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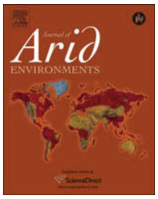

The impact of abandoned pastoral settlements on plant and nutrient succession in an African savanna ecosystem

A.N. Muchiru[a,b,*], D. Western[a], R.S. Reid[b,c]

[a] *African Conservation Centre, P.O. Box 62844, Nairobi, Kenya*
[b] *International Livestock Research Institute, P.O. Box 30709, Nairobi, Kenya*
[c] *Center for Collaborative Conservation, Colorado State University, Fort Collins, CO, USA*

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ABSTRACT

We detail the impact of abandoned traditional settlements (or bomas) on plant and nutrient succession in the Amboseli ecosystem, southern Kenya, over the course of a century. Plant and soil data were sampled on and around abandoned settlements. The term, 'onsite', refers to the area within the perimeter fence, 'offsite' to the area up to 200 m beyond the fence. Herbaceous standing biomass onsite increased in the course of succession to peak at twice offsite levels within two decades. Biomass remained elevated for six decades then dropped to the background levels at the limit of sampling distance. Plant species richness onsite increased rapidly in the course of succession, then stabilized on older bomas. Species composition changed throughout succession, with pioneer herbs and grasses giving way to boma-edge species and woody vegetation later in succession.

Soil nutrients, including carbon, nitrogen, magnesium and phosphorus, were highly elevated on abandoned settlements. The various nutrients declined at different rates during the course of plant succession. Potassium, phosphorus and magnesium levels remained at twice offsite levels for over a century, creating islands of high fertility and high plant biomass in the savanna landscape. We conclude that the perturbation caused by shifting nomadic settlements creates localized nutrient and plant diversity hotspots in savanna ecosystems that remain distinct from the surrounding savanna for decades, possibly centuries.

1. Introduction

By the end of this century, grasslands will lose proportionately more biodiversity than any other ecosystem on earth (Sala et al., 2000). Human impact will be the principle cause of loss. The African savannas, the richest of the world's grasslands (McNaughton, 1979; Norton-Griffiths, 1979), also support the highest concentrations of large mammals (Cole, 1986). Despite their natural resilience (Noy-Meir, 1982; Walker and Noy-Meir, 1982), there is considerable debate over whether African savannas are losing productivity permanently due to intensified livestock production, settlement, sedentarization, water development and wood consumption, or whether they are resilient systems, driven primarily by climate and not people (Lamprey, 1983; Sinclair and Fryxell, 1985; Coppock et al., 1986, 1987; Ellis et al., 1987; Reid, 1992; Behnke et al., 1993; Milton et al., 1994; Sullivan and Rohde, 2002; Vetter, 2005).

Early tool-bearing hominids evolved in the African savannas millions of years ago (Harris, 1980). Human impact intensified with the advent of pastoralism 3000–4000 years ago to the point of accounting for the major portion of the large mammal biomass (Cole, 1986). The human imprint is therefore an ancient and formative ecological factor in the savannas. Given the dominant role humans have played in African savannas, there is a need to establish the background influence of traditional pastoralism on the structure and dynamics of ecosystems in order to assess the ecological significance of growing human populations and increasing sedentarization. Only a few studies have addressed these questions, largely because most research has focused on "natural" ecosystems (Gallagher and Carpenter, 1997) rather than human-dominated ecosystems that typify Africa.

Bell (1971), suggested that wild ungulates tend to cluster on pastures modified by pastoral activity. Western and Gichohi (1993) argued that human activity in the savannas could have a positive or negative influence on biodiversity, depending on the level and type of activity. One study that has looked at pastoralism as an integral

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[*] Corresponding author. Andrew N. Muchiru, P.O. Box 15289, Nairobi, Kenya. Tel.: +254 20 891360/3002431; fax: +254 20 891751.

E-mail addresses: andrew.muchiru@acc.or.ke (A.N. Muchiru), dwestern@africaonline.co.ke (D. Western), robin.reid@colostate.edu (R.S. Reid).

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rather than aberrant factor in savanna ecosystems has been underway in Amboseli since 1967 (Western, 1973, 1994). Here, as with other studies (Stelfox, 1986; Blackmore et al., 1990; Muchiru, 1994; Reid and Ellis, 1995; Young et al., 1995; Augustine, 2003; Augustine et al., 2003), it is evident that settlements play an important ecological role (Western and Dunne, 1979). Livestock settlements are certainly the most visible impact pastoralists have on the savannas, due to the enormous daily concentration of animals (Augustine, 2003; Augustine et al., 2003) and the destruction of woody vegetation for houses and fencing (Ellis et al., 1984; Muchiru, 1994). But, unlike the equally conspicuous impact of water holes in the savannas (Georgiadis, 1987; Tolsma et al., 1987; Andrew, 1988), the impact of settlements is transient and followed by rapid vegetation re-colonization on abandoned sites (Reid and Ellis, 1995).

Here we expand recent research on the impacts of pastoral settlements on vegetation in east and southern Africa (Western and Dunne, 1979; Stelfox, 1986; Blackmore et al., 1990; Muchiru, 1994; Reid and Ellis, 1995; Young et al., 1995; Augustine, 2003; Augustine et al., 2003) by looking at the successional cycle of settlements and suggesting the complex ecological role they play in shaping African savannas.

2. Study area

The study area extends (2°20′–2°35′S, 37°05′–37°20′E), lying at an altitude of 1150 m along the northern boundary of Amboseli National Park straddling the Kenya–Tanzania border north of Kilimanjaro. The area has a high concentration of abandoned settlements and good aerial photographic coverage dating from 1950. The settlements studied fell within a 400-km^2 area stretching some 40 km from Meshanani Ridge east to Iremito and 10 km north to Charkita. Between 50 and 60 settlements occupied this area during the study period and were largely used on a seasonal basis.

Amboseli has a hot dry climate with maximum temperatures varying between 26 °C and 44 °C and minimum temperatures between 6 °C and 24 °C (Western, 1973). Rain falls in two seasons, October–December and March–May, averaging 350 mm. The bushed grassland in Meshanani and Nkiito is dominated by the trees *Acacia mellifera* (Vahl) Benth and *Commiphora* spp. In Charkita, tree cover is dominated by *Commiphora* spp. and in Iremito, by *Acacia* nubica Benth. The most abundant grass species between settlement sites are *Sporobolus nervosus* Hochst, *Aristida kenyensis* Henr and *Leptothrium senegalense* (Kuth) W.D. Clayton. Forbs species include *Tribulus terrestris* (Caltrops), *Blepharis ciliaris* (L) B.L. Burt and *Sericocomopsis pallida* Schinz. Soils in the area have low infiltration rates due to sparse vegetation cover, a low humus content and poor soil structure (Western and Dunne, 1979).

A variety of wild and domestic animals are found in the study area. Wild species include elephants (*Loxodonta africana*), common elands (*Taurotragus oryx*), gerenuks (*Litocranius walleri*), plains zebras (*Equus burchellii*), blue wildebeests (*connochaetes taurinus*), oryx (*Oryx gazella*), giraffes (*Giraffa camelopardalis*), impalas (*Aepyceros melampus*), buffaloes (*Syncerus caffer*), black-backed jackals (*Canis mesomelas*), spotted hyenas (*Crocuta crocuta*), grant's gazelle (*Gazella granti*) and thomson's gazelle (*Gazella thomsoni*). Domestic species include cattle, sheep, goats (*Capra hircus*), donkeys (*Equus*) and dogs. Livestock is closely herded by Maasai pastoralists.

3. The settlement cycle

The Maasai economy rests heavily on the production of cattle, sheep and goats. The locus of Maasai life is the boma, Swahili for a settlement enclosure. Bomas are typically circular thorn enclusures ranging from 40 to 80 m in diameter. The outer perimeter is demarcated by a thorn fence. Family huts rim the inner fence. Adult cattle are packed into the boma at night and small stock, including calves, sheep and goats, are fenced off within smaller compounds in the centre of the settlement. Stock numbers in a settlement range from 200 to 1500 or more (Western, 1973). Construction and repair of the fences and firewood make heavy demands on the surrounding trees, creating a maximum visible impact zone of some 225 m (Western and Dunne, 1979; Jensen, 1983a,b). The impact zone is also heavily trampled and grazed, stripping herbaceous cover to the point of looking like a heavily used waterhole. This study, focuses on the impact zone and draws on the results of other studies to compare the impact zone against the background vegetation unaffected by settlements. Thus, all comparisons are made between impact on the abandoned boma itself (referred to as 'onsite') and impact zone tailing off to 200 m beyond the bomas fence ('offsite').

Bimodal rainfall each year triggers two distinct pastoral migrations, which shadows those of wild herbivores. During the dry season, pastoralists, livestock and wildlife concentrate around the permanent swamps and redisperse during the rains (Western and Dunne, 1979). In the dry season study area north of the basin, bomas are consequently used on average twice a year for a few weeks to several months. The distribution, seasonality, longevity and physical characteristics of bomas are circumscribed by grazing and watering conditions, herding strategies, decline habitat conditions and by settlement decay (Western and Dunne, 1979). By the time a settlement is abandoned after a few years of seasonal occupation, huge quantities of dung and urine have been deposited in and around the boma. Dung within the boma can mound up to 2 m above the ground surface, creating bare ground and a rich nutrient store.

4. Methods and materials

4.1. Settlement age

Thirty-eight bomas were chosen for study, ranging from those currently occupied to those abandoned for several decades. Some abandoned bomas were identified from 1:20 000 scale aerial photographs taken in 1950, 1961 and 1970. Other bomas were shown to us by long-term Maasai residents. The informants showed us bomas that had occupied and subsequently abandoned. We identified and located many such abandoned bomas on the ground, but found only thirty-two with no signs of later reoccupation. Reoccupied bomas were excluded from the study to avoid the confounding effect of multiple occupations on the same site. Six currently occupied bomas that did not sit on earlier settlement sites based on examination of aerial photos dating back to 1950 were included in the study to give baseline conditions for the start of successional measurements.

Time since abandonment was determined either by extrapolation from aerial photographs or with the help of Maasai informants. Jensen's (1983b) technique for estimating settlements 40 years or older from photographs was adopted. Here, a recently abandoned settlement first observed in 1950 was judged to be 11 years old on the 1961 photos, 20 years old on the 1970 photos and 40 years old when located on the ground in 1990. We were also able to 'backdate' old settlements appearing on the earliest aerial photos in the following way. Settlements that we identified on 1950 photos that were identical in appearance to the 20-year-old settlements on the 1970 photos were classified as 20 years old in 1950, 40 years old on the 1970 photos, and 60 years when located on the ground in 1990.

Settlements were grouped into four boma age classes: still in use ($n = 6$), 5–20 years old ($n = 11$), 21–60 years old ($n = 11$), and 60+ years old ($n = 10$). All sites 60+ years were combined into one class, though several over a century old. Lumping 60+ years old settlements did not substantially affect the results since there was little change in the soils of sites 50+ years (see below).

4.2. Herbaceous species abundance and composition

Herbaceous species data was collected within and around abandoned settlements. The abundance of each species was measured using the slanting pin-intercept technique angled 65° from vertical (McNaughton, 1979). Each pin-frame held 10 pins suspended 10 cm apart. Within the boma, we randomly placed 15 pin-frames within the perimeter fence. Outside the fence, data was sampled at three points 50 m apart along each of the two radial transect. Hits were based on the number of times a pin was intercepted by each species. The first transect ran along a randomly selected compass bearing from the settlement, the second one perpendicular to the first. Although the transects were 200 m long, herbaceous data was collected only up to 150 m from the settlement due to time constraints. Woody species data was collected the full length of the transect. At each sampling point along the transect, three transects oriented perpendicular to the radial transect were set up. Five pin-frames were placed along each of the perpendicular transects.

4.3. Woody species abundance and composition

Woody species abundance and composition was sampled in the same on and offsite locations as herbaceous data. All woody species within the boma area were identified and the total number of each species tallied. Basal stem diameter, height and canopy dimensions for each tree or shrub were recorded. Canopy diameter was averaged from the two perpendicular measurements. Along each of the two radial transects, woody vegetation was measured with the Point Centered Quarter (PCQ) method (Mueller-Dombois and Ellenberg, 1974). Sample points were located every 50 m. The transects extended to the point at which tree stem density was not measurably affected by settlements (175 m) close to the limits of 225 m measured in earlier studies (Western and Dunne, 1979). At each point, woody plants (trees or shrubs) were recorded in each of the four quarters. For each species, measurements were recorded for: the distance from the quadrat centre-point to the nearest tree/shrub's stem; for the height of the tree or shrub; and for canopy diameter (average between two perpendicular diameters). Any tree or shrub species shorter than a meter was considered a seedling and not recorded.

4.4. Biomass estimates

Herbaceous biomass in g/m^2 (HB) was estimated using a regression equation from Western (unpublished) where: $HB = \text{total hits} \times 0.847$. When analyzing herbaceous biomass against settlement age, we omitted three settlements aged 20–40 years because a temporary boma had been established in the proximity of these sites, resulting in heavier grazing on this compared to other sites. The temporary settlements were established shortly before peak biomass during the rains and significantly reduced standing mass levels. Other study sites may also have been grazed by wild herbivores and cattle moving through the area. However, in these cases, there was no visible impact on standing biomass.

Biomass per individual tree and shrub was estimated using regression equations from Western (unpublished). Here $\log \text{AGDM (kg)} = 1.0433 \log \text{CV} + 0.0707$, where AGDM is Above Ground Dry Mass and CV (Canopy Volume). $\text{CV} = P_iX\ (\text{radius}^2) \times \text{height (m)}$. Total woody biomass per boma was the sum of the estimated biomass of all the individual trees and shrubs found onsite. Onsite biomass, kg/m^2 was calculated for each boma by dividing biomass by the area. Since we were interested in re-colonization by *Acacia tortilis* onsite following abandonment, we excluded mature *A. tortilis* trees (over 20 cm basal diameter) left over from the occupied phase of the boma. Pastoralists often leave mature trees intact to provide shade within new settlements. Woody biomass offsite was estimated for each of the four trees or shrubs at each point then summed for total biomass. Biomass in kg/m^2 was calculated by multiplying total biomass by the density at each point. Density at each point was estimated by taking the reciprocal of the mean distance to the four trees or shrubs to get around the problem that PCQ methods are a plotless sampling methods.

4.5. Soils

Soil characteristics were sampled from twenty-four abandoned bomas. Several bomas were randomly selected from each of the three age classes. Seven bomas were selected from bomas aged 5–20 years, eight 21–60 years and nine 60+ years. Two pits were dug 50 cm deep at each boma. One pit was located centrally onsite, the other, which served as a control, was randomly located 100 m perpendicular to slope to avoid nutrient erosion from the settlement. At each pit, soil was sampled at depths of 0–10 cm, 20–30 cm and 40–50 cm. The samples were analyzed by the Kenya Government National Agricultural Laboratory in Nairobi. The soils samples were sun dried before analysis. Determination of sodium, potassium, magnesium and extractable phosphorus was measured using Mehlich method (Mehlich et al., 1962). Soil extraction was measured using a mixture of 0.1N HCl and 0.03N H_2SO_4. Na, Ca and K were measured colorimetrically. Mg and P were measured photometrically. We used the Walkley–Black method (Walkley and Black, 1934) to measure organic carbon. Here, samples were finely ground and a 1 g sub-sample was mixed with 10 ml potassium dichromate ($K_2Cr_2O_7$). 20 ml H_2SO_4 was added to the mix. The resulting mixture was allowed to stand for 20 min before adding 200 ml distilled water and 5 ml H_3PO_4. Finally, the solution was titrated with 0.5N $FeSO_4$. Nitrogen was determined using Kjeldahl method (Bremner, 1960). The soil sample was mixed with 1.5 ml distilled water and H_2SO_4 as a digestion agent. The solution was distilled into a test tube containing boric acid, then titrated with 0.007144 H_2SO_4.

4.6. Statistical analysis

Vegetation biomass and species richness data were subjected to a two-factor-analysis of variance, with the main effects being boma age since abandonment and distance from a boma. Post hoc tests were done on the effects of boma age, distance to boma and their interactions on vegetation biomass. Spatial and temporal variation of both herbaceous and woody species in relation to bomas was determined by regressing the relative frequency of each species on boma age and distance away from a boma. Individual species frequency was obtained by dividing total pin interceptions of individual species by the total number of pin interceptions for all species counted per site. The model was fitted using the SAS procedure GLIMMIX (SAS Institute, 2005). A three-way ANOVA was used for the soil data analysis, with the main effects being boma age, soil depth and location (onsite or offsite). Variation of the mineral elements between the boma age classes was analyzed by fitting a linear regression separately for each element. This was considered appropriate since only one core was collected at each boma.

5. Results

5.1. Plant biomass

Plants colonized the bare ground of old bomas after abandonment (Fig. 1, Table 1). Herbaceous biomass increased rapidly for the first 20 years, with a peak at 21–60 years (Fig. 1A). Post hoc tests were done on the effect of boma age and distance to boma. The test showed that occupied bomas supported significantly less plant biomass than the other three boma age classes ($P < 0.01$). Grass and forbs biomass was greater on bomas than in the surrounding impact zone ($P < 0.01$) for the first 60 years after abandonment and declined sharply with distance offsite (Fig. 2A and B). After 60+ years, biomass onsite approached background levels at the periphery of the impact zone. For grasses, the effect of bomas tailed off at 50 m from a boma, but for forbs the influence of the boma is still apparent at 150 m (Fig. 2A and B).

Total woody biomass of all species onsite increased significantly with boma age but was weakly significant for *A. tortilis* alone (Fig. 1B, Table 1). Biomass of *A. tortilis*, a slow-growing, long-lived species, increased steadily with boma age to make up most of the biomass on the oldest bomas (Fig. 1B, Table 1). Biomass of other species remained the same for 21–60-year-old as 5–20-year-old settlements, then gradually increased on older bomas (Fig. 1B). Distance from settlement was significant for all species, including *A. tortilis* (Table 1). There was also a significant interaction between boma age and distance for the biomass of all woody species. This interaction arose because occupied bomas showed a different pattern of biomass with distance compared to other boma classes. Biomass with distance for occupied bomas showed a humped distribution peaking at 100 m to significantly higher levels than 200 m distance ($P = 0.053$). Biomass with distance increased steadily away from the bomas, with significantly more biomass offsite than onsite ($P < 0.001$).

Table 1
Significant effects of settlement age (years) and distance (m) from a settlement on woody and herbaceous biomass and species richness.

	Source	df	*F*	*P*
Woody biomass	Age class	3	86.91	<0.001
	Distance	4	23.59	<0.001
	Age class × distance	12	2.92	<0.001
Acacia tortilis biomass	Age class	3	2.13	0.094
	Distance	4	21.53	<0.001
Grass biomass	Age class	3	2.93	0.033
Forbs biomass	Age class	3	3.54	0.020
Grass and forbs biomass	Age class	3	3.86	0.009
Grass richness	Age class	3	12.71	<0.001
Forbs richness	Age class	3	9.57	<0.001
Woody richness	Age class	3	4.71	0.003
Grass, forbs and woody richness	Age class	3	9.61	<0.001
	Distance	4	2.72	0.030

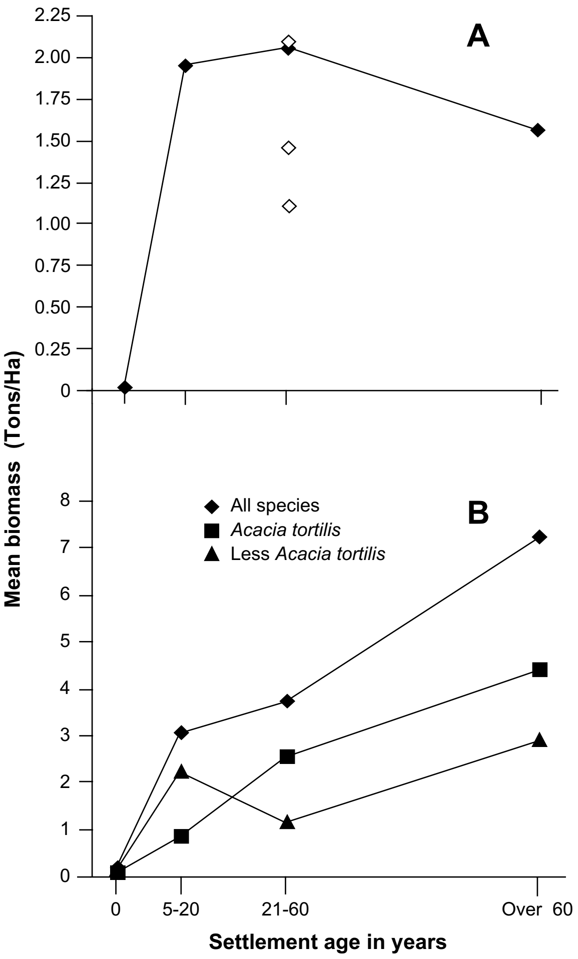

Fig. 1. Mean herbaceous (A) and woody (small tree and shrub) biomass (B) on settlements (onsite) of varying age. Occupied ($n = 6$); 5–20 years ($n = 11$); 21–60 years ($n = 11$) and 60+ years ($n = 10$). Settlement age was by the number of years since abandonment, where '0' years were occupied settlements. Three heavily grazed bomas (A) are shown as outliers: ◇ (age class 21–60 years). Large trees with more than 20 cm basal diameter were not included in the analysis.

5.2. Species richness

The mean number of herbaceous species on bomas appeared to increase strongly for the first 20 years after abandonment. There was no significant difference in post hoc tests between 5–20, 21–60 and 60+ years after abandonment (Fig. 3). Woody species increased weakly for the first 20 years, then more slightly thereafter. In the post hoc test, woody vegetation of occupied bomas increased significantly from 5–20 years to 60+ years ($P > 0.012$). The total number of species continued to increase after 20 years, but marginally on the oldest bomas. Distance had a significant effect on richness of all species combined (Table 1), but not on woody or herbaceous richness individually, neither of these insignificant results are shown in the table.

5.3. Species composition

Herbaceous species exhibited three abundance patterns as bomas grew older (Fig. 4). To show both temporal and spatial patterns involved, we focused on species occurring on all boma age classes and the full distance along offsite transects (Fig. 4). Two of these patterns are supported significantly by a generalized linear mixed model. We found a significant variation in the mean abundance of the different species by boma age ($F_{4,145} = 25.481$, $P < 0.001$) and with distance from settlement ($F_{4,620} = 80.81$, $P < 0.001$). We also found significant interactions between boma age and species ($F_{8,145} = 4.65$, $P < 0.001$) and between distance and species ($F_{12,620} = 19.14$, $P < 0.001$).

Decomposition of these interactions revealed the variation in mean abundance with boma age. The first pattern was a humped distribution, shown by *Amaranthus graecizans* ($F_{2,145} = 4.81$, $P < 0.01$) (L) (Fig. 4A). This species rapidly colonized the abandoned bomas, rose to a peak in the first twenty years, then declined with boma age thereafter. Though not significant *Cynodon plectostachyus* (K. Schum) showed a similar pattern. At 5–20 years it was the most abundant herbaceous species. A second insignificance pattern was characterized by *T. terristries* and *Eragrostis papposa* (Roem and Schult) (Fig. 4B), which also invaded the bare ground though more slowly and sustainably. The third group of species, including *S. nervosus* ($F_{2,145} = 11.93$, $P < 0.001$) and *Commicarpus pedunculosus* ($F_{2,145} = 2.392$, $P < 0.095$) (A. Rich) increased steadily as the bomas

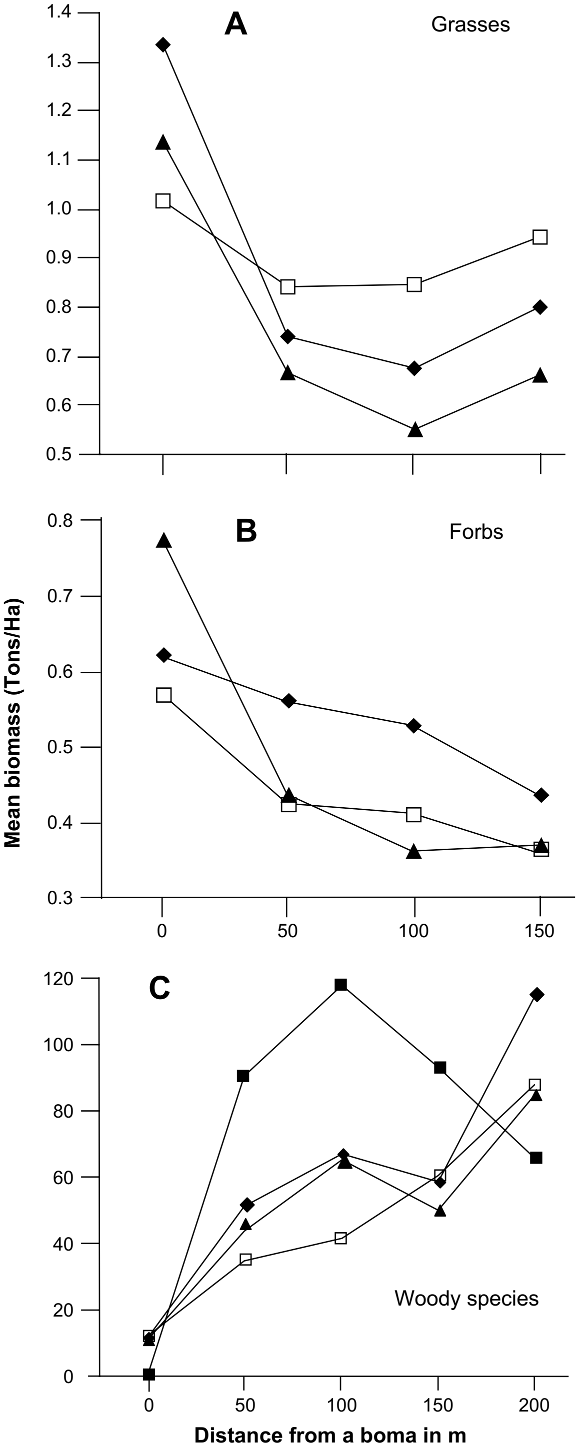

Fig. 2. Mean herbaceous (A and B) and woody biomass species (C) at increasing distance from settlement, where '0' is onsite. Mean biomass was calculated separately for settlements of varying age classes. Age classes were: ■ Occupied ($n = 6$); ◆ 5–20 years ($n = 11$); ▲ 21–60 years ($n = 11$) and □ 60+ years ($n = 10$).

Fig. 3. Mean number of herbaceous and woody species per age class. Settlements were grouped into three age classes: 5–20 years ($n = 11$); 21–60 years ($n = 11$) and 60+ years ($n = 10$).

aged (Fig. 4C). *S. nervosus* increased to become the dominant herbaceous species on the oldest bomas sampled.

Further decomposition of the interactions revealed variation of abundance with distance. The most abundant species onsite, including *C. plectostachyus* ($F_{3,620} = 61.49$, $P < 0.001$) and *A. graecizans* ($F_{3,620} = 29.55$, $P = 0.001$), decreased in abundance with distance away from the boma (Fig. 4D), *T. terristries* ($F_{3,620} = 9.66$, $P < 0.001$). *C. plectostachyus* was also abundant under shady trees close to the settlement (Muchiru pers. obs). Other species, including *C. pedunculosus* and *Pavonia patens* (Andr.) showed an insignificant humped distribution (Fig. 4E). These species were most abundant close to the outer perimeter fence. Finally, species such as *S. nervosus* ($F_{3,620} = 7.16$, $P < 0.001$) and *A. kenyensis* ($F_{3,620} = 39.02$; $P = 0.025$) (Henr) (Fig. 4F), were rare on the bomas and increased steadily and continuously in abundance with distance.

We also focused on three woody species to look at spatial and temporal patterns of succession on abandoned bomas (Fig. 5). The relative abundance of *A. tortilis*, *A. mellifera* (Vahl) and *Commiphora africana* (A. rich) Engl. was regressed on boma age and distance from a boma, using a generalized linear mixed model. Species significantly influenced each other's abundance by age boma age ($F_{2,361} = 5.47$, $P = 0.005$) and distance from boma ($F_{2,2111} = 13.23$, $P < 0.001$). Mean abundance for the three species significantly varied by distance only ($F_{2,2111} = 70.22$, $P < 0.001$). Only the interaction of species and distance was significant ($F_{8,2111} = 3.08$, $P < 0.002$). Decomposing the interactions revealed that boma age had a significant effect only on *A. tortilis* ($F_{3,361} = 4.024$, $P = 0.008$), while distance had a significant effect on *A. tortilis* ($F_{4,2111} = 123.87$, $P < 0.001$), *C. africana* ($F_{4,2111} = 11.06$, $P < 0.001$) and *A. mellifera* ($F_{4,2111} = 16.40$, $P < 0.001$).

A. tortilis steadily established itself on old boma sites and eventually assumed dominance (Fig. 5A). Some species like *Commiphora* were conserved by pastoralists as mature trees during settlement occupation (Fig. 5B). These mature trees decreased in abundance after abandonment. Finally, several species represented by *A. mellifera* (Fig. 5C), *Lycium europium* L. and *Salvadora persica* L., established themselves after boma abandonment, peaked soon afterwards and then declined rapidly on older sites. Spatially, some woody species such as *A. tortilis* (Fig. 5D), *A. nubica* and *L. europium*, were abundant on old bomas and decreased with distance from the bomas. Others, such as *C. africana*, were most abundant at intermediate distances and decreased with settlement distance (Fig. 5E). *A. mellifera* was abundant on abandoned boma sites (Fig. 5F), decreased at intermediate distances and increased again further from settlements.

5.4. Soil nutrients

A three-way ANOVA by boma age, soil depth and location (onsite and offsite) for all elements showed significant effects of depth ($F_{2,1437} = 10.17$; $P > 0.001$; df = 2), location ($F_{1,1437} = 9.21$; $P = 0.002$; df = 1). At the interaction level, only depth and location

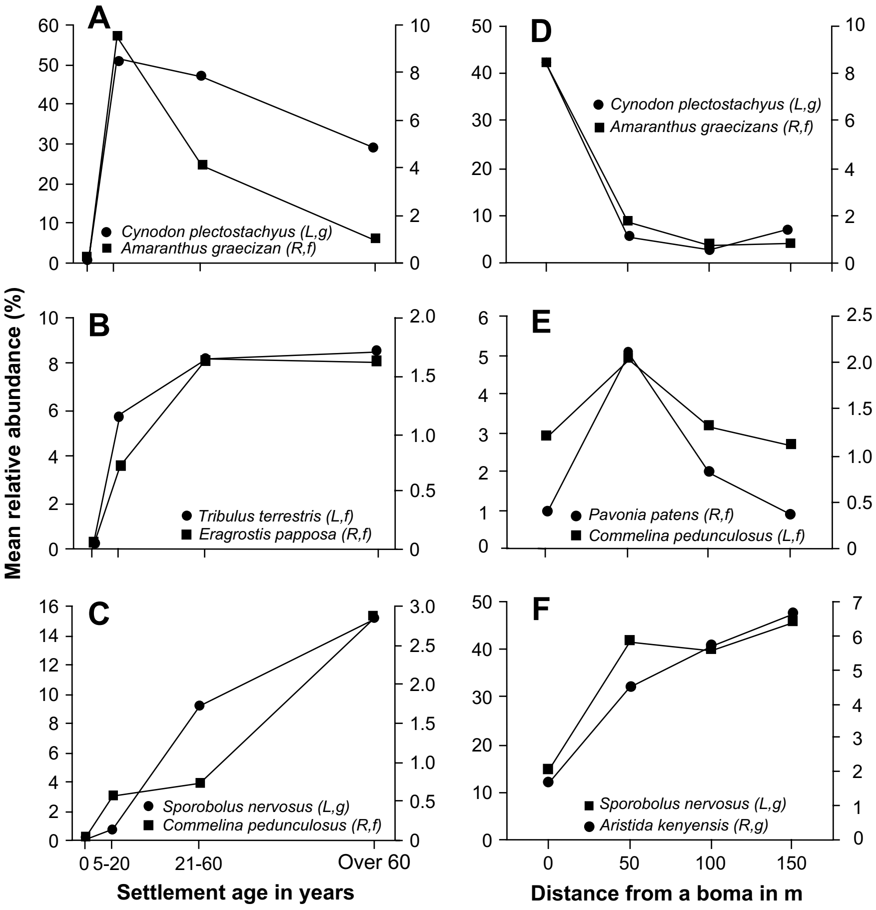

Fig. 4. Temporal (A–C) and spatial (D–F) variation of representative herbaceous species expressed as percent relative abundance on old bomas sites of varying age. Percent relative abundance is expressed as the ratio of total biomass of a species on all bomas in an age class over the total herbaceous biomass for all the bomas of that age class. Age classes were: Occupied ($n = 6$); 5–20 years ($n = 11$); 21–60 years ($n = 11$) and 60+ years ($n = 10$). Offsite biomass was calculated separately as a function of distance from boma. L = left and R = right axis; g = grass and f = forbs species.

had significant effects ($F_{2,1437} = 6.91$; $P > 0.001$; df = 2). A post hoc analysis by depth showed that soil nutrients were different only between shallow soils (0–10 cm) and deeper soils ($P < 0.001$). Depth was more influential onsite ($F_{2,157} = 8.227$; $P > 0.001$) than offsite ($F_{2,157} = 3.256$; $P = 0.04$). Focusing on the effects of shallower soils, a two way post hoc ANOVA by boma age and location showed a significant difference by location ($F_{1,480} = 7.791$, $P = 0.005$). Nutrients concentrations in shallow soils on young bomas (5–20 years old) fell significantly by middle age (21–60 years old), but little thereafter. Phosphorus declined faster than other elements beyond middle age (Fig. 6A). These trends were supported by decomposition of the analysis to the elemental level. A one way ANOVA revealed a significant boma age effect for nitrogen ($F_{2,13} = 5.88$, $P = 0.009$), potassium ($F_{2,13} = 4.28$, $P = 0.03$) sodium ($F_{2,13} = 5.64$, $P = 0.01$) and organic carbon ($F_{2,13} = 7.04$, $P = 0.005$), but not for phosphorus or magnesium.

We calculated element concentration ratios to show their values on and offsite. Values greater than one means that concentrations of nutrients were higher onsite than offsite soils. Phosphorus and organic carbon were 9 times higher on than offsite, nitrogen and potassium 4 times, and magnesium 1.6 times more concentrated onsite than offsite in young bomas sites. The difference fell as bomas aged. Only potassium was less concentrated onsite than offsite for all boma ages. Levels of phosphorus and potassium (4 times), nitrogen and organic carbon (1.5 times), were still elevated onsite 60+ years after abandonment. For the two oldest settlements included in the 60+ age class, sodium, phosphorus, nitrogen and organic carbon were still 2–4 times higher than in the control sites a century or more later. Nitrogen, organic carbon and magnesium levels dropped most rapidly as bomas aged, while phosphorus declined the slowest (Fig. 6A).

6. Discussion

6.1. Plant succession on pastoral settlements

In Amboseli, when first abandoned, bomas contain only a dung layer above the mineral soil, with no plants present, except for remnant shade trees conserved by pastoral families. Herbaceous biomass increases steeply once the heavy dung concentration begins to mix with soil. Within five years of abandonment herbaceous biomass exceed levels at the periphery of the impact zone (Western and Dunne, 1979), and doubles within twenty years, then fall steadily to the levels at the edge of impact zone over the ensuring century. In Amboseli, abandoned bomas seen from the air or hilltop after rain, are visible as rich green arenas dominated by *C. plectostachyus* for 20–50 years or so (Muchiru, per. obs.). Even though livestock trampling and grazing reduces herbaceous standing biomass on and around the boma during occupation (Western and Dunne, 1979), our results show that Maasai bomas in Amboseli support a far higher standing crop than the surrounding savanna for a century or more.

Increased species richness on abandoned settlements mirrors the increase in biomass. Overall, onsite species richness increases

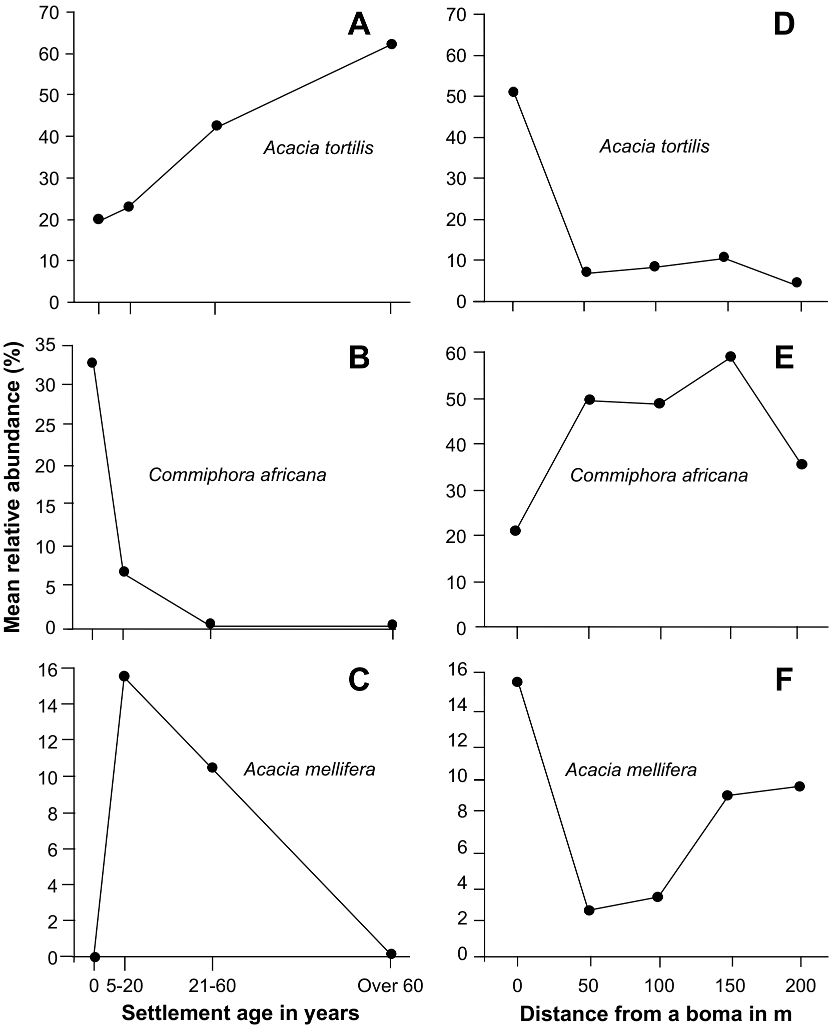

Fig. 5. Temporal (A–C) and spatial (D–F) variation in the relative abundance of representative woody species on old bomas of varying age. Percent relative abundance is expressed as the ratio of total biomass of a species on all bomas in an age class over the total woody biomass for all the bomas of that age class. Age classes were: Occupied ($n = 6$); 5–20 years ($n = 11$); 21–60 years ($n = 11$) and 60+ years ($n = 10$). Offsite biomass was calculated separately as a function of distance from boma. L = left and R = right axis.

from zero on recently abandoned settlements to a peak at 60+ years (Fig. 3), then declines in the oldest settlements. The decline in the oldest settlements at the limit of our age spread likely reflects the shading effects of maturing *A. tortilis*. If so, it may take the death of these large, long-lived trees before herbaceous richness on ancient abandoned settlements rises to background levels.

In Amboseli, when building bomas, pastoralists clear trees 20 cm basal diameter and less within 150 m of the boma (Fig. 2C). After abandonment, trees slowly colonize the site. *A. tortilis* eventually reaches biomass dominance over grasses and forbs in old-aged settlements (Figs. 1 and 2). The dominance of *A. tortilis* on old settlements has been reported in other locations. In South Africa, *A. tortilis* assumes dominance on old settlement sites in Burkea woodlands (Blackmore et al., 1990) and in Kenya on old bomas in Turkana, northern Kenya (Reid and Ellis, 1995) and in the Laikipia Highlands (Young et al., 1995). However, old bomas do not support *A. tortilis* in the Mara, southwestern Kenya, (Muchiru, per. obs.), an areas outside its ecological range. The abundance of *A. tortilis* on old settlement sites is related to feeding habits of livestock, especially goats. Pods and seeds are eaten by goats and defecated in the boma at night. Herders also harvest pods and seeds to feed young goats retained near the settlement during dry seasons. In Turkana, *A. tortilis* pods are similarly reported to be a source of nutrients for goats (Reid and Ellis, 1995). However, pod consumption depends on the availability of this species in the different ecosystems.

Unlike mature *A. tortilis* retained for shade on occupied settlements (Muchiru, 1994), herbaceous plants are totally destroyed during the life of a settlement. Colonization must therefore start from seeds or stolons after abandonment. The regeneration of other woody species must also start from seeds or in, the case of *Balanites*, from fence cuttings (Muchiru, per. obs.)

Several plants species can serve as useful indicator species of old bomas sites. These include grass and forb ‘boma specialists’ such as *A. graecizans* L., *C. plectostachyus* (Fig. 4D) and also *T. terrestris*, found almost exclusively onsite on abandoned settlements. Other species are more abundant at intermediate distances from bomas, others still at the outer reaches of the impact zone (Fig. 4E and F). *T. terristries* tends to invade bare ground at the start of boma colonization. *C. plectostachyus* occurs almost exclusively on or immediately around abandoned bomas or under trees where livestock rest around the settlement. Ordinarily, *C. plectostachyus* is confined to Pleistocene and Holocene lake beds (Edward and Bogdan, 1951). The one exception to this limited distribution is its ubiquitous occurrence on old boma sites (and other livestock concentration points) over much of the pastoral lands of eastern Africa (Stelfox, 1986; Muchiru, 1994; Young et al., 1995; Augustine, 2003).

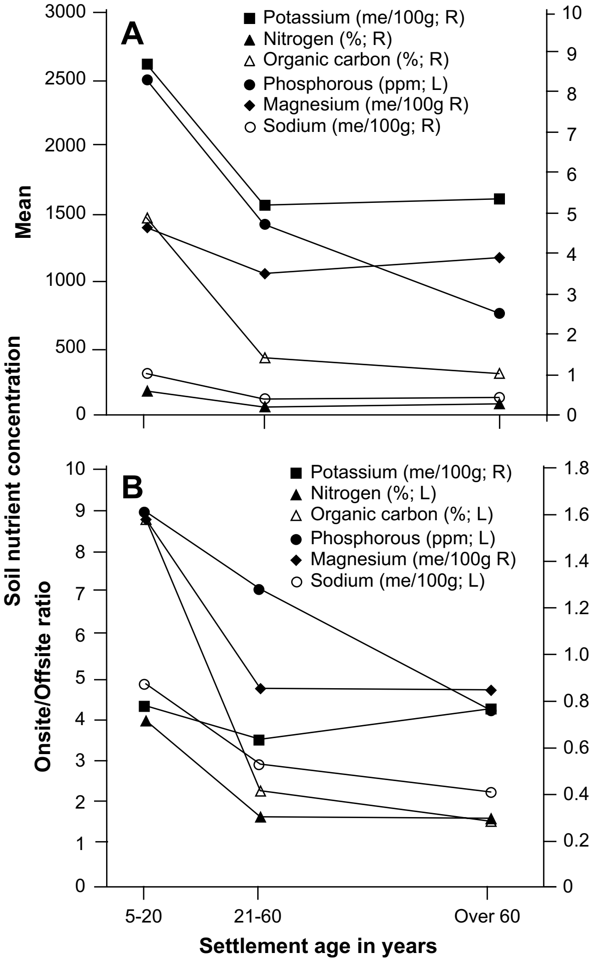

Fig. 6. Concentration of soil nutrients in relation to settlements age class. Soil samples were collected on randomly selected bomas from each class. Age classes were: 5–20 years ($n = 11$, sampled bomas = 7); 21–60 years ($n = 11$, sampled bomas = 9) and 60+ years ($n = 10$, sampled bomas = 8). Soil samples were collected onsite and offsite for twelve settlements to a depth of 0.5 m. Only samples from the top 10 cm were included in the analysis. L = left and R = right axis.

Its predilection for old bomas has in fact earned it the name of manyatta grass, manyatta being the Maasai name for special bomas built by young men during warriorhood.

Forbs such as *A. graecizans*, *T. terristries*, *Datura stramonium* L. and *Zaleya pentandra* Burm. are also relatively good indicators of early succession and gradually disappear as other species, such as *S. pallida* and *B. ciliaris*, invade settlements in middle age. *Gynandropsis gynandra* (L) is relatively abundant on middle aged bomas. This species is also a common forb on old bomas in the Laikipia district of Kenya (Young et al., 1995).

It is likely that the colonizing forbs tolerate or require the high levels of nitrogen, potassium, organic carbon and phosphorus found in the soils of recently abandoned bomas (Fig. 6). In terrestrial ecosystems, nitrogen is generally recognized as the primary nutrient limiting plant growth (Vitousek and Howarth, 1991). This is confirmed by fertilization experiments in Laikipia (Augustine et al., 2003). In some grassland, however, phosphorus has been shown to limit plant growth (Penning de Vries et al., 1980; Donaldson et al., 1984; Synman, 2002). Whatever the limiting element, it is likely that the longevity of boma patches in the savannas stems from elevated soil nutrients deposited during the occupation phase. Longevity may be boosted yet further by the late invasion of long-lived *A. tortilis*, a N-fixing species (Vitousek and Howarth, 1991).

6.2. *Islands of fertility and biomass in savanna landscapes*

Abandoned bomas are rich islands of fertility and biomass dotting savanna ecosystems in eastern Africa. We speculate that old settlement sites are important nutrient-rich islands that have a major influence on plant and animal structure and their community dynamics in nutrient-poor savannas.

From a plant perspective, the nutrient-rich islands of old bomas sites are colonized by a succession of grasses and forbs over many decades. Although we did not measure productivity directly, plant production is likely to be boosted by nutrient enrichment and mirror the elevated biomass of old settlement sites.

From an animal perspective, the nutrient enrichment of old settlements is also likely to increase plant palatability. In a wetter savanna north of Amboseli, Stelfox (1986), for example, found boma herbs richer in crude protein and poorer in fibre than background levels. Boma plants are thus likely to be both more productive and nutritious for herbivores (Muchiru et al., 2008). *C. plectostachyus*, which accounts for nearly 80% of the grass biomass for the first 50 years of colonization, is a preferred forage species among the Maasai (Muchiru, per comm.), a valuation supported by qualitative analysis of Kenya grasses (Edward and Bogdan, 1951). This species, can, however, reach concentrations of cyanide poisonous to cattle where nutrient concentrations are high around water points in Amboseli (Georgiadis and McNaughton, 1988). *S. nervosus* and *Kyllinga alba*, which become subdominant grasses after 50 years of colonization, are also highly nutritious grasses like *C. plectostachyus* (Edward and Bogdan, 1951). The leaves of *Acacia* trees on older bomas also provide richer nutrition for browsers than leaves of other savanna tree species (Coppock et al., 1987; Tolsma et al., 1987; Reid, 1992; Scholes and Archer, 1997).

The enhanced biomass and higher quality of grass and tree foliage on old settlement sites have recently been documented to be significant factors in large mammal ecology and conservation. We and others (Young et al., 1995; Augustine et al., 2003; Muchiru et al., 2008) found that wildlife and livestock spend more time on old bomas compared to the surrounding landscape. In Amboseli, ungulates prefer abandoned bomas during the dry season (Muchiru et al., 2008), similar to the patterns found in Laikipia (Young et al., 1995; Augustine, 2003). Early successional bomas provide grazing lawns that attract a range of grazers. Later successional bomas attract a number of browsers, including giraffe and elephant as well as shade-seeking ungulates (Muchiru et al., 2008). In addition, grazers may also prefer early successional bomas sites because the habitat here is relatively open and thus predators are readily visible from these patches, as was observed for impala in Laikipia (Augustine, 2002). The heavy herbivore traffic in turn deposits large amounts of dung, which is likely to extend the duration of boma sites as nutrient hotspots and perpetuate their impact on the savannas for decades or centuries (Blackmore et al., 1990). These authors suggest that these *Acacia* patches on old settlements are maintained, perhaps indefinitely, by continual nutrient deposition by ungulates selecting *Acacia* patches over woody plants in the surrounding nutrient-poor *Burkea* savanna. This is borne out by *Acacia* patches thriving on settlement sites abandoned 700 years ago (Blackmore et al., 1990). In Laikipia, ungulate deposition of N in dung and urine was found to exceed total N consumed offsite by 43% (Augustine, 2003).

7. General conclusions

A number of tentative general conclusions are drawn from studies of the impact of abandoned settlements on savanna ecosystems.

First, occupied settlements tend to reduce woody plant abundance in savanna bushland and woodlands. Both individual settlements and clusters of settlements on sites preferred for settlement by herders (Western and Dunne, 1979) are clearly visible as a patchwork of openings in the woody cover that dominates many unoccupied East African savannas.

Second, these patches, typical fairly devoid of vegetation, soon become hyper-productive grasslands once abandoned. The resulting high-fertility patches persist for decades. A typical pastoral area will support many old boma sites.

Third, settlements tend to be asynchronously used by traditional pastoralists and span a wide range of ages and successional stages. Some abandoned settlements support grass, others grass and shrub mixes, still others small to large trees. Given that historically virtually all of the savannas were occupied by pastoral peoples (Harris, 1980), we consider that settlement activity and succession to be an important force creating the bush-grass mosaic and patch dynamics of the savannas.

Fourth, the quantitative importance of pastoral settlements on the Amboseli landscape can be shown by calculating the impact area of settlements over the course of a century, the period of most distinctive boma imprint. Based on a study of all settlement activity in the Iremito region between 1969 and 1970, a period of relatively traditional use (Western, 1973), we calculate that 9 new settlements were established annually in the 157 km^2 study area. Assuming an impact zone with a radius of 225 m (Western and Dunne, 1979), the area affected will be 0.126 km^2. Computed over the course of a century, the total impact zone of new settlements, assuming no settlement reoccupation, amounts to 113 km^2 or 72% of the study area. Even allowing for resettlement of former sites (68% in this study), the impact of pastoral settlements amounts close to 23% of the study area. Given that the impact on woody vegetation on old settlements extends well over a century, it is likely that impact of pastoral settlements on the savanna is one of the major factors structuring vegetation composition and dynamics.

Fifth, abandoned settlements create nutrient hotspots in the savannas, boosting primary productivity and nutrient quality for several decades, possibly a century or more. This suggests that pastoral settlement cycles are major driving force in nutrient redistribution in the savannas and may persist as hotspots in national parks and ranchlands long after the demise of traditional migratory pastoralism.

Finally, fluctuations in livestock and human populations over time and changes in their movement patterns due to stochastic factors such as climate, warfare and disease, undoubtedly added to complexity to boma succession. This complexity historically must have been a strong driving force in the macro-ecology and patch dynamics of East African savannas. The traditional high mobility of pastoralism is, however, rapidly giving way to sedentarization (Salzman, 1980; Galaty, 1994). Sedentarization is likely to reduce savanna patchiness and ultimately the abundance and diversity of wildlife.

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