility obstruction by the tree layer. We then used structural equation modeling to consider the potential influences that tree density may have on herbivores and herbaceous community properties. Tree density was associated with substantial variation in herbaceous species composition and richness. Cattle exhibited a fairly uniform use of the landscape, whereas wild herbivores, with the exception of elephants, exhibited a strong preference for areas of low tree density. Model results suggest that this was not a response to variation in herbaceous-community characteristics, but rather a response to the greater visibility associated with more open places. Elephants, in contrast, preferred areas with higher densities of trees, apparently because of greater forage availability. These results suggest that, for all but the largest species, top-down behavioral effects of predator avoidance on herbivores are mediated by tree density. This, in turn, appears to have cascading effects on the herbaceous vegetation. These results shed light on one of the major features of the “landscape of fear” in which African savanna herbivores exist.

Key words: *Acacia drepanolobium*; Africa; Laikipia, Kenya; landscape of fear; optimal foraging; predator avoidance; structural equation modeling; tree–grass interactions; ungulates; woody encroachment.

INTRODUCTION

Herbivores have been said to exist in a “landscape of fear” (Laundre et al. 2001, Brown and Kotler 2004). Within this landscape, herbivores must often trade off between avoiding predators and maximizing the quality or quantity of their forage intake (Sih 1980, Houston et al. 1993, Lima 1998). The nature of this trade-off is thought to depend on herbivores’ perceived degree of predation risk (Brown and Kotler 2004). For ungulate herbivores, factors that affect predation risk include body size (Berger and Cunningham 1988, Sinclair et al. 2003, Radloff and du Toit 2004), group size (Childress and Lung 2003), and the ability to detect and/or be detected by predators (FitzGibbon 1989, Creel and Winnie 2005). Habitat features, particularly the amount of cover, have the potential to affect how well prey

detect predators, and vice versa (Kunkel and Pletscher 2000, Creel and Winnie 2005). Relatively few studies, however, have examined the effects of cover on ungulate herbivore habitat preferences, or the potential consequences of those preferences.

In African savannas the habitats available to herbivores range from relatively open plains with few trees to dense thickets of trees with sparse grass. Although variation in woody cover across regions has been associated with differences in precipitation (Sankaran et al. 2005), woody cover within a region can be patchy, depending on factors such as fire, herbivory, soil characteristics, and the interactions among these factors (Dublin et al. 1990, Roques et al. 2001, van Langevelde et al. 2003, Sankaran et al. 2005). African savannas support a high diversity of ungulate herbivores that span a large range of body sizes. Herbivores include strict browsers, strict grazers, and mixed feeders. Given their differences in body size and foraging habits, these herbivores might be expected to exhibit a range of responses to the variation in woody cover that charac-

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terizes the landscape in which they live. The nature of these responses, however, and the extent to which they are driven by foraging preferences vs. predator avoidance, remain poorly understood (Lima 1998).

Variation in cover or abundance of woody vegetation (hereafter “trees”) can affect the forage available to herbivores in several ways. Most obviously, there is more forage available to browsing herbivores where tree density is high (although accessibility to this forage may depend on other factors such as the height of the trees). In contrast, areas with low tree density may have more or better forage available to grazing herbivores. This could occur simply because grasses occupy a higher percentage of the habitat where tree cover is low. Alternatively, grass productivity may be higher in such places (Scholes and Archer 1997, Smit and Rethman 2000). Herbaceous species composition, including the relative abundance of grasses and forbs, can also respond to tree density (Angassa and Baars 2000, Smit 2004), with potential consequences for forage quality.

At the same time, tree density may affect the risk of predation for ungulate herbivores. High densities of trees impede visibility and, potentially, predator detection. In African savannas, where most predators rely on stealth, the ability to detect predators may be more important than the ability to hide from predators (van Orsdol 1984). In the Serengeti, Underwood (1982) found that wildebeest, impala, topi, and reedbuck all exhibited greater predator vigilance and, consequently, less forage intake, in areas with more woody vegetation. This suggests that herbivores may spend more time and/or consume more forage in areas with low tree density, with potentially cascading consequences for the vegetation.

In this paper we consider two alternative possibilities: first, that tree density affects the herbaceous vegetation, thereby exerting “bottom-up” effects on herbivore habitat preferences; or, second, that tree density affects visibility, mediating “top-down” effects of predator avoidance on herbivore habitat preferences. We sampled sites spanning a 10-fold range of natural tree densities and quantified herbaceous vegetation, domestic and wild herbivore use, and visibility in these sites. We first examined the bivariate associations among these variables. We then used structural equation modeling (Grace 2006) to consider some of the potential influences that tree density may have on herbivores via its effects on plant community properties and visibility. Specifically, we asked: (1) Do herbaceous cover, composition, and species richness appear to be influenced by tree density? (2) Do herbivores respond to tree density? and (3) In structural equation models, do herbivores appear to respond more strongly to differences in herbaceous vegetation or visibility?

METHODS

Study site

This study was conducted at the Mpala Research Centre (36°52' E, 0°17' N) and the adjacent Jessel

Ranch, in Laikipia, Kenya. Mean annual rainfall is ~500 mm. Soil in our study area is poorly drained, clay-rich “black cotton” soil. The whistling-thorn acacia (*Acacia drepanolobium* Sjöstedt) comprises 97% of the woody cover, and five species of perennial bunchgrasses make up 90% of the herbaceous cover (Young et al. 1998): *Bracharia lachnantha*, *Pennisetum stramineum* (Maasai grass), *Pennisetum mezianum* (bamboo grass), *Themeda triandra* (red oat grass), and *Lintonia nutans*. The herbaceous layer also includes several less common forb and grass species. *Acacia drepanolobium* is one of the most abundant and widespread tree species in eastern Africa. It is typically found on black cotton soils, where it forms nearly monospecific stands over hundreds of square kilometers and can be a serious rangeland invader. Individual trees can grow up to 10 m in height, but at our study site the vast majority of trees are <4 m tall.

The Mpala Research Centre (MRC) and Jessel Ranch are managed for domestic cattle production and wildlife conservation. Common wild herbivores include: grazers, mostly plains zebras (*Equus burchelli*), hartebeest (*Alcelaphus buselaphus*), and oryx (*Oryx gazella*); browsers, mostly giraffes (*Giraffa camelopardalis*) and steinbuck (*Raphicerus campestris*); and mixed feeders, mostly Grant's gazelles (*Gazella granti*), elephants (*Loxodonta africana*), and eland (*Taurotragus oryx*). Common large predators include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and spotted hyenas (*Crocuta crocuta*).

Data collection

Using a high-resolution (60 cm) image taken in June of 2003 from the Quickbird satellite (acquired from Digital Globe, Fort Collins, Colorado, USA), we mapped tree cover for the MRC and Jessel Ranch properties (see Okello et al. [in press] for methods). We then located 34 sites representing a range of tree covers in an area 3.5 × 4.5 km. At each site, we established a 50 × 50 m plot.

In February–March of 2006, we quantified tree density, herbaceous cover and composition, and herbivore use in these plots. Trees and shrubs of all species were identified, counted, and categorized into four height classes: <1 m, 1–2 m, >2–3 m, and >3 m. We established six parallel 50 × 4 m transects through each plot, along which we identified and counted dung piles of cattle and all native wild herbivores. In a review of the accuracy of dung counts for estimating terrestrial vertebrate densities, Barnes (2001) found that dung counts were at least as accurate as aerial and ground counts—especially for quantifying the relative densities of a given herbivore species across different habitats. At our site, the landscape-wide relative dung densities of the common wild herbivore species (Fig. 3) were strongly correlated with the relative densities of the same species based on four years of aerial surveys ($r^2 = 0.95$, $n = 9$ species, $P < 0.0001$; G. Aike, unpublished data).

We sampled herbaceous vegetation using a 10-point pin frame at 10 m intervals along four 50-m transects (for a total of 240 pins per plot). We counted total pin hits for each species encountered, which is strongly correlated with biomass in this system (I. Kimathi and T. P. Young, *unpublished data*). This “snapshot” sampling of herbaceous vegetation has the disadvantage of not informing us about the effects of tree density on grass productivity; thus in our analyses we focus on understanding grass and forb abundance patterns.

In October 2006 we quantified visibility, or mean distance to the nearest line-of-sight obstruction, using a rangefinder. At this time 20 of the original 34 plots had been experimentally manipulated to modify tree densities. Thus we could only measure visibility in the 14 remaining plots. For each plot, we measured visibility in 24 directions (every 15° on the compass) from the center of the plot. The rangefinder was held level at a height of 1.10 m, approximately the height of a Grant's gazelle's head. All 24 measurements were averaged for each plot. In addition, at this time, we counted the number of trees exhibiting evidence of elephant damage (trunk and/or branch breakage) in the 14 control plots.

For all plots, we also quantified soil characteristics (texture, total N, total P, available P, and total C). The details of these analyses are given elsewhere (C. Riginos, J. B. Grace, D. J. Augustine, and T. P. Young, *unpublished manuscript*). For the purposes of the present study, we use these results simply to statistically control for the effects of soil characteristics on tree density and herbaceous community characteristics in structural equation models (see *Statistical analysis: Structural equation modeling*, below).

Statistical analysis: bivariate relationships

We used ANCOVA and linear regression to evaluate several dependencies: (1) soil characteristics on woody and herbaceous vegetation, (2) tree density on herbaceous vegetation and dung density, and (3) herbaceous vegetation on dung density. All analyses were carried out in JMP version 7.0 (SAS Institute 2007). In ANCOVA models we found significant main effects of property (MRC vs. Jessel Ranch) and the predictor variables listed above, but no interactions between these factors. One plot was discarded as an outlier for certain analyses as this plot had exceptionally high wild-herbivore dung densities and grass cover, probably because it is almost never grazed by cattle (P. Jessel, *personal communication*). For all bivariate relationships, we fit the data to linear, log-linear, and quadratic (polynomial) models. Significance tests were used to select the most parsimonious model for each case. To explore the relationships among variables, we calculated Pearson's correlations. One multivariate outlier (the aforementioned plot) was excluded and certain variables were log-transformed to achieve multivariate normality (an assumption of structural equation modeling; see

next section). Results from these exploratory analyses are presented in the Appendix for reference.

Statistical analysis: structural equation modeling

We used structural equation modeling (SEM) analyses to consider some of the effects that tree density may have on herbivores, the herbaceous community, and visibility. SEM provides a means to examine possible causal pathways among intercorrelated variables, examine the associations among variables while statistically controlling for other model variables (i.e., to partition relationships), and examine the likelihood of alternative models given the data at hand (Bollen 1989).

To guide our analyses and interpretations, we developed a structural equation meta-model (J. B. Grace, T. M. Anderson, H. Olf, and S. M. Scheiner, *unpublished manuscript*). A meta-model is one that represents the general theoretical propositions being considered without specifying statistical details. The meta-model that guided our analyses (Fig. 1) is based on the following a priori premises: (1) Both woody and herbaceous vegetation may be influenced by soil texture but not vice versa. (2) Tree density can influence vegetation via mechanisms other than soil texture and fertility; for example, by affecting the light or soil moisture environment. (3) The effects of tree density on wild herbivores and cattle may either be indirect, mediated through tree effects on herbaceous vegetation, or they may be direct, due to some other behavioral selection of foraging locations, such as predation-risk avoidance. (4) Wild herbivores and cattle may alter herbaceous community composition or affect diversity (thus, there may be reciprocal interactions between herbivores and herbaceous vegetation). (5) Wild herbivores (excluding elephants) and cattle are not likely to affect tree density in the short term.

Our application of SEM in this case involved what is referred to as a “nested-models approach” (Grace 2006). Using this approach, the world of possible models was constrained by the premises associated with the meta-model described above. Evaluations focused sequentially on (1) indicator selection and (2) nested-model comparisons. Nested models include those containing a common set of variables and assumptions about dependencies (e.g., vegetation depends on soil), but differ in the pathways deemed to be significant.

Indicator selection is a process whereby different variables or forms of variables in a set (e.g., soil conditions) are chosen to represent the conceptual entities of interest. For soil conditions, we screened the data using stepwise regression to select the measures to include in the structural equation models. Results indicated that silt, clay, total nitrogen, and extractable phosphorus were a sufficient set of variables to represent the dependence of vegetation components on soil conditions. We selected the “wild herbivores” measure based on both biological knowledge and consistency in response. Since the dung densities of most wild-

herbivore species showed similar responses to tree density, we used total dung count as our measure. We excluded elephant dung from this total, however, since elephant dung densities were positively associated with tree density, supporting prior ecological knowledge that elephants select habitat largely without concern for predator avoidance. For the herbaceous community, we were interested in the responses of the dominant grasses and in understanding the controls on plant species richness. We considered possible ways of grouping the various grass species—for example, by “increasers” vs. “decreasers” in response to tree density, herbivores, or certain soil properties—but found that each species’ response to these variables was unique. In the models, therefore, we included the following herbaceous characteristics: (1) cover of each of the four most abundant grasses, (2) percentage of total cover that was grass (hereafter “relative grass cover”) to capture the relative cover of grasses and forbs in one variable, and (3) total species richness from the 240 pin samples at each site.

Based on the above-described measures for the constructs in the meta-model (Fig. 1), we considered nested models in which herbaceous vegetation predicted herbivore dung densities, and models in which herbivore dung densities predicted herbaceous vegetation characteristics. This allowed us to examine the alternative hypotheses that herbivores respond to differences in herbaceous vegetation as opposed to driving these differences. We used maximum likelihood procedures for estimation and to evaluate model goodness-of-fit. Sequential application of single-degree-of-freedom χ^2 tests was used to determine which pathways should be retained in the models. We also allowed the effects of tree density to be nonlinear by including a second-order polynomial term in the models. This process allowed us to arrive at a single model, which we deemed the most likely relationship among the variables considered. These analyses were carried out using the structural equation modeling software Amos 7.0 (SPSS 2007). Because of the small number of samples relative to the complexity of the models evaluated, we also obtained Bayesian estimates (Lee 2007) using Amos for confirmatory purposes, since these estimates do not depend on large-sample theory.

An additional simple structural equation model was investigated to see whether the relationship between tree density and wildlife could be explained by the effects of trees on our measured estimates of visibility. This analysis was conducted separately because visibility estimates were only available for 14 of the 34 plots.

RESULTS

Bivariate relationships

Sites ranged from 60 to 696 trees per 0.25-ha plot, equivalent to 240–2784 trees/ha. *Acacia drepanolobium* comprised 98% of the trees encountered. Some relationships between tree density and the proportion of trees in each size class were statistically significant; however, the

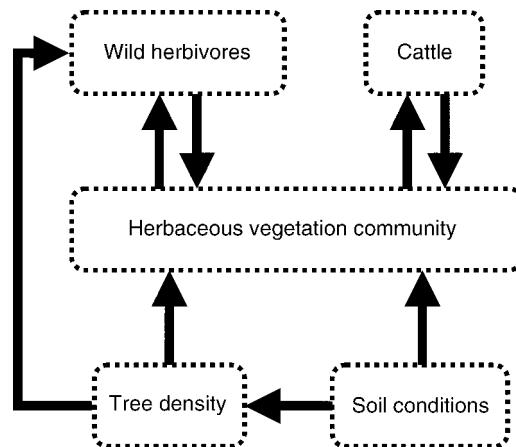


FIG. 1. Schematic model guiding structural equation modeling (SEM) analyses. The boxes represent major conceptual categories of variables; the arrows represent the relationships and the directions of those relationships that were examined in SEM analyses.

magnitudes of these differences were small, <7% in all cases. Moreover, tree cover, as estimated from the satellite image, was found to correlate strongly with tree density ($r^2 = 0.80$, $P < 0.001$; Okello et al., *in press*). Therefore, we consider size structure to be relatively constant across the spectrum of tree densities.

Total grass cover did not vary significantly with tree density (Fig. 2a) but forb cover was higher at intermediate tree densities than at high and low densities (Fig. 2b). Of the dominant grasses, *Pennisetum mezianum* and *Themeda triandra* had significantly lower cover at higher tree densities (Fig. 2e, f). *P. stramineum* cover exhibited a humpbacked response, largely positive except at the very highest tree densities (Fig. 2d). *Bracharia lachmantha* and *Lintonia nutans* did not exhibit any discernible trend in relation to tree density.

Total grass and forb cover were significantly negatively correlated with the density of cattle dung (Fig. 2g, h). *Bracharia lachmantha* was the only grass species significantly correlated with cattle dung (Fig. 2i) and is probably driving the relationship between total grass cover and cattle dung. Plant species richness exhibited a negative relationship with tree density (Fig. 3a) and a positive relationship with wild herbivore dung (Fig. 3b). Species richness was also negatively related to relative grass cover (Fig. 3c); that is, where grass made up a higher proportion of the total cover, species richness was reduced.

Cattle dung density was not related to tree density (Fig. 4a). Wild-herbivore dung density, on the other hand, exhibited a strong, negative relationship with tree density (Fig. 4b). Total wild herbivore dung was on average 3 times more abundant at sites with low tree density than at sites with high tree density. This trend applied to the four most common species: zebras, Grant’s gazelles, hartebeest, and giraffes (Fig. 4c–f). Eland dung, however, was most abundant at sites with

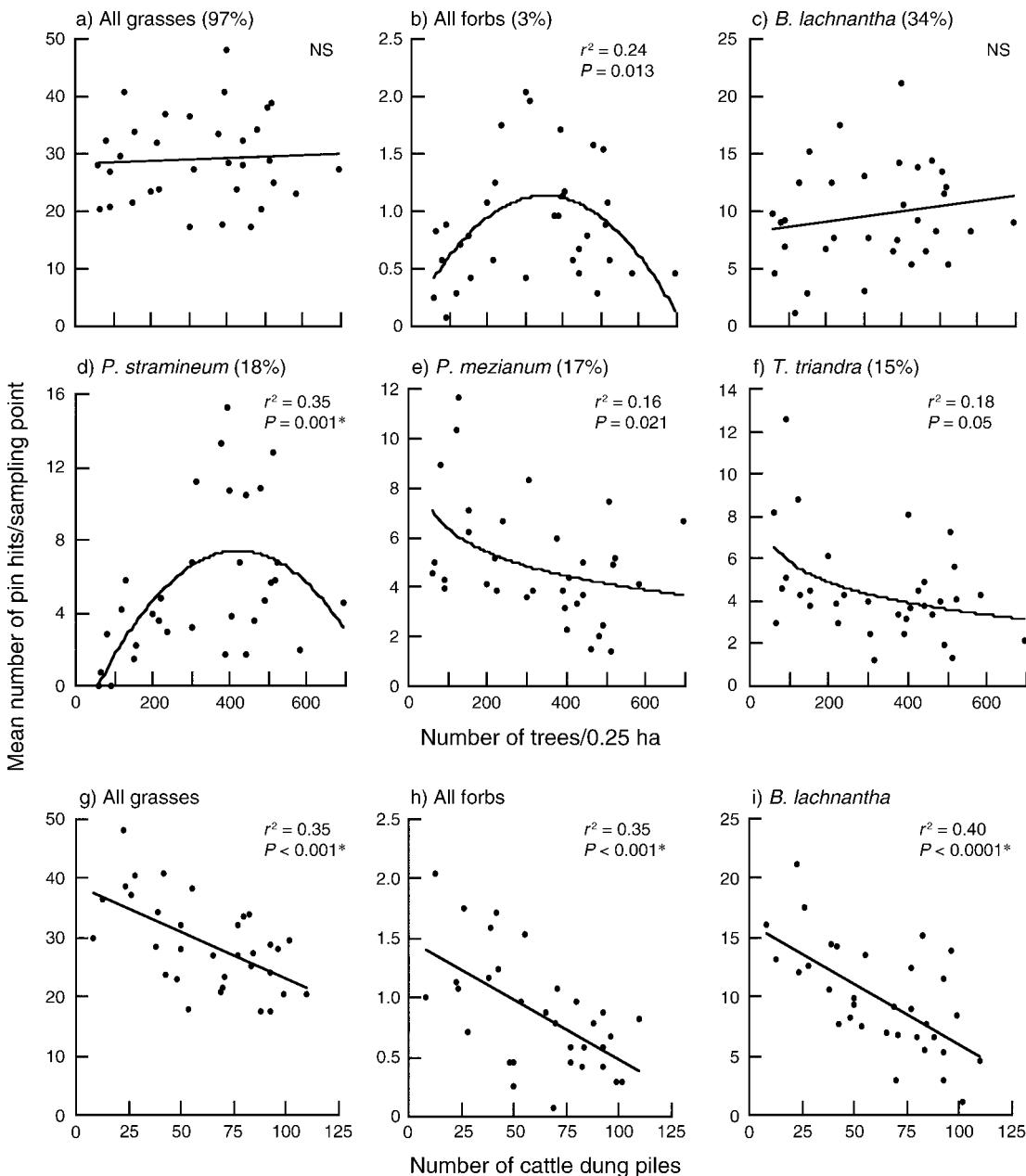


FIG. 2. Bivariate scatter plots showing the relationships between tree density, recent cattle activity (measured by dung counts), and herbaceous cover (measured by total pin hits [240 pins per 50×50 m plot]). (a–f) The relationships between tree density and (a) total grass cover, (b) total forb cover, and (c–f) cover of the dominant grass species (*Bracharia lachnantha*, *Pennisetum stramineum*, *P. mezianum*, and *Themeda triandra*). The relative contribution of each herbaceous guild or species to total cover is given in parentheses. (g–i) The relationships between cattle dung abundance and (g) total grass cover, (h) total forb cover, and (i) cover of the grass *Bracharia lachnantha*. The best-fit relationships (linear, log-linear, or quadratic) are given as solid lines, along with r^2 and P values. Asterisks indicate significance after sequential Bonferroni corrections; NS, not significant.

intermediate tree density (Fig. 4g), while steinbuck dung showed no significant relationship with tree density (Fig. 4h). Unlike any other species, elephant dung was most abundant at sites with high tree densities (Fig. 4i).

Visibility exhibited a strong negative relationship with tree density (Fig. 5a). Visibility was 2–3 times greater at

sites with lower tree densities. Wild herbivore dung, in turn, was positively related to visibility (Fig. 5b).

Structural equation modeling

The structural equation model obtained through our modeling process had 67 degrees of freedom and a χ^2

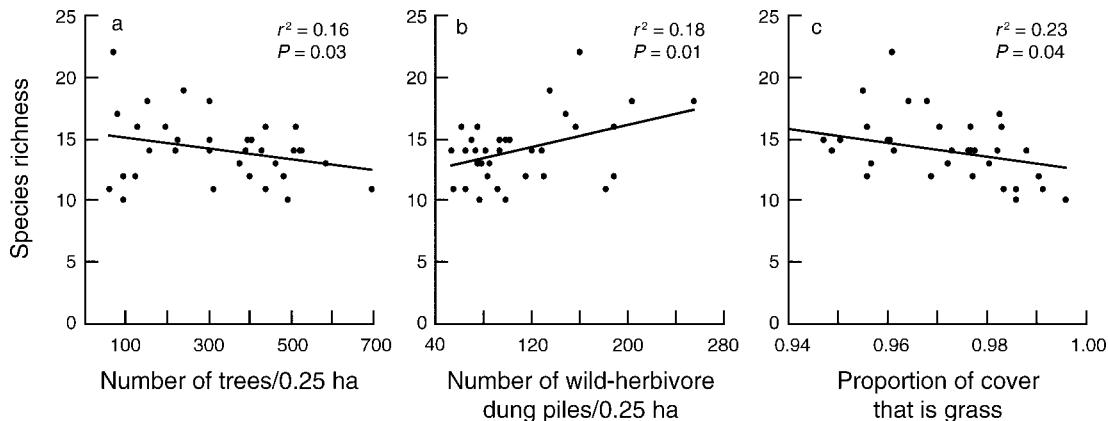


FIG. 3. Bivariate scatter plots showing the relationships between species richness and (a) tree density, (b) wild herbivore dung density, and (c) the cover of grasses relative to total cover. The best-fit relationship (linear in all cases) is given as a solid line, along with r^2 and P values.

value of 63.68 with a P value of 0.59. Here, the χ^2 value measures the magnitude of the discrepancy between model and data; thus a $P < 0.05$ indicates significant discrepancy between model and data. Our P value of 0.59 along with all model fit indicators reported by the Amos software (which include the Akaike information criterion and the Bayesian information criterion) indicate good model fit. In addition, Bayesian estimation procedures confirmed that all paths retained in the model possessed coefficients with 95% credible intervals that did not include zero. On average, Bayesian estimates differed from those derived by maximum likelihood by <1%.

SEM results (Fig. 6) show that soil characteristics explained a moderate proportion of the variation in tree density and grass cover. For *Themeda triandra*, the correlation between tree density and grass cover was explained by a shared dependency on soil characteristics. Even after controlling for soil, however, *P. stramineum* exhibited a strong positive relationship with tree density. Similarly, the cover of grass relative to forbs appears to be influenced by both soil and tree density. The humpbacked relationship between forb cover and tree density (Fig. 2b) translated to a lower cover of grasses relative to forbs at intermediate tree densities. This, in turn, was negatively related to overall species richness; where grass made up a greater percentage of the total cover, species richness was lower.

There is no indication that these effects of soil and tree density on herbaceous vegetation influenced herbivore habitat preferences (Fig. 5). In models allowing cattle and wild herbivores to respond to herbaceous vegetation, these pathways were all non-significant. Instead, wild herbivores exhibited a strong negative relationship with tree density, independent of herbaceous vegetation. When visibility was included in a separate model, however, the effect of tree density on wild herbivores became nonsignificant (Fig. 4c). This result supports the

inference that wild herbivore responses to tree density can be explained by reduced visibility in more dense habitats.

While herbivores do not appear to have responded to variation in herbaceous vegetation, both cattle and wild herbivores do appear to have influenced the herbaceous vegetation (Fig. 6). All other things being equal, *B. lachnantha* cover was lower where either wild herbivore or cattle dung densities were higher. Cover of *P. mezianum* was positively associated with wild herbivores. Thus it appears that the negative bivariate relationship between *P. mezianum* and tree density reflects a negative influence of tree density on wild herbivores and a positive influence of wild herbivores on *P. mezianum*, rather than a direct influence of trees on *P. mezianum*. Model results also indicate that wild herbivores had a direct positive influence on species richness.

DISCUSSION

Wild herbivores choose their habitat and modify their movements in the landscape in response to both forage availability and predation risk (Sih 1980, Houston et al. 1993). The conditions affecting herbivore behavioral trade-offs between these two aspects of survival remain poorly understood (Lima 1998). Among African savanna herbivores, Sinclair et al. (2003) have argued that populations of smaller-bodied species are limited by predation, whereas populations of larger-bodied species (>150 kg) are limited by forage availability. In this study we examined the behavioral responses of several herbivore species to these top-down and bottom-up forces in the context of savanna tree density. Our results suggest that all but the largest-bodied species preferred areas of low tree density because of greater visibility in these areas, rather than any vegetation characteristics associated with low tree density. These herbivore habitat preferences, in turn, appear to have cascading effects on herbaceous species composition and richness.

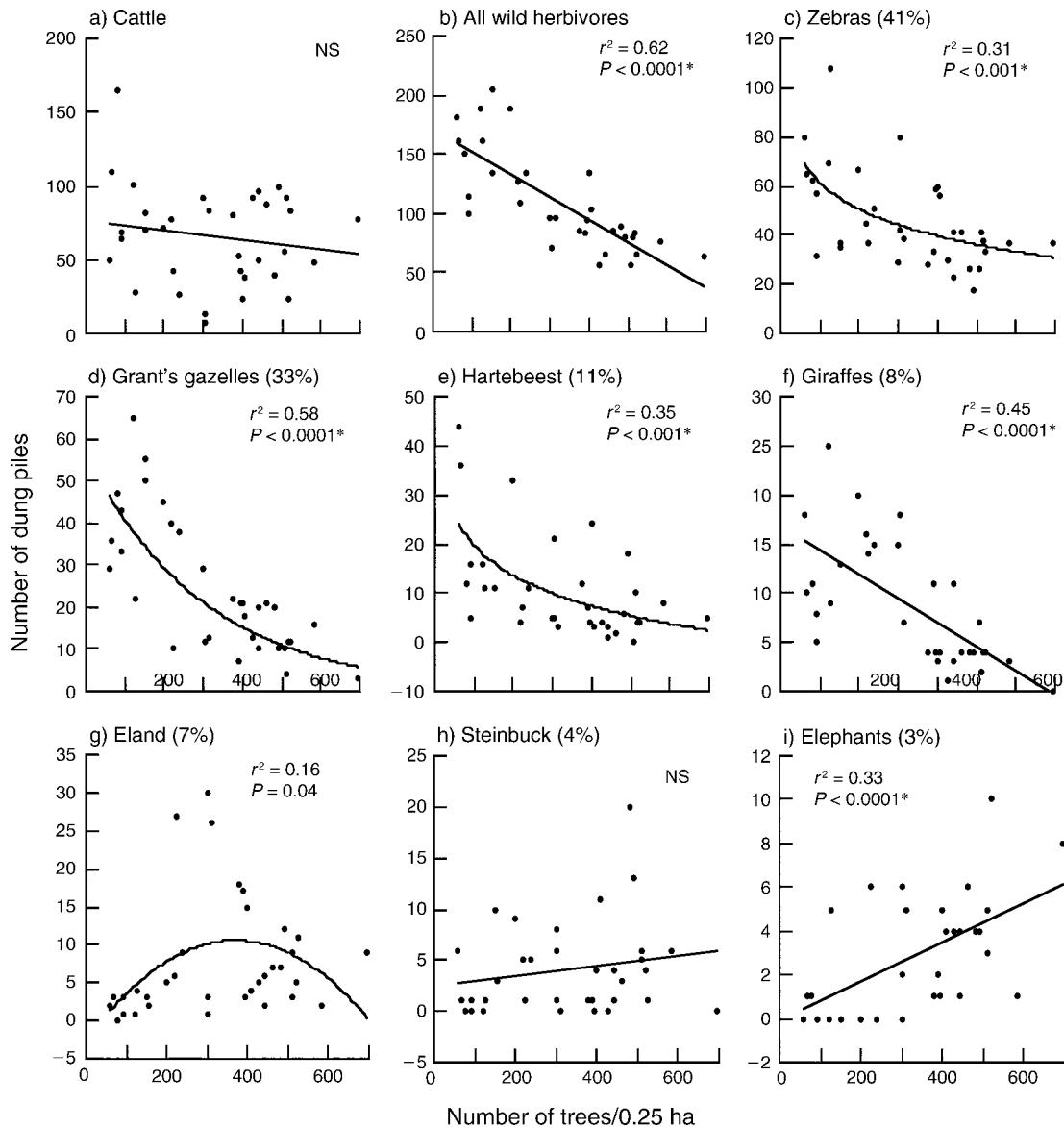


FIG. 4. Bivariate scatter plots showing the relationships between tree and dung density for (a) cattle, (b) all wild herbivores, and (c–i) the seven most common wild herbivore species. The relative percentage contribution of each of the wild herbivore species to total wild herbivore dung abundance is given in parentheses. The best-fit relationships (linear, log-linear, or quadratic) are given as solid lines, along with r^2 and P values. Asterisks indicate significance after sequential Bonferroni corrections; NS, not significant.

Herbaceous vegetation and tree density

We found herbaceous species composition to vary markedly with tree density. For *Themeda triandra*, this correlation appears to be due to the shared effects of soil texture on tree density and cover of this grass. Cover of the other dominant grass species, as well as the cover of all grasses relative to forbs, was also explained to some extent by edaphic factors. Only one of the dominant grasses, *Pennisetum stramineum*, appears to have responded directly to tree density. In this case, the effect of trees was generally positive, consistent with findings from southern Ethiopia, where *P. stramineum* was also

found to be associated with high tree densities (Angassa and Baars 2000). The direct effect of tree density on *P. stramineum* cover in the structural equation model suggests that the trees themselves facilitate this species, perhaps by modifying the shade or soil moisture environment.

Effects of tree density on herbivores

Cattle use of the landscape was not related to tree density. Model results also suggest that cattle did not respond to the differences in herbaceous species composition associated with tree density. This is not surprising, since cattle movements in this landscape are

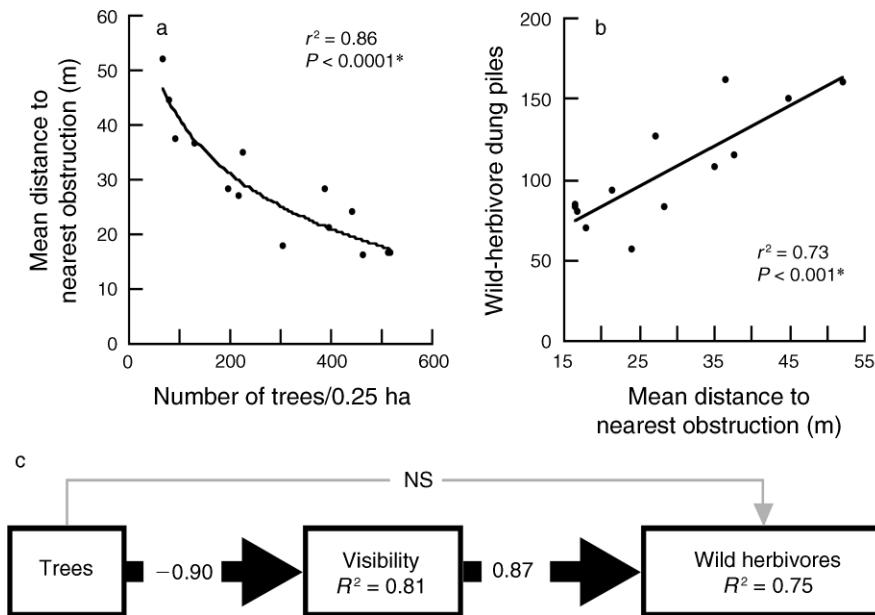


FIG. 5. Relationships among tree density, visibility (measured as the mean distance to the nearest line-of-sight obstruction), and wild-herbivore dung abundance. (a–b) Bivariate scatter plots (a) between tree density and visibility and (b) between visibility and wild-herbivore dung abundance. The best-fit relationships (linear or log-linear) are given as solid lines along with r^2 and P values. Asterisks indicate significance after sequential Bonferroni corrections. (c) Results of structural equation modeling ($\chi^2 = 0.62$, $df = 1$, $P = 0.43$) in which variation in tree density is used to explain variation in wild herbivore dung density via its effects on visibility. Black arrows represent significant effects of one variable on another ($\alpha = 0.05$) while gray arrows represent nonsignificant effects. The relative strength of a given effect is indicated by arrow thickness and by a standardized path coefficient. The proportion of the variance explained for each response variable is given by r^2 values. This analysis was conducted separately from the analysis presented in Fig. 6 because visibility estimates were only available for 14 of the 34 plots.

managed by herders. Herded cattle are rarely attacked by predators during the day (P. Jessel, *personal communication*) and spend their nights in predator-proof corrals. Unlike cattle, wild herbivores responded strongly to tree density, generally preferring more open places. The only exceptions were steinbuck (which have small, well-defined territories), eland, and elephants.

A bottom-up hypothesis to explain wild herbivore preferences is that forage quantity or quality is higher in more open areas. We would expect this to apply to grazers but not to browsers. However we found that even giraffes, which are strict browsers, spent more time at the sites with the fewest trees. Even among grazers, we found little to suggest that foraging preferences drive their habitat associations. Model results suggest that herbivores did not respond to differences in species composition associated with tree density, and, in fact, no association between tree density and total grass cover was detected. One limitation of our present study is that it captures only a snapshot of vegetation cover. It is possible that grass production and quality are higher at more-open sites due to higher nutrient inputs from herbivore dung, stimulation of green leaf growth by grazing, or both (Hamilton et al. 1998). These hypotheses are currently being tested experimentally. Preliminary results suggest that sites with higher densities of trees have a greater proportion of green grass than sites

with lower densities of trees (W. Odadi and C. Riginos, *unpublished data*).

A top-down hypothesis to explain wild herbivore habitat preferences is that herbivores seek out areas with less obstruction of predator visibility and/or escape. Because smaller herbivores are more susceptible to predation (Sinclair et al. 2003, Radloff and du Toit 2004) and exhibit greater anti-predator vigilance (Underwood 1982, Berger and Cunningham 1988), we would expect smaller-bodied species to prefer open areas more than larger-bodied species do. Our results support this hypothesis. In our model, habitat preferences for all herbivores except elephants were strongly correlated with visibility, but not tree density, when visibility was held constant (Fig. 5c). Only elephants, the largest-bodied species, did not avoid bushy habitat. Even eland, the third largest species after elephants and giraffes, avoided the areas with the most trees. Giraffes, although larger than eland, are more susceptible to predation (Hayward and Kerley 2005) and tend to forage in more-open habitat when accompanied by juveniles (Young and Isbell 1991). Among the common herbivores, we found a positive correlation between body size and slope of response to tree density ($r^2 = 0.62$, $n = 6$ species, $P = 0.06$), with smaller-bodied species exhibiting the strongest negative responses. Taken together, these results suggest that herbivores avoid

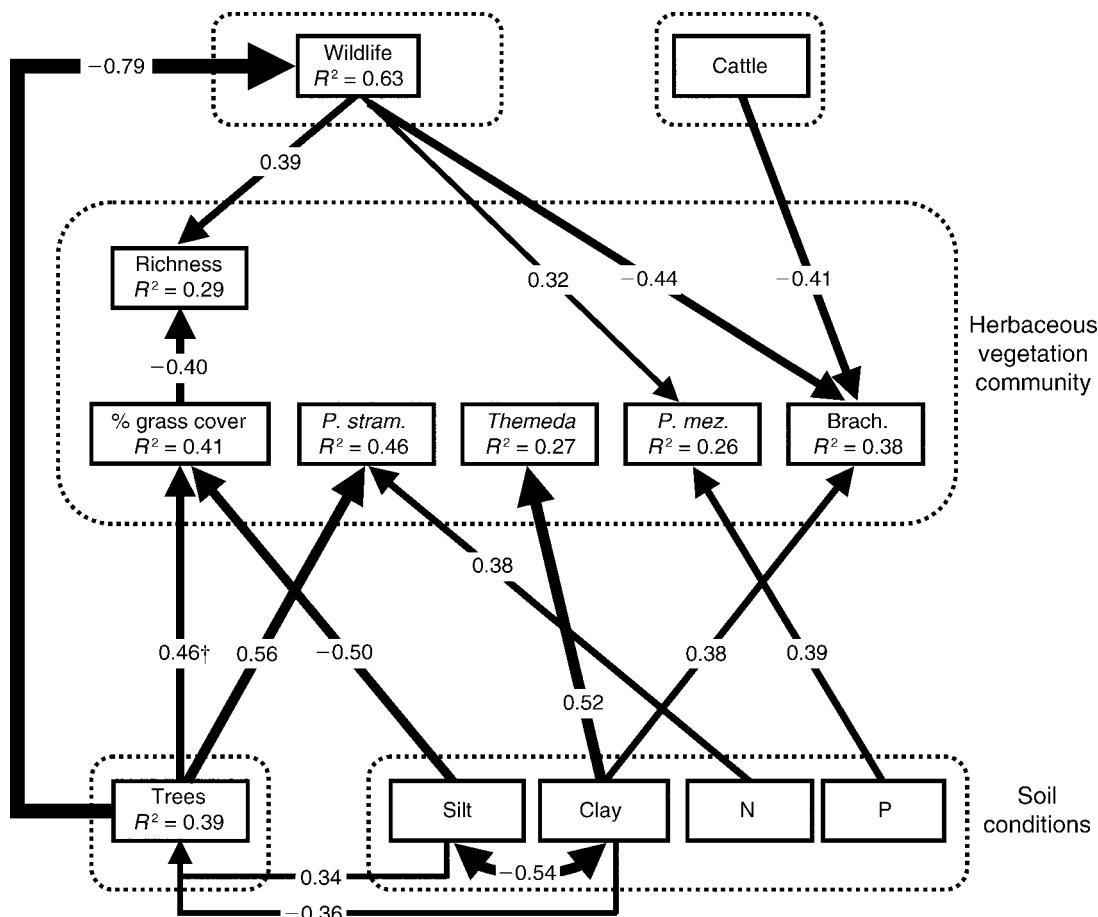


FIG. 6. Results of structural equation modeling ($\chi^2 = 63.68$, $df = 67$, $P = 0.59$, where the χ^2 value measures the magnitude of the discrepancy between model and data) in which variation in soil characteristics and cattle dung density are used to explain variation in tree density, herbaceous community characteristics (where “% grass cover” indicates the cover of grass relative to the cover of grass and forbs combined), and wild herbivore dung density. Straight, single-headed arrows represent significant effects of one variable on another ($\alpha = 0.05$), while the curved, double-headed arrow represents significant correlations between variables. The relative strength of a given effect is indicated by arrow thickness and by a standardized path coefficient. The proportion of the variance explained for each response variable is given by r^2 values. Only pathways that are significant at $\alpha = 0.05$ are shown. Full names of the grass species are given in the Fig. 2 legend.

areas of high tree density to minimize their risk of predation, but this response depends on herbivore body size.

Elephants, unlike any other species, appear to prefer areas with more trees. This seems to be a direct response to tree density rather than an indirect response to any correlated factors, such as grass species composition (model results not shown). We also found that the percentage of trees damaged by elephants was positively correlated with tree density ($n = 14$ plots, $r^2 = 0.25$, $P = 0.068$); elephant damage per tree was more than twice as great at higher tree densities compared to lower tree densities. This suggests that elephants seek out sites with greater availability of browse. Elephants are considered key players in reducing the density of trees in African savannas (Dublin et al. 1990, Western and Maitumo 2004). Our results suggest that elephants may exert a

negative feedback on the system by disproportionately reducing the number of trees in areas where tree density is already high. Especially in areas with numerous elephants, this negative feedback may act to homogenize the landscape, contributing to the maintenance of the mixed tree–grass savanna state and potentially facilitating smaller-bodied herbivores.

One limitation of our study is that we are unable to assess predation risk for different herbivores in areas with different tree densities. To further test our findings, we would ideally assess herbivore habitat preferences when predators are present or absent (Creel and Winnie 2005), or manipulate tree and/or grass habitat characteristics and quantify herbivore responses. We are currently taking the latter approach in a replicated experimental manipulation of tree density (C. Riginos, unpublished data).

Effects of herbivores on herbaceous vegetation

Although we found no evidence that wild or domestic herbivores responded to variation in herbaceous vegetation in the landscape, our results suggest that these herbivores impacted herbaceous cover and composition. In some cases, tree density appears to have had cascading effects on herbaceous vegetation via its effects on wild herbivores.

Cover of the grass *Bracharia lachnantha* was negatively impacted by both cattle and wild herbivores. This is not surprising, given that this species is highly palatable (Odadi et al. 2007). The negative effect of wild herbivores on *B. lachnantha* appears to have mediated an indirect positive effect of tree density on this grass; where tree density was higher, herbivores were fewer, and *B. lachnantha* cover higher. Similarly, results indicate that tree density indirectly affected *Pennisetum mezianum* cover via its effects on wild herbivores. This species is the least palatable of the predominant grass species at this site (Odadi et al. 2007) and is abundant in heavily grazed areas. Thus it is not surprising that it was associated with areas of low tree density and abundant herbivores. Herbivore effects on this and other grass species may, however, be less pronounced after rain; we measured grass cover in the height of the dry season, when cover of preferred forage species is lowest.

Forb cover was negatively impacted by cattle, consistent with experimental findings in this ecosystem (Young et al. 2005). Low forb cover and high relative grass cover were also associated with reduced species richness, most likely because the few dominant grass species suppress multiple species of competitively subordinate grasses and forbs (Olf and Ritchie 1998). Thus, cattle appear to have indirectly suppressed species richness via their negative effects on forbs, rather than enhancing species richness via their negative effects on grass.

Wild herbivores, in contrast, appear to have had a direct positive effect on species richness. Such an effect is not uncommon in highly productive grassland systems (McNaughton 1983, Olf and Ritchie 1998). Since wild herbivores did not significantly affect forb cover, their influence on species richness was likely due to some activity other than foraging. One possibility is that wild herbivores facilitate seed dispersal in the landscape, since, unlike cattle, they can cross property boundaries. Another possibility is that the hoof action of wild herbivores—which span a wide range of body sizes, foraging behaviors, and movement speeds—creates a variety of soil microhabitats (Olf and Ritchie 1998), facilitating the establishment of less common plant species (Harper et al. 1965).

Conclusions

We have shown that a naturally occurring mosaic of tree densities in an African savanna landscape mediates a number of direct and indirect effects on herbaceous species composition and herbivore habitat use. Sinclair et al. (2003) have argued that populations of smaller-

bodied ungulates are limited by predation, whereas larger-bodied ungulates are limited by forage availability. Here, we have shown that these top-down and bottom-up effects may also modify herbivore habitat use, with cascading effects on herbaceous vegetation. Although a number of studies from aquatic systems have demonstrated that predator-avoidance behavior among prey can have cascading effects on producers, our results represent a rare example of such a cascade in a terrestrial ecosystem (Lima 1998).

These results also illuminate one of the features defining the landscape of fear that large African ungulates exist within. Here, wild herbivores and some herbaceous species responded directly to local tree density, suggesting that similar responses would be expected where anthropogenic disturbances or land-management practices have altered the density of trees. We are currently testing experimentally the causal relationships we have inferred from our SEM analyses. Given the variety of ways in which people can and do affect woody cover in savanna systems (via, e.g., cattle grazing, altered elephant densities, fire suppression, climatic changes, and fuelwood harvesting), it is important that we gain an understanding of how and why native flora and fauna respond to this variation in woody cover.

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APPENDIX

Table of correlations and standard deviations among the major variables (*Ecological Archives* E089-128-A1).