Long-Term Glades in Acacia Bushland and Their Edge Effects in Laikipia, Kenya

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LONG-TERM GLADES IN ACACIA BUSHLAND AND THEIR EDGE EFFECTS IN LAIKIPIA, KENYA[1]

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Abstract. Throughout the Laikipia ecosystem in Kenya, isolated glades occur within acacia bushland and woodland communities. These glades are at least several decades old. They are reported to be old settlement sites of traditional pastoralists no longer present, and their size, location, and orientation are consistent with the settlement sites of related pastoralists studied elsewhere. The purpose of this study was to document the effects of these glades at the local and landscape levels. Working in central Laikipia, we documented differences in vegetation, animal use, and soils at four of these glades, and at increasing distances from glade edges. Four "glade specialists" dominated the plant communities within glades, and were very rare outside of glades. *Pennisetum stramineum,* one of six glade edge species, formed a ring of dense tall grass around most glade edges. The transition to acacia bushland at the glade edges was not always abrupt (depending on the trait considered), resulting in edge effects that differed in depth and sharpness. Edge depth, defined as the distance required to attain two-thirds of background levels for a trait, ranged from 0 to 200 m. Understory plant species richness and diversity were lowest inside glades, and gradually increased with distance from glades. However, because glades supported species not found elsewhere, the presence of glades increased overall species diversity. The density of wild and domestic large mammal dung was up to 10 times greater inside the glades, and declined with distance from glade edges. Similarly, soil nitrogen, potassium, carbon, calcium, and sodium were greatest inside glades. Soil phosphorus, magnesium, and manganese were not elevated inside glades or within 100 m of glades, but instead were much more abundant in background samples. These glades may be maintained by high densities of large mammals, either through herbivory or through changes in soil chemistry. Glades may be attractive to mammals because of the high quality of food there, or as part of an anti-predator strategy. The result is a relatively permanent community mosaic that increases ecosystem heterogeneity and resource use by domestic and wild animals. The spatial nature of this heterogeneity differs among species, depending on their distributions relative to the glades.

Key words: Acacia; cattle enclosures; community mosaic; dung counts; edge depth; elephants; grazing lawns; Laikipia, Kenya; large mammals; patch dynamics; soil chemistry.

Introduction

Mosaic and patch dynamic ecosystems are not uncommon in nature. Human activity often produces mosaics of ecological communities with superficially abrupt boundaries. Ecologists, including resource managers and conservation biologists, are increasingly recognizing that community boundaries in artificial and natural community mosaics are not always coincident with the distribution limits of all species, even when community boundaries are superficially abrupt, as at forest edges. The biotic and abiotic effects of one community may extend well into an adjacent community (Williams-Linera 1990, Chen et al. 1992). Consideration of edge depth can change significantly our perceptions of the structure and function of mosaic ecosystems and our recommendations concerning their conservation and management (Alverson et al. 1988, Chen et al. 1992).

One class of community mosaics is the pattern of patches of heavily grazed areas imbedded in a background of semiarid woodland, bushland, or grassland. Such mosaics have been reported from Africa (Vesey-Fitzgerald 1969, McNaughton 1984), North America (Coppock et al. 1983a, b), and South America (J. E. Jackson, *personal communication*), and may be created or maintained by herbivory. There is considerable experimental evidence that large mammals can have profound effects on the structure and composition of semiarid plant communities in Africa (Hatton and Smart 1984, Dublin et al. 1990, Stuart-Hill 1992, see review by O'Connor 1985). However, it is not clear that all mosaics in semiarid ecosystems are either created by or are maintained by large mammal herbivory.
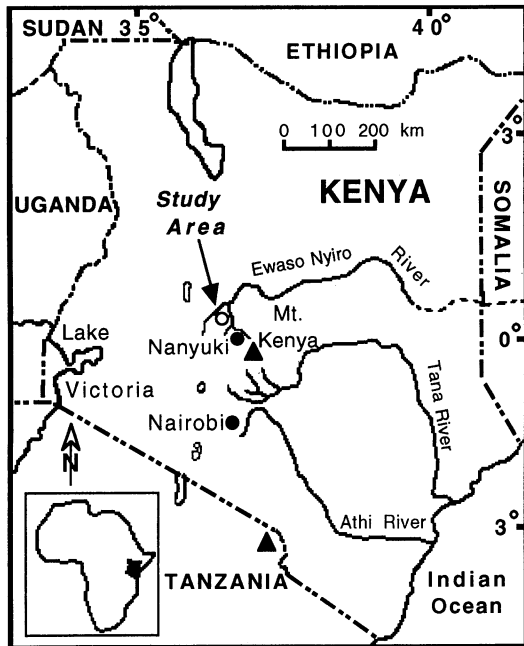
FIG. 1. Map showing location of the study area in Laikipia District, Kenya.

Our interest in glade edges initially arose from the need to know how great a distance from glades was necessary to avoid the ecological effects of their vicinity. We were in the process of setting up permanent experimental exclosures, and it was vital that these exclosures not be affected unduly by their proximity to factors that would influence plant or animal distribution.

We describe here a study of the edaphic, floristic, and physiognomic qualities of glades within acacia bushland in Laikipia, Kenya, with particular emphasis on the nature and depth of edges in this community mosaic. We also explore the interactions of this mosaic with both wild and domestic large mammals.

STUDY SITE

This research was carried out November 1992–August 1993 at the Mpala Research Centre, on property administered by the Mpala Foundation. This site is located 40 km northwest of the town of Nanyuki in the middle of the Laikipia District (37° 53′ E, 0°17′ N), in the Republic of Kenya (Fig. 1). The average rainfall is ≈500 mm/yr (Odinga 1971). The soils are described as "well-drained, moderately deep to very deep, dark reddish brown, friable gravely, sandy clay loam to clay loam" (Ahn and Geiger 1987). The vegetation has been characterized as "open *Acacia brevispica* thicket" (Taiti 1992). The woody vegetation is dominated by *Acacia* species (primarily *A. brevispica* and *A. etbaica,* but also *A. mellifera, A. gerrardii,* and *A. nilotica*), and includes the shrubs *Croton dichogamus, Grewia* spp. and *Rhus vulgaris.* The understory is dominated by

grasses in the genera *Cynodon, Pennisetum, Digitaria,* and *Sporobolus,* and by the herbs *Plectranthus* spp., *Pollichia campestris, Portulaca* spp., and *Blepharis* spp.

Several glades are scattered in what would be otherwise regular cover by acacia bushland. These glades differ from the surrounding vegetation in several ways: (1) They lack adult and juvenile trees and shrubs. (2) They are covered by low herbs and grasses that are visibly greener than the surrounding ground cover, at least during some seasons. (3) They are often ringed by a tall dense band of taller grass. These glades form distinct, discrete communities readily recognizable even to inexperienced observers.

Local land managers (J. Fairhall and J. Wreford-Smith, *personal communications*) report that these glades have existed in their present locations at least since European settlement in the 1920s, and believe that they are the sites of old bomas (cattle enclosures) of "Maasai" people. These people are more appropriately identified as the Laikipiak and the Purko-Kisongo (Herren 1987), and they and related groups had grazed in the Laikipia ecosystem since at least 1800. However, a variety of factors (including rinderpest and internecine warfare) had greatly reduced their presence by 1900, and a treaty with the British in 1911 led to their deportation from parts of the ecosystem in 1914 and 1915, and opened up these areas for European settlement (Herren 1987). The glades studied here occur on broad, gently sloping ridges, consistent with the preferences of modern Maasai for the placement of their bomas (Western and Dunne 1979).

METHODS

Glades

We surveyed an east-facing watershed of ≈8.3 km², counting all glades. This survey encompassed all of the land on the Mpala Research Centre of similar landscape and soils type. We measured eight of these glades for length, width, slope, topographic location, and orientation. We carried out detailed surveys of four of these glades, quantifying vegetation, soils, and animal use inside each glade, and at increasing distances from glade edges. Soils and vegetation data were also collected along transects far from the glades to measure background values.

Vegetation

Woody vegetation was measured with the point-center method (Brower et al. 1990). Two (in one glade, three) transects were run at each glade. Each transect started 25 m inside the glade and ran 200 m in a straight line (to 175 m from the glade edge). These lines were chosen to sample a variety of topographies (along ridge lines, along contour lines, and down adjacent slopes).

A sample point was located every 25 m along each line ($n = 9$). At each point, four woody plants (trees

or shrubs) were sampled, one in each quarter. The distance from the point to the center of the tree's stem, the height of the tree, and the identity of the tree were recorded. In addition, a running survey of *Croton dichogamus* was made, recording the number of individuals present within 5 m of either side of the line from −25 to 225 m, at 25-m intervals.

Herbaceous cover was measured with a pin frame. The pin frame sampled all plant material <80 cm from the ground at 25 regular points along a 1-m frame. Pin frame sample points included the nine points sampled for woody vegetation, plus a point located 25 m into the glade, along each glade transect. At each sample point, the frame was placed four times, 3 m from the point, in four regularly spaced compass directions. The number of times pins touched individuals of each species ("hits") was recorded, as was the number of pins that hit no vegetation. Multiple hits per pin were not uncommon. For a small number of points (<2%), dense thorny vegetation made it impossible to place the pin frame in the selected location. The number of hits by each species was estimated in these sites.

In addition, background vegetation was sampled along a series of eight line transects through the surrounding vegetation. These transects varied in length from 200 to 1300 m (mean 540 m) and were located at least 200 m from any glade. Every 25 m, woody vegetation and herbaceous cover were measured using the techniques described above. Pin frame estimates of cover were carried out at 11–19 locations (44–76 pin frames) along five of these transects. In glade transects and background transects combined, 254 points were sampled for woody vegetation (1016 individuals sampled), and 608 pin frames were placed (15 200 pins).

Species were identified with the help of published floras and checklists (Dale and Greenway 1951, Polhill 1957–1989, Agnew 1974, Ibrahim and Kabuye 1989, Coe and Beentje 1991, Mwasya et al. 1994), and with vegetative keys designed specifically for the flora of Laikipia (T. P. Young, *unpublished manuscript*). Vouchers were collected and deposited at the East African Herbarium of the National Museums of Kenya.

The mean density of each tree and shrub species in the point center samples was calculated separately for each background transect and for each distance at each glade. In addition, the densities of all adult and juvenile trees and shrubs were estimated. These estimates were then used to calculate the mean and standard deviation of each species' abundance, with each glade ($n = 4$) and each background transect ($n = 8$) being considered a replicate.

Mean cover for each understory species was calculated for each glade at each distance from the glade edge. These estimates were then used to calculate the mean and standard deviation of each species' abundance, with each glade being considered a replicate ($n = 4$). Mean cover by each understory species was also calculated for each of the five background transects for

which there were pin frame data. Data from two of the transects located in close proximity were pooled. Means and standard deviations were calculated, with each transect being considered a replicate ($n = 4$).

Species richness and Shannon diversity (Brower et al. 1990) of both the overstory and the understory were calculated at each distance from the glade edge, over all transects, and for each background transect. Care was taken to ensure similar sample sizes for these estimates, which tend to increase with increased sampling.

Soils

Along two sampling lines at each of the four glades, five soil samples were taken. At 25 m inside the glade and 100 m beyond the glade edge, soil was collected at 0–10 cm and 20–30 cm depth. At 25 m beyond the glade edge, soil was sampled at 0–30 cm depth. For each glade, samples from the two sampling lines were mixed for each category. In addition, soil was collected at two sites along each of four background transects. At each soil site, soil from two holes 2 m apart (0–30 cm deep) was thoroughly mixed. The soil samples were placed in paper bags and delivered 4 d later to the National Agricultural Laboratories in Nairobi. The 28 soil samples were analyzed for pH and nine elements.

Large mammal dung

Along each transect line, the number of dung piles within 3 m of the line was counted for each 25-m interval. Dung was classified into seven categories: elephant, zebra, cattle and buffalo, large ungulates (kudu, eland, waterbuck), medium ungulates (Grant's gazelle, impala), small ungulates (steinbuck, goats, sheep), and dik-dik.

Most of the bovine dung was from domestic cattle; a recent drought had reduced the density of buffaloes to ≈10% of the number of cattle grazing this area (J. Fairhall, *personal communication*). Similarly, it is likely that most of the "small ungulate" dung was from domestic sheep. Only a few goats were kept on the property, and steinbucks were almost never seen in the vicinity of these transects. On the other hand, zebras, elephants, waterbucks, elands, greater kudus, impalas, and dik-diks were common.

Edge depth

For each measured factor that differed significantly between glades and background levels, we calculated the depth of the edge effect. Edge depth was defined (after Chen et al. 1992) as the distance from the glade edge at which each variable reached two-thirds of the background level, compared with the level in the glade (or at the glade edge, for glade edge specialists).

RESULTS

Glade density and characteristics

Our survey of the study area revealed 16 glades in an area of 8.3 km², for an average density of 1.9 glades/
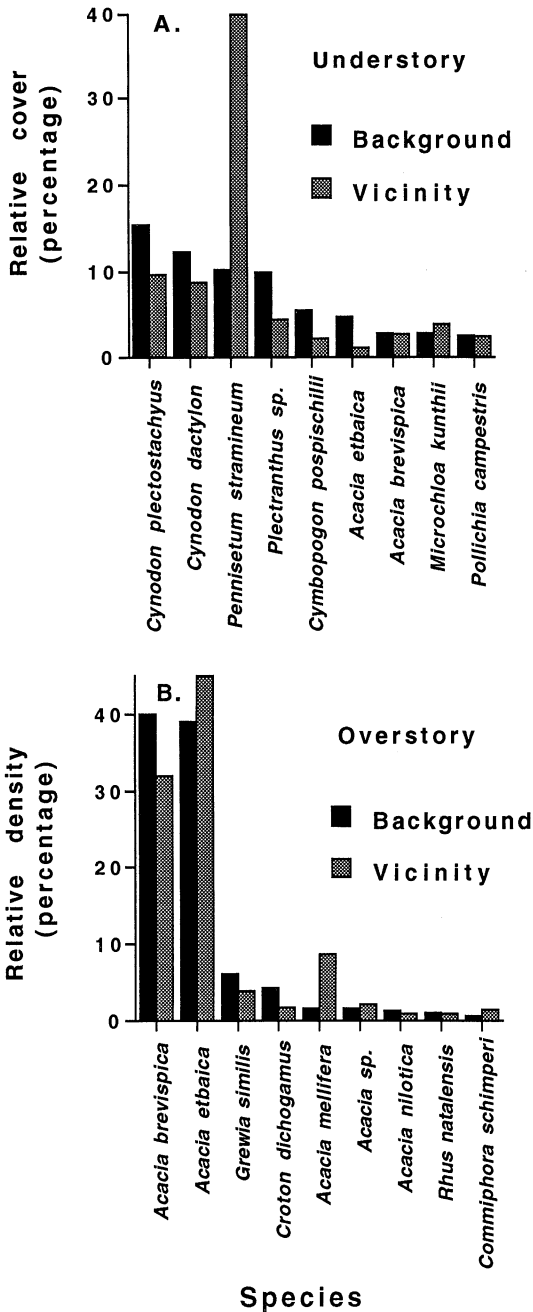
FIG. 2. Abundance histograms for the most abundant species (A) in the understory (relative cover) and (B) in the overstory (relative density), in the background transects (solid) and in the vicinity of glades (shaded). Values for "vicinity" are averaged over all distances from glade edges, excluding sample points inside glades. The vegetation inside glades was entirely different (see Fig. 3).
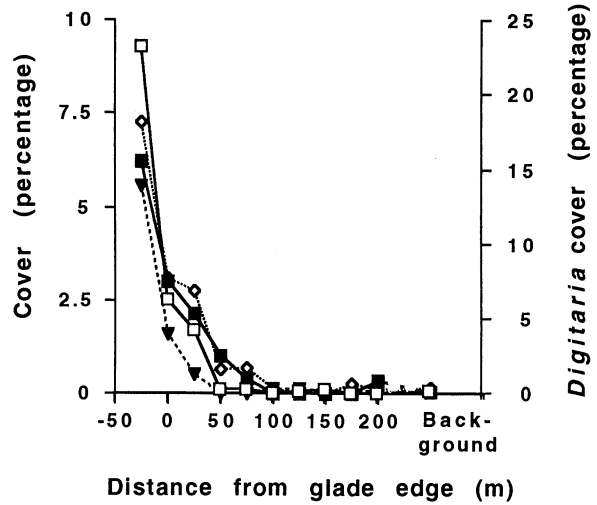

FIG. 3. Abundances of glade specialists relative to glade edges. □, *Digitaria milanjiana* (note different scale); ◇, *Tribulus terrestris*; ■, *Portulaca oleracea*; ▼, *Cyperus blysmoides*.

efficient of variation = 20%). These glades always lay atop a broad gentle ridge, with slopes of 0.75–4.00% (2.38 ± 1.21%). The long axes always lay along the tops of these ridges, within 10° of the fall line. Similarly, traditional Maasai in another Kenya ecosystem select broad, gently sloping ridges (mean slope = 3.29 ± 2.04%) for their settlement sites, which vary in diameter from 30 to 106 m (Western and Dunne 1979).

Vegetation

Vegetation was dominated by relatively few species, both in the understory and in the overstory (Fig. 2). *Acacia brevispica* and *A. etbaica* accounted for 77% of the overstory individuals in the vicinity of glades, and 79% in the background transects. Three species of grasses (*Cynodon plectostachyus, C. dactylon,* and *Pennisetum stramineum*) dominated the understory vegetation, in the vicinity of (but not inside) glades (59% of understory vegetation) and in the background transects (38% of understory vegetation).

The definition of these glades was based on obvious vegetation differences, so it is no surprise that our data show profound differences between glade and the surrounding vegetation. Four plant species dominated the plant communities in these glades, accounting for 95% of the plant cover: *Digitaria milanjiana, Tribulus terrestris, Portulaca oleracea,* and *Cyperus blysmoides.* These species occurred outside the glades only at very low densities (<1% cover), and can be considered "glade specialists," at least in the study area (Fig. 3). In addition, the small shrub *Ipomoea kituiensis* appeared to be a glade specialist that occurred too rarely to be sampled.

We identified five gap edge plant species that were absent from inside glades, and more common near glade edges than farther away: *Pennisetum stramineum,*

km². None was >2.5 km from the permanent Ewaso Nyiro River. The eight surveyed glades varied in size from 0.15 to 1.30 ha (0.64 ± 0.38, mean ± 1 SD) with diameters ranging from 43 to 128 m. The ratio of length to width was relatively consistent (1.64 ± 0.32; co-
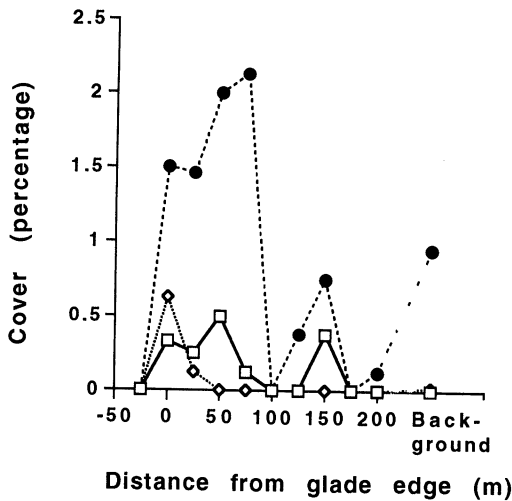
FIG. 4. Abundances of glade edge species, relative to glade edges. ●, *Eragrostis racemosa*; ◇, *Cyperus cristatus*; □, *Pollichia campestris*.

Eragrostis racemosa, Pollichia campestris, and *Cyperus cristatus* (Fig. 4). The latter species was most restricted to glade edges. In addition, *Solanum incanum* often occurred at glade edges, but at densities too low to be sampled. *Pennisetum stramineum* often occurred as a dense ring of tall grass around the edges of glades and was less abundant, but not uncommon, farther from glade edges (Fig. 5). A similar pattern has been reported, at a much smaller scale, from around gopher mounds in a semiarid North American grassland (Reichman et al. 1993).

Two species of grass in the genus *Cynodon (C. plectostachyus* and *C. dactylon*) were virtually absent from these glades, and increased in abundance with distance from the glade edges (for combined data: $r^2 = 0.63$, $P < 0.01$). Cover by the less common grass *Tragus berteronianus* also increased with distance from the glade

edges ($r^2 = 0.60$, $P < 0.01$). Mean overall percentage cover by grasses, forbs, and bare ground was relatively constant at all distances from glade edges (Fig. 6).

The glades were treeless, and adult tree and shrub density increased with distance from glade edges ($r^2 = 0.72$, $P < 0.002$; Fig. 6). In contrast, juvenile trees and shrubs, also absent from glades, occurred at similar densities independent of distance from glade edges, beyond the first 25 m (Fig. 7). The density of *Acacia brevispica* increased with distance from glade edges ($r^2 = 0.86$, $P < 0.001$; Fig. 8). *Acacia etbaica,* the other dominant woody species, reached background levels much closer to the glade edge (within 50 m) than *A. brevispica* (Fig. 7), as did other common woody species. The shrub *Croton dichogamus* was virtually absent from the vicinity of glades, only appearing in appreciable numbers >200 m from glade edges (Fig 9).

Ninety-five plant species were recorded along these transects. Understory species richness and species diversity were lowest inside glades, and thereafter increased gradually at increasing distances from glade edges, reaching levels similar to those in the background transects (Fig. 10). Neither the species richness nor the Shannon diversity of woody trees and shrubs were significantly related to distance from glade edges. However, background transects had significantly lower woody species diversity than glade transects overall (1.24 ± 0.04 vs. 1.34 ± 0.40; mean ± 1 SE; $t = 2.33$; $P < 0.05$).

Soils

Soil became more acidic with distance from the glades. Inside the glades, soil pH was nearly neutral, but it was ≈6 at 100 m from the glade edges, and in the background samples. Inside the glades, the surface (0–10 cm deep) soil was significantly less acidic than the deeper soil (20–30 cm deep). At 100 m from the glade edges, there was no pH difference between soil depths (Fig. 11).
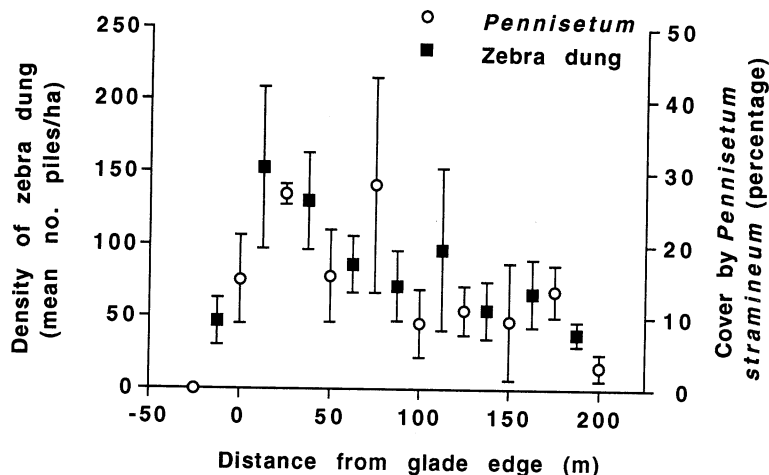

FIG. 5. The abundances of *Pennisetum stramineum* and zebra dung piles, relative to glade edges.
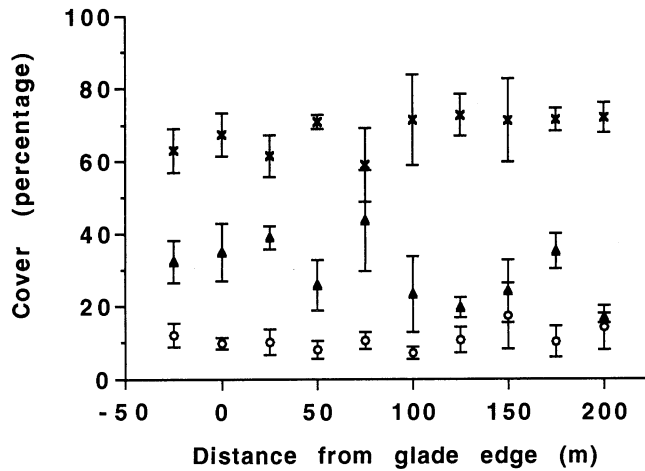
FIG. 6.   Percentage cover by bare ground (x), forbs (o), and grasses (▲), with respect to distance from glade edges.

Nitrogen, carbon, calcium, sodium, and potassium declined with distance from the glade edges (Fig. 11). Inside the glade, surface soil had greater nitrogen and carbon than deeper soils, an effect that was much less evident at 100 m from the glade edges. In contrast, sodium occurred at higher levels in the deeper soil than in the surface soil, both in the glades and at 100 m from the glade edges. Neither calcium nor potassium showed significant differences related to soil depth either in the glade or at 100 m from the glade edges.

Phosphorus, manganese, and magnesium levels of the soil inside the glades were similar to levels 25 and 100 m from the glade edges (Fig. 11). However, all three nutrients showed significantly higher levels in the background samples. Surface soil 100 m from the glade edges had higher levels of both phosphorus and magnesium than did deeper soil, a phenomenon not observed within the glade. Manganese levels were largely independent of soil depth both inside the glade and at 100 m from the glade edges.

Large mammal dung

The abundance of dung piles from all classes of large herbivores declined with distance from the glade edges (Table 1), the steepest decline occurred in the first 50 m from the edges (Fig. 12; Table 2). Elephant dung showed the weakest relationship, and dung of the medium and large wild ungulates the strongest relationships, between distance and density (Table 1). Dung of the two categories dominated by domestic livestock ("cattle and buffalo" and "small ungulates") showed weaker declines when considered separately, but the relationship between dung density and distance from glade edges was strong and significant when all live-
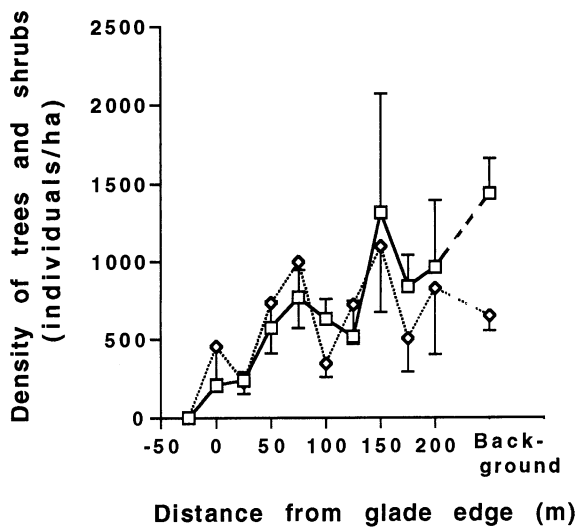

FIG. 7.   The densities of □, adult and ◇, juvenile trees and shrubs relative to glade edges.
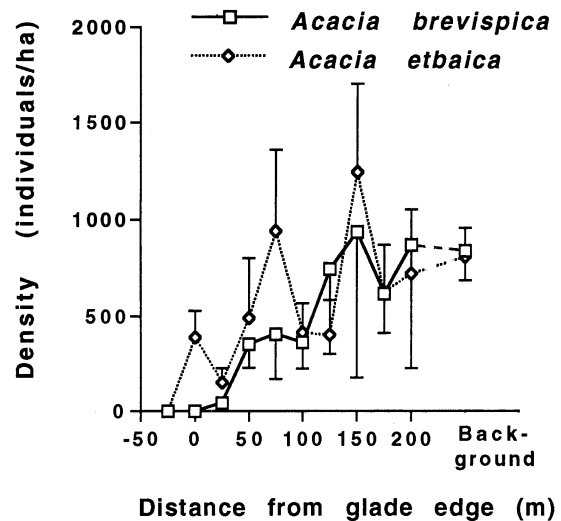

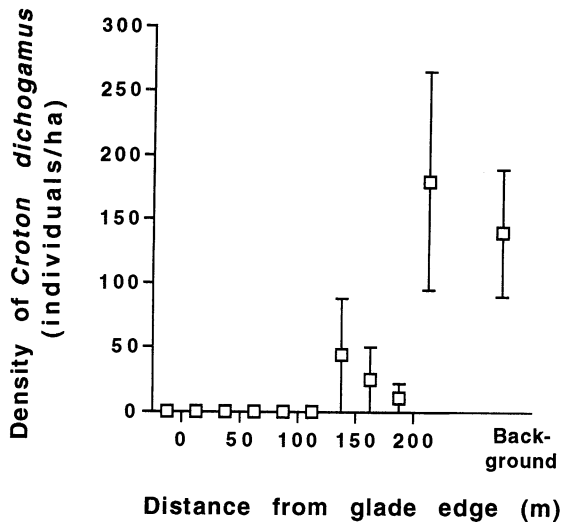FIG. 8.   The abundance of □, Acacia brevispica and ◇, A. etbaica relative to glade edges.

FIG. 9. The density of the shrub *Croton dichogamus* relative to glade edges.

FIG. 10. Species richness (●) and Shannon diversity (△) of understory plants relative to glade edge.

stock were considered together (Table 1). Although dik-diks were common in the study area, only two dung piles occurred in the sample transects. Dik-diks are territorial animals that use a small number of middens (Estes 1991), and their dung piles are therefore very patchy.

Zebra dung was anomalous in that it did not peak inside the glades, but in the first 25 m beyond the glade edges, forming a unimodal distribution. This pattern paralleled the pattern for percentage cover by the tall grass *Pennisetum stramineum* (Fig. 5). Excluding the points inside the glades, zebra dung declined strongly and significantly with distance from glade edges (Table 1). We do not have data yet on seasonal variation in the use of glades by herbivores.

Edge depth

For some traits, the edge between glades and bushland was abrupt, and for others it was gradual (Table 2). Edge depth varied from 0 to 200 m (Table 2). Values of zero are for traits that changed abruptly at glade edges, such as the abundance of glade specialists and the abundance of juvenile woody species. The majority of other vegetation variables and of dung variables indicated edge depths of 50–150 m. The exception was *Croton dichogamus,* which was virtually absent from areas within 200 m of glades. Most glade soil chemistry variables reached background levels relatively close to the edge of the glade, but three elements (phosphorus, magnesium, and manganese) showed dramatic increases between the background samples and all samples taken in the vicinity of glades, indicating edge depths of >100 m.

At an average of 1.9 glades/km², the glades cover 1.2% of the landscape (mean diameter 86 m, mean area 0.64 ha/glade). For those traits with an edge depth of 100 m, 13% of the landscape (6.4 ha/glade) is affected.
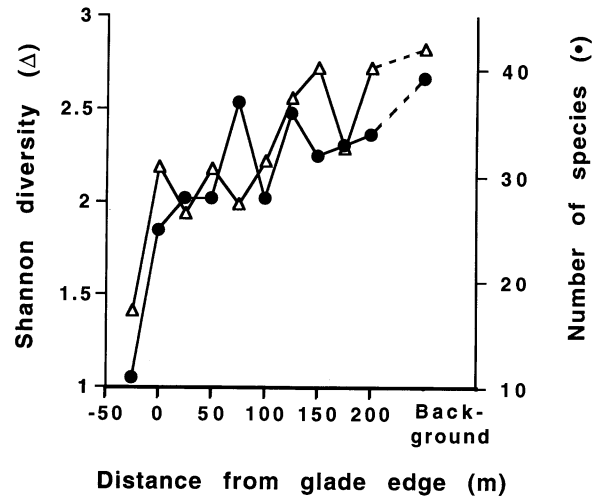
For *Croton dichogamus,* which is virtually absent from within 200 m of glade edges, 37% of the landscape (18.5 ha/glade) is affected, ignoring potential overlap between glades within 400 m of each other.

DISCUSSION

Species respond to the presence of these glades in different ways: negatively or positively, abruptly or gradually, and at different distances (edge depths). Therefore the spatial nature of this ecosystem mosaic differs among species (Fig. 13). For *Digitaria milanjiana* and other glade specialists, the landscape consists of small, isolated, hospitable sites with sharp boundaries (Fig. 13a). For *Croton dichogamus,* the landscape is dominated (37% of land area) by a number of large (diameters ≈ 500 m) inhospitable sites with sharp boundaries (Fig. 13d). For *Acacia brevispica* shrubs and *Cynodon* grasses, these inhospitable sites are much smaller (diameters ≈ 100 m, twice that of the glade itself) and have fuzzy edges (Fig. 13c). For *Pennisetum stramineum,* the landscape consists of a series of rings around glades, each with sharp inner edges and gradual outer edges that merge into low background levels (Fig. 13b). For gap edge specialists such as *Cyperus cristatus,* the landscape is limited to these narrow rings (Fig. 13e). For ungulate herbivores, the entire landscape is used, but the glades especially so (Fig. 13f). Zebras preferentially use glade edges (Fig. 13g).

The estimates of edge depth reported here may be low, depending upon their interpretation. Following Chen et al. (1992), edge depth was estimated as the distance from the glade edge at which each variable reached two-thirds of background levels. If, instead, a value of 9/10 were used, many edge depths would be greater. The latter, more conservative estimate would be more appropriate when trying to ensure that a site was out of the range of edge effects. However, this
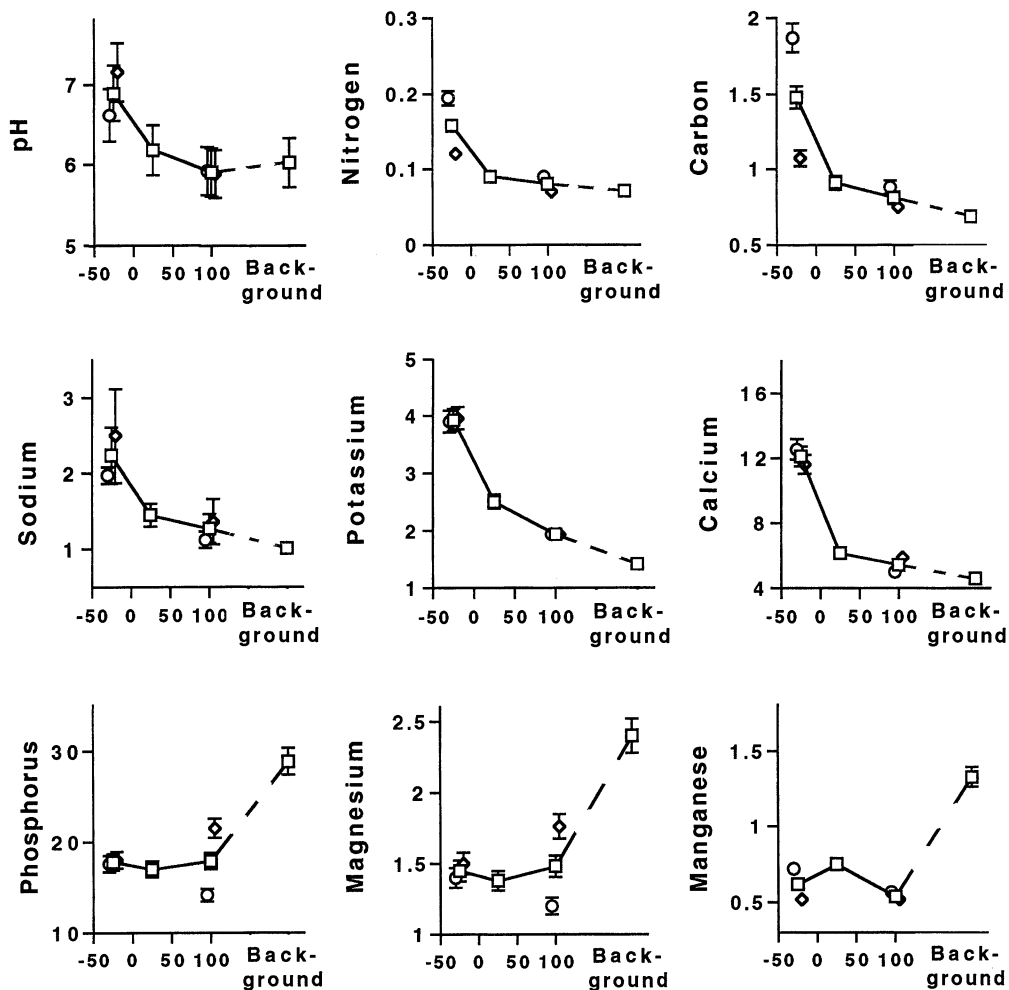
FIG. 11. Soil chemistry relative to distance from glade edge. □, values from soils 0–30 cm deep; ○, values from soils 0–10 cm deep; and ◇, values from soils 20–30 cm deep. Ordinate units are percentage dry biomass for all graphs except pH, and phosphorus (mg/kg). Data represent mean ±1 SE, $n = 4$. Symbols overlap some error bars.

TABLE 1. Correlation coefficients for the relationships between distance from glade edges and mean density of dung piles, averaged over all transects, for each class of large mammal. $n = 9$, except where noted. "Inside/outside" is the ratio of dung density inside the glades to dung density at the farthest sample sites (175–200 m from the glade edges).

Herbivore class	r	r^2	P	Inside / Outside
Medium ungulates	−0.680	0.462	<0.05	11.5
Large ungulates	−0.858	0.736	<0.005	2.1
Zebras	−0.504	0.254	~0.17	1.2
less point inside glades; $n = 8$	−0.881	0.777	<0.005	4.0
Small ungulates (mostly sheep)	−0.623	0.388	~0.07	1.7
Cattle (and buffalo)	−0.545	0.297	~0.13	2.8
Domestic livestock (combined)*	−0.697	0.486	<0.05	2.3
Elephants	−0.495	0.245	~0.18	1.5
All dung	−0.808	0.652	<0.01	3.4

* The class "domestic livestock" combines "small ungulates" and "cattle and buffalo," which were dominated by sheep and cattle, respectively.
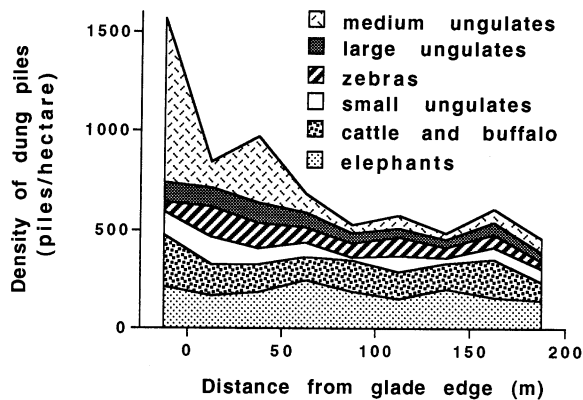
FIG. 12. Densities of dung piles of various classes of large herbivores, relative to glade edge.

would require a more thorough documentation of measured parameters because it makes a more subtle distinction.

This ecosystem mosaic of glades within a bushland landscape is an example of "spatially focused animal activity" (Andrew 1988). Other examples include watering points, salt licks, and shade sites (Belsky 1983, Georgiadis and McNaughton 1990, Belsky and Canham 1994).

The high levels of dung within glades in Laikipia indicate that glades are important local habitats for large mammals. Overall, dung piles were three and a half times (and for medium-sized wild ungulates, more than ten times) denser inside glades than they were 175–200 m outside the glades. Two explanations for this apparent preference for glades are enhanced food quality and greater ability to detect predators. These glades resemble the "grazing lawns" described by others (Coppock et al. 1983a, b, McNaughton 1984), and the dominant grass species in the glades, *Digitaria milanjiana*, is a preferred food for many grazers. In addition, the high nitrogen levels in the soils inside glades may support food plants that are more nitrogen-rich (c.f. Coppock et al. 1983a, Jaramillo and Detling 1992a).

These open, treeless glades may also provide better locations for predator detection than the surrounding bushland. This could explain, in part, why elephants, which have virtually no natural predators, showed the least preference for glades. Although elephants feed extensively on acacia species, they also feed on glade herbs and grasses, especially *Digitaria milanjiana* (T. P. Young, *personal observation*). Similarly, domestic cattle and sheep herds are individually escorted by herders in this habitat and corralled in "bomas" at

TABLE 2. Edge depth, measured as the distance at which each variable reached two-thirds of the background level, compared with the level inside the glade (or for zebras, the glade edge) for glades in acacia bushland in Laikipia, Kenya. "Background" levels for dung are from samples 200 m from glade edges. Soils were not surveyed on a fine enough spatial scale to determine sharpness of edge effects relative to soil chemistry. Soil values are based on dry mass. Omitted from this table are variables that showed no significant pattern with respect to distance from glade edges, and plant edge specialists.

Variable	Glade value	Background value	Edge depth (m)	Gradual or abrupt
Vegetation				
Digitaria sp. (% cover)	24	<1	0	abrupt
Cyperus blysmoides (% cover)	6	<1	0	abrupt
Tribulus terrestris (% cover)	6	<1	0	abrupt
Portulaca oleracea (% cover)	7	<1	0	abrupt
Cynodon spp. (% cover)	0	10	75	gradual
Acacia brevispica (no. individuals/ha)	0	840	115	gradual
Acacia etbaica (no. individuals/ha)	0	800	50	intermediate
Adult trees and shrubs (no. individuals/ha)	0	1400	150	gradual
Juvenile trees and shrubs (no. individuals/ha)	0	650	0	abrupt
Croton dichogamus (no. individuals/ha)	0	140	200	abrupt
Species richness (no. species)	11	39	50	gradual
Shannon diversity (understory)	1.41	2.82	100	gradual
Dung				
All dung (no. piles/ha)	1570	460	50	gradual
Large wild ungulates (no. piles/ha)	96	45	50–75	gradual
Medium wild ungulates (no. piles/ha)	830	72	50	intermediate
Zebras (from glade edge, no. piles/ha)	153	39	75–125	gradual
Domestic livestock (no. piles/ha)	387	165	25	intermediate
Soils				
pH	6.8	6.0	15	
Nitrogen (%)	0.16	0.07	15	
Carbon (%)	0.15	0.07	15	
Sodium (%)	2.25	1.00	25	
Calcium (%)	12.0	4.5	10	
Potassium (%)	3.95	1.45	25	
Phosphorus (mg/kg)	17.5	28.5	>100	
Magnesium (%)	1.45	2.35	>100	
Manganese (%)	0.6	1.3	>100	

a. *Digitaria milajiana*   b. *Pennisetum stramineum*

c. *Acacia brevispica*   d. *Croton dichogamus*

e. *Cyperus cristatus*   f.   Ungulates
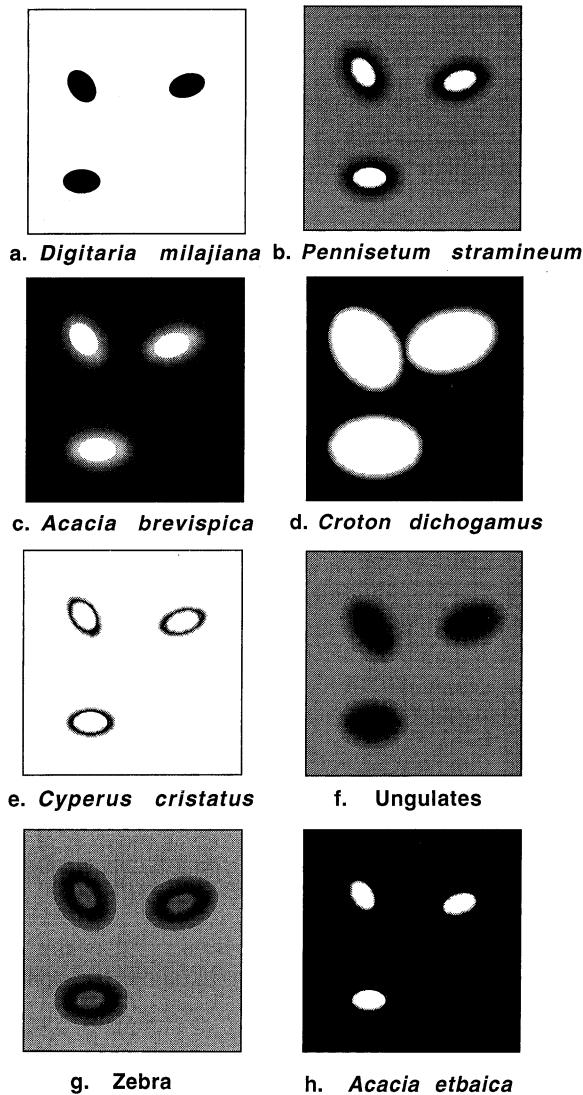
g.   Zebra   h.   *Acacia etbaica*

FIG. 13. The bushland–glade mosaic, from the perspective of different species. Black areas represent the greatest measured abundance, and white areas represent absence. There are additional scales of heterogeneity within the glade and bushland communities.

night, which might explain their weaker preference for glades, when compared to wild herbivores (Table 1). However, local herders report that these glades are preferred grazing areas for domestic stock.

It is possible that for most wild herbivores, these glades provide both better food and protection from predators. In addition to large mammals, it appears that hares (*Lepus capensis*) also benefit from this community mosaic, feeding almost exclusively in glades at night, and finding cover during the day in the surrounding bushland (T. P. Young, *personal observation*). In North America, bison preferentially feed in young prairie dog towns and preferentially lie up in older towns (Coppock et al. 1983*b*).

Whatever the reasons for the preference of large herbivores for these glades, the glades are apparently important for both domestic and wild large mammals. It is likely that these glades increase the density and the diversity of the native large mammal community, and may increase economic productivity for the ecosystem in the form of cattle.

Conversely, large mammals may play a role in maintaining the glades. Heavy browsing and grazing pressure can favor grassy and herbaceous "lawns" at the expense of woody vegetation and less palatable herbs (McMaughton 1984). A review by Gordon and Lindsay (1990: 272) states: "Heavy grazing pressure on swards also tends to select for prostrate, small-leaved, dwarfed species that have dense foliage. These sward changes tend to increase the concentration of available forage and thereby increase the rate of intake of plant material by large herbivores." Such areas of short grass and high nutrients can be maintained by the high levels of herbivory that they encourage (Bakker et al. 1983, Willms et al. 1988).

In addition, increased deposition of dung (and presumably concomitant urine) may be responsible for the dramatic differences in soil chemistry associated with patches of high herbivory, in particular high N, Na, Ca, and K (McNaughton 1984, Georgiadis and McNaughton 1990). It is not yet known whether these soil differences also help maintain these glades. Natural and simulated urine patches have been shown to create fine-scale structural heterogeneity through increased nitrogen content and grazing in a semiarid grassland in North America (Day and Detling 1990, Jaramillo and Detling 1992*a, b*). Models of ecosystem function in the Serengeti imply that patchy dung and urine depositions can create local grassland heterogeneity through changes in nitrogen mineralization, mediated by soil microbes (Ruess and McNaughton 1987, Seagle et al. 1992). Increased nitrogen mineralization in heavily grazed sites at prairie dog colonies in South Dakota was associated with decreased carbon allocation to roots and lowered nitrogen immobilization by decomposers (Holland and Detling 1990).

Fine-scale heterogeneity in grassland community structure and grazing preference in the Serengeti has been shown to be associated with high levels of C and Na in the short grass microsites, with the latter difference being concentrated in the upper soil (Belsky 1983), in patterns similar to those found in the present study. However, that study also showed lower levels of K and Ca in the short grass microsites, in patterns opposite to those in the present study. In appears that there is not a single outcome of the complex relationships between herbivory, soil chemistry, and vegetation structure. Long-term exclosure experiments are currently under way in Laikipia to examine some of the cause-and-effect relationships in this system.

The geometries, orientations, and topographic locations of these glades are entirely consistent with pat-

terns of settlement site decisions by current traditional Maasai, who select broad, gently sloping ridges and produce sites of similar size (Western and Dunne 1979). Interviews with local ranch owners and herdsmen indicate that these glades have existed in their present locations for several decades, and are thought to be sites of precolonial Maasai bomas (cattle enclosures). Stelfox (1986) has shown that contemporary cattle bomas have profound effects on soil chemistry and vegetation composition. If the Laikipia glades have origins in Maasai cattle bomas, they have been self-maintaining for >70 yr. The Maasai settlement sites surveyed by Western and Dunne (1979) retained low levels of canopy cover even after being abandoned long enough (called "old scars") for vegetation to cover the sites.

Fractal analysis of a woodland–grassland mosaic in Zimbabwe indicated that small grassland patches (of a size similar to the glades in Laikipia) "remained remarkably stable over time" (Meltzer and Hastings 1992). However, these authors suggested that this may be an artifact of the ongoing breakup of larger grasslands, and it is unclear whether these patches are fundamentally similar to the glades in Laikipia.

There exist in South Africa small nutrient-rich patches of acacia woodlands embedded in a broad-leaved ecosystem, producing a mosaic similar in scale to that described here. These patches were similarly attributed to old settlement sites (Blackmore et al. 1990, Scholes and Walker 1993). However, they are distinguished, not by a lack of woody plants, but rather by a shift from broad-leaved trees to acacias. *Acacia tortilis* patches in northern Kenya have been attributed to the high seed loads deposited by livestock in enclosures (Coughenour and Ellis 1993). Isolated trees in semiarid savannas create patches beneath their canopies that are moister, cooler, and richer in nutrients than the surrounding grassland (reviewed in Belsky and Canham 1994).

There appear to be different outcomes from abandoned settlement sites, depending on the relative importance of initial seed deposition, the nutrient requirements of plant species, and the effects of increased herbivore activity. For example, livestock may be less likely to eat large amounts of *Acacia* pods in less arid sites, such as Laikipia and the Amboseli ecosystem studied by Western and Dunne (1979) where grazing livestock predominate, than in the much drier northern Kenya ecosystems where browsing livestock predominate. Livestock enclosures of the Turkana ("anok") are also used for shorter periods of time than enclosures of the Maasai, and long-term enclosures accumulate deeper dung levels that may inhibit seedling germination and growth (J. Ellis, *personal communication*). The effects of herbivores on savanna ecosystems can vary considerably (O'Connor 1985, Gordon and Lindsay 1990). Herbivore patches in more productive ecosystems may be more likely to be dominated by low,

palatable, fast growing plants than patches in less productive ecosystems (Huntly 1991).

Although wildlife and cattle conflict in many ways (Prins 1992), both appear to benefit from the continuing presence of these glades. Gordon and Lindsay (1990) have examined the possibility of "management" of vegetation by wild herbivores. It is also possible that traditional Maasai pastoralists of Laikipia (no longer present) intentionally managed their livestock in ways designed to increase the presence of desirable glades. These glades also contribute to the physiognomic and floristic diversity of the Laikipia ecosystem by maintaining plant species and growth forms that are rare or absent elsewhere. Management and conservation strategies for the region should incorporate an understanding of the nature and function of this woodland–glade mosaic.

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