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ORIGINAL PAPER

How pastoralism changes savanna vegetation: impact of old pastoral settlements on plant diversity and abundance in south-western Kenya

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Abstract For centuries, pastoralists have influenced savanna ecology through their construction of settlements, traditional movement patterns in search of forage, water and safety for their livestock. Construction of settlements initiates localised changes in the vegetation due to clearance of vegetation at construction and collection of construction materials. During the occupation period a lot of dung is deposited in and around settlements. When pastoral families abandon settlements and move away, they leave behind mud huts and livestock corrals surrounded by fences. These sites become nutrient-rich patches supporting a different abundance and diversity of plants and large mammals compared to the rest of the savanna. This study aimed to broaden our understanding of how pastoral land use influences plant diversity in East African savannas. Past work on the effects of settlements has been done in dry places (<600 mm rainfall) with relatively poor soils. To complement and extend these studies, we selected a contrasting site with high

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rainfall and rich soils in the Mara ecosystem of south-western Kenya. We sampled the occurrence of different plant species along transects radiating from 28 settlements abandoned by pastoralists and ranging in age from 2 months to 48 years on two different soil types. Mean plant species richness and abundance peaked at intermediate distances, 12.5 and 25 m from the edges of settlements. We recorded a total of 210 plant species during the study, 65 of which occurred only within the impact ring of the abandoned settlements. The effects of settlements on plants were stronger on shallow sandy soils than on deep clay soils. Our findings show that abandoned settlements were key sites for regeneration and replenishment of shrubs harvested by the Maasai, but support few other plants of biodiversity value. These unique habitat patches in the savanna ecosystem are under threat as pastoral Maasai become increasingly sedentary and as wildlife conservancies are established, thus reducing the number of abandoned settlements. In essence, the Maasai, by changing their traditional lifestyle, will reduce these nutrient hotspots and hence landscape heterogeneity and biodiversity.

Keywords East Africa · Serengeti-Mara ecosystem · Maasai · Livestock enclosures · Species response

Introduction

Pastoral people can profoundly influence savanna landscapes. By grazing savannas heavily, pastoral livestock can convert grasslands into woodlands or scrublands (Roques et al. 2001; Tobler et al. 2003). Heavy burning by pastoralists can shift woody landscapes into open grasslands (Lamprey and Waller 1990). These changes are often patchy in nature, because pastoralists concentrate their livestock around settlements (Muchiru et al. 2008; Reid and Ellis 1995) and water points (Georgiadis 1987; Ogutu et al. 2010, 2014).

In East Africa, many pastoral people still live in temporary settlements, moving frequently within the system, as often as once a month to once in several years (Muchiru et al. 2008; Reid and Ellis 1995). Pastoralists move when grazing areas are exhausted, seasonal water points dry up, tick loads or other disease risks for their livestock become too high, leaving areas that are unsafe from other raiding tribes or for social reasons (Gulliver 1975; McCabe 1994; McCabe et al. 1999). While they live in settlements, pastoral families cut wood for building structures, fuel wood and thorn fencing, leaving a measurable impact ring about 150–175 m around their settlements (Western and Dunne 1979). Pastoralists corral their livestock each night within a thorn enclosure and thus leave behind circular patches of dung, fencing and huts when they move.

These old settlement or ‘boma’ sites have strong impacts on soils, plants and wildlife. Nutrient levels in soils in two dry savannas in Kenya remained elevated more than 40–100 years (Augustine 2003; Muchiru et al. 2009, 2008) after pastoral families had abandoned their settlements. In central Kenya this redistribution of nutrients has no long-term effect on nitrogen distributions but significantly concentrates phosphorus over the long term in old settlement sites, thus probably ‘mining’ phosphorus from the surrounding landscape (Augustine 2003). After abandonment, vegetation on old bomas remains distinct for decades. Old settlements pass through several stages of regeneration over time, from grassy patches to shrub and then tree dominated areas in the dry Amboseli ecosystem of southern Kenya (Muchiru et al. 2009). In wooded landscapes, old settlements create open, grassy patches that remain open for decades (Young et al. 1995). Many species of wildlife cluster differentially on old boma sites in dry savannas, probably preferring to graze on the more nutritious grasses that grow in the nutrient-rich soils (Muchiru et al. 2008; Young et al. 1995). Due to the contrasting forage preferences of their constituent species, multiple species associations of wildlife and livestock feeding on old boma sites can have differential effects on the heterogeneity of savanna landscapes (Veblen and Young 2010). Thus, it is plausible that pastoral settlements may be shaping the structure of savannas over much of East Africa, and even parts of southern Africa (Blackmore et al. 1990). Not surprisingly, recent studies have shown bird species richness and abundance to peak near abandoned and seasonal pastoral settlements (Morris et al. 2009; Soderstrom and Reid 2010). High nutrient concentrations near these settlements elevate the availability or accessibility of invertebrates for birds, especially insects from the orders Diptera and Coleoptera (Soderstrom and Reid 2010). Treeless glades originating from isolated bomas have been shown to have pronounced edge effects on the growth and size structure of trees together with the distribution of arboreal arthropods and geckos, thus creating large-scale spatial heterogeneity in a landscape with otherwise uniform tree species composition (Donihue et al. 2013).

Despite past research, our ability to estimate the impacts of pastoral settlements on savannas over a broad range of biophysical conditions remains limited. All previous studies on old bomas have been in dry ecosystems, principally on nutrient-poor soils. We hypothesised that bomas would have less impact on soil nutrients, plants and wildlife in wetter savannas and on nutrient-rich rather than on nutrient-poor soils. We reasoned that wetter systems will have more rapid nutrient leaching and cycling rates, causing the impact of old bomas to weaken rapidly over time (our ‘nutrient disappearance’ hypothesis to be indirectly tested by comparing our results with findings of other studies conducted in drier ecosystems). In addition, nutrient ‘hotspots’ in old boma soils may appear ‘cool’ biologically when they are set in a matrix of already rich soils, with cascading effects on plants and other organisms (our ‘context matters’ hypothesis to be indirectly tested by comparing patterns on two soil types in this study). To find a good wet and rich soil to contrast to previous studies, we used soil and rainfall maps to identify the place in East Africa where we thought the impacts of settlements would be most different from those of previous research (Table 1). One such ecosystem is the northern part of the Serengeti-Mara ecosystem of south-western Kenya, where rainfall is high and soils are mostly deep clays of recent volcanic origin, which are nutrient rich. We also found settlements in the same ecosystem on nearby sandy and clay soils, which allowed us to make a direct comparison of the effect of settlements on plants located on soils with different textures and nutrient status. We then set out to measure the influence of old bomas on plant abundance, diversity and composition, which is the scope of this paper.

Materials and methods

Study area

The study took place in the northern part of the vast Serengeti-Mara ecosystem that crosses the Kenya and Tanzania border (Sinclair and Arcese 1995), along the Olare Orok River at the northern edge of the Maasai Mara National Reserve (Fig. 1, 1°16′–1°23′S, 35°7′–35°11′E). The ecosystem is home to the greatest migrating herds of ungulates on Earth (Sinclair 1995). The Mara plains are blanketed by extensive flows of Tertiary phonolitic

Table 1 Climate and soil characteristics for the study sites in Laikipia (Augustine 2003; Young et al. 1995; Veblen and Young 2010), Amboseli (Muchiru et al. 2008, 2009) and Mara (this study)

Climate and soil characteristic	Laikipia	Amboseli	Masai Mara
Annual precipitation (mm)	548	576	1,018
Annual evapotranspiration (mm)	1,540	1,514	1,447
Annual mean max. temperature (°C)	25.8	28.6	26.4
Annual mean min. temperature (°C)	11	16.3	12.5
Soil type	Vertisol	Luvisol	Vertisol
Sand (mass%)	28	66	20
Silt (mass%)	22	18	20
Clay (mass%)	50	16	60
FAO texture class	Fine	Medium	Very fine
Available water capacity (vol.%)	12	11	13
Cation exchange capacity (cmolc/kg)	11.1	35.2	35
pH measured in water	6.1	6.7	7
Total carbonate equivalent (g/kg)	0	3	5
Total C (g/kg)	13.9	10	20
Total N (g/kg)	1.67	0.91	1.23

Climate data were obtained from ILRI database 2014, and soil data from Batjes and Gicheru (2004)

lava (Williams 1964). Low-lying areas have black cotton soils, which are dark, nutrient-rich, deep clay vertisols with impeded drainage, while lighter shallow sandy loams occur on hilltops (Lamprey 1990). Consequently, bulk density decreases, whereas clay content, nitrogen and water holding capacity of soils all increase from hilltops towards low-lying locations (McNaughton 1985). Altitude varies between 1,550 and 1,650 m a.s.l. The landscape is open or lightly wooded with forests occurring along rivers and seasonal watercourses. *Croton dichogamus* shrubs are scattered mostly on hill sides and hill tops with *Acacia gerrardii* bushland communities on the northern border of the study area (Lamprey 1990). The most abundant grass species are *Themeda triandra* and *Eragrostis tenuifolia*.

The short rains usually fall in November–December but may continue and merge with the long rains in March–June; the dry season lasts from July to October. In the dry season there are stagnant pools along rivers in the area, but they dry up completely during droughts. Our study area receives about 1,000–1,341 mm annually, dropping to 800 mm in the Loita plains to the northeast (Ogutu et al. 2011).

Pastoral land use

Neolithic pastoral groups began herding cattle, sheep and goats in this ecosystem more than 2,000 years ago (Marshall 1990). Maasai people are thought to have moved into this area around the 1,750 s (Lamprey and Waller 1990). The 1890 rinderpest pandemic killed most ruminant animals, including most of the wildlife and Maasai livestock herds (Lamprey and Waller 1990). This was followed by a severe epidemic of smallpox. From 1950's onwards, the Purko section of the Maasai began to re-occupy the Mara plains (Lamprey and Waller 1990; Lamprey and Reid 2004). In the early 1960's dense *Acacia–Commiphora* bushland and tsetse flies were almost eliminated by a concerted effort by the Maasai to

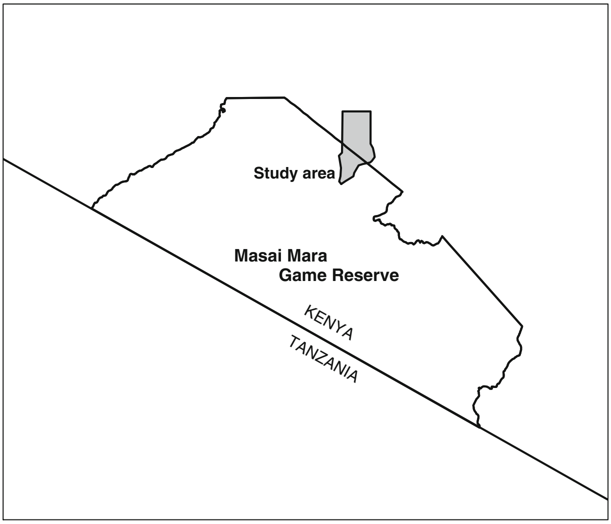

Fig. 1 Study area

remove disease and open up grazing areas through repeated burning (Langridge et al. 1970). Since then, the number of settlements in the area has increased by 4–7 % per annum, and since 1977, the numbers of cattle, sheep, and goats have also increased (Ogutu et al. 2011, 2009). Recently, households started to split in anticipation of land privatisation or sub-division, creating more numerous but smaller bomas, and families had cultivated and fenced about 1 % of the land by 2002 (Reid et al. 2003). The Maasai land owners in the Mara group ranches in our study area established the first community wildlife conservancy through a partnership with private investors in tourism in 2006 and several others thereafter. The landowners voluntarily vacate their land for wildlife conservation and settle elsewhere on the landscape in return for a monthly land rent from the tourism operators (Norton-Griffiths et al. 2009; Ogutu et al. 2009). In the 1980's, pastoral groups leased land to commercial wheat farmers in the wet season calving grounds of the resident wildebeest population (Homewood et al. 2001; Serneels and Lambin 2001).

Study design

Settlement locations were established by mapping all the abandoned and occupied, temporary and permanent settlements along the edge of the Mara reserve, but away from the centre of Talek town from March to May 2001. The information recorded for each settlement included: period of use, livestock and human numbers, diameter of the boma, residence time, time since abandonment, reason for selecting and abandoning the site, resettlement and burning history, landscape position, soils and distance to the nearest river (Table 2). The team identified 106 settlements in the study area of about 40.8 km^2 or 2.6 bomas km^{-2}, abandoned between 1953 and 2001.

Permanent settlements had two nested circular fences, an outer fence of thorn scrub to repel predators and an inner fence of poles to keep thorns outside the boma and allow people to walk barefoot within the boma, with livestock separated by species in corrals inside the inner fence and huts built between the fences. Temporary settlements were

Table 2 Physical characteristics of study settlements, livestock population characteristics at the settlements and where settlements were burned or resettled after abandonment and reasons for selecting or abandoning settlement sites

Characteristic	Temporary settlements			Permanent settlements		
	N	Mean	SE	*N*	Mean	SE
Diameter (m)	70	36.2	1.39	36	44.8	2.16
Number of cows	63	630	58.6	36	344	38.3
Number of sheep and goats	18	378	86.2	28	220	35.3
Number of people	67	11.6	0.829	34	19.2	2.01
Number of houses	57	4.37	0.298	29	4.31	0.455
Altitude (m)	69	1,599	3.01	36	1,617	2.86
Period occupied (years)	70	0.982	0.097	36	4.18	0.365
Time since abandonment (years)	70	14.2	0.918	36	15	1.43
Burned after abandonment						
Yes	15			8		
No	14			17		
Not known	41			11		
Resettled						
Yes	28			5		
No	38			31		
Not known	4			0		
Why site was selected						
Water, pasture	43			12		
Water, pasture after burning	6					
Water, pasture, salt lick	10			10		
Water, pasture, no tsetse	4			4		
Hygienic reasons	2					
Reserve border extension	2			8		
Escaping of cattle rustlers/fighting	1			2		
Not known	2					
Why site was abandoned						
Rains started, moving back to permanent settlements	25					
Drought, no water/pasture	16			6		
Wildlife disturbance	8			4		
Moving back to family	7			5		
Cattle rustling/fighting	3			3		
Family breakup	3			3		
Tsetse disturbance	2			3		
Hygienic reasons	1			7		
Inside the reserve	2					
Floods				4		
Other/not known	3			1		

simpler with one fence. Mostly the temporary settlements were built during the dry season close to water and in areas of better pastures and/or close to saltlicks. On average, permanent settlements supported 344 cattle, 220 sheep and goats, 19 people; were 45 m in diameter, active for 1–10 years, and located near rivers. Pastoral families abandoned bomas for many reasons (Table 2), but principally because of excessive dung accumulation, lack of pasture or water, to live near relatives, and to avoid disturbance by wildlife. About a third of abandoned settlements were burned several months after the family moved. We found sites that had been abandoned between 2 months and 48 years.

Out of 106 abandoned settlements, we selected 28 for further study. The selected sites were evenly distributed across the study area and no site adjacent to an occupied settlement was included to avoid confounding with the effects of the active settlement (Porensky and Young 2013). Twelve of the selected bomas were on shallow, sandy soils and 16 on deep clayey soils. Settlement characteristics were broadly similar on the two soil types. However, the settlements on shallow sandy soils were mostly situated closer to hilltops and were younger (9.9 ± 2.0 years) than those on deep clayey soils (19.6 ± 2.5 years). In the analyses, we compared plots according to soil type, settlement age and distance to the nearest settlement site. When comparing plots between soil types, we only used settlements aged between 9 and 22 years to minimize the effect of the age difference between settlements on the two soil types (sand: 13.5 ± 1.74 years, deep clay: 15.8 ± 1.01 years). There were 8 settlements on shallow sandy soils and 13 on deep clayey soils that fell within this similar age range. However, for the ordination analyses, we used all the 28 settlement sites.

At each selected settlement, we placed a 200-m transect extending from the settlement based on the following criteria: (1) all points on the transect were more than 300 m away from any other settlement, and (2) the transect, as it extended away from the site, remained in a similar topographic position and broad vegetation type as the settlement (i.e., if the site was at the edge of shrubs, the transect stretched along the edge as well). We placed seven, 100 m^2 plots along each transect. The first plot, shaped like a pie, was placed on the circular settlement. The apex of this plot was at the centre of the settlement and the wide end on the settlement edge, facing the direction of the transect. The rest of the plots were 10 m × 10 m with their midpoints placed at 12.5, 25, 50, 100, 150 and 200 m from the edge of the settlement. Plant cover and species composition were measured using a pin frame (McNaughton 1979), with 2.1 mm pins at a 65° angle, randomly placed within the plots. Plants intercepting pins were counted and the species name recorded. We used 8 pins per pin frame, a number of pin drops that efficiently captured the abundance of the dominant grass species based on a running means test (Mueller-Dombois and Ellenberg 1974). Also, based on the running means test, we used more pin frames when sampling of plots with less grass cover. A maximum of 16 pin frames (128 pins), for example, were used in sampling of plots with less than 50 % plant cover. After sampling, we carefully searched each plot for any additional rare species that may have been missed. Percent cover of the rare species was visually estimated and recorded. A total of 1,638 pin frames were used in the whole exercise for a total of 14,242 pins and 75,609 plant interceptions. We classified and recorded the type of micro-habitat sampled by each pin frame for use in ordination analyses. These habitats were classified as open and flat, water related (seasonal collection of water due to flooding or depression), presence/absence of bush cover, presence/absence of erosion or rocks and nutrient enrichment (an old termite mound or old resting place for livestock). Herbaceous plant height (or leaf table) was measured by allowing a Styrofoam sheet, 17 cm × 26 cm, weighing 4.5 g, to come to rest on the herbaceous canopy (McNaughton 1976). The amount of dung deposited on the settlements and their vicinity was calculated using the following formula (King et al. 1984) $\sum N_x P_x W_x I(1 - D_i) D_a$, where N_x is the number of livestock, P_x is the proportion of different livestock types (calves, steers/heifers, bulls, cows and sheep/goats), W_x is the body weight, I is the fodder intake rate, D_i is the amount of fodder consumed by the different livestock species grouped by age and D_a is the number of days the settlement was occupied (Table 3). Each plot was assigned a wetness index, calculated from the number of pins hitting a place with or without a water puddle in the wet season.

Statistical analyses

Variation in the number of grass and shrub species (richness) with distance from abandoned settlements, soil type (clay or sand) and their interaction was modelled using a Poisson regression model with a log link function in the SAS GLIMMIX procedure (SAS Institute 2012). The interaction between distance and soil type was partitioned into its simple effect slices to compare expected species richness between the two soil types at each sampling distance from a boma. We used the one-sample Kolmogorov–Smirnov and Levene's tests to test shrub cover and the number of hits/pin for each plant species or group of plant species for normality and homogeneity of variances. If the assumption of normality and/or homogeneity of variances was violated, then shrub cover was square-root transformed whereas the number of hits/pin was $\log_{10}(x + 1)$ transformed for use in parametric linear regression analyses and one-way ANOVAs. For all the transformed variables we report results on the original scale. When the data did not satisfy the assumptions of parametric tests even after undertaking the transformations, then we used a non-parametric Mann–Whitney *U* test. These latter analyses were performed in SPSS Release 11.0.1 (SPSS Inc. 2001). Canonical Correspondence Analyses (CCA, (Ter Braak 1986, 1994) was used to analyse the influences on plant species of the amount of dung, herbaceous cover, shrub cover, herbaceous height, settlement age, soil type, landscape position, dryness index and grazing intensity. CCA and TWINSPAN were done with PC-ORD Version 4.20 (McCune and Mefford 1999) including all the species and all the default settings (Gauch and Whittaker 1981; Hill 1979).

Results

Of the 210 different plant species recorded, the highest diversity occurred near the edge of settlements, but not within or far from settlements. Mean plant species richness around settlements abandoned between 9 and 22 years peaked at intermediate distances of 12.5 (mean ± 1 SE, 22.8 ± 1.60 species) and 25 m (23.0 ± 1.32 species) from the edge of settlements (Fig. 2). We found the least number of species on top of the old settlements (18.1 ± 1.08).

When we separated settlements by soil type, plants responded to settlement disturbance more strongly on shallow sandy than on deep clayey soils (Fig. 2). Overall species richness was similar on sandy and clay soils on top of and at 12.5 m from abandoned settlements, but was significantly higher on sandy than on clay soils beyond 12.5 m, most especially at 25, 50 and 100 meters from abandoned settlements, (Table 4). Grass species richness showed the strongest quadratic relationship with distance from settlements on shallow sandy soils (quadratic curve fit, $p < 0.001$). Grass species richness was significantly higher on sandy than on clay soils at 25 and 50 m from abandoned settlements, while shrub richness did not vary significantly between the two soil types, but was marginally higher on sandy than on clay soils at 50 and 150 m (Table 4).

We performed a stepwise multiple linear regression of species richness on a suite of variables using backward elimination with an F-to-enter criterion of 0.05 ($R^2 = 0.398$,

Table 3 The percentage composition, average body weight, forage intake rate and digestibility of forage eaten by each age and sex class of a typical Masai cattle herd

Age/sex class	Typical cattle herd composition (%)[a]	Body weight (kg)[a]	Intake rate (% of body weight)[b]	Forage digestibility (%)[b]
Calves	18	70	2.5	55
Steers and heifers	39	175	2.5	55
Bulls	7	350	2.5	55
Cows	36	250	2.5	55
Sheep and goats		35	3.0	60

[a] King et al. (1984), M. Koriatah (pers. comm.) Koyiaki Group Ranch, Narok District

[b] D. Romney (pers. comm.) International Livestock Research Institute

$F_{5,141} = 18.6$, $p < 0.0001$) to establish the micro-habitat variables influencing plant species richness. Soil type ($p < 0.001$), habitat diversity ($p = 0.006$), herbaceous cover ($p = 0.001$), openness ($p = 0.016$) and dryness ($p = 0.049$) were all significantly correlated with plant species richness on and around settlements for the intermediate aged plots according to the relation: species richness = 1.61(0.254(SE)) + 0.0825(0.018) × soil-type + 0.0627(0.022) × habitat diversity − 0.027(0.001) × herbaceous cover − 0.00442 (0.002) × % area without shrub cover + 0.00183(0.001) × dryness. Hence, there were fewer plant species where there was more vegetation cover and in open habitats without any shrubs, and there were more species where there were more micro-habitats (Fig. 3). There were more species in drier than wetter sites and more species in sandy than clayey sites.

Different factors affected species richness on each soil type, so we also ran two multiple linear stepwise regressions for each soil type. On deep clay soils, there were more plant species ($R^2 = 0.336$, $F_{3,87} = 14.7$, $p < 0.0001$) where there were more micro-habitats ($p < 0.001$), it was drier ($p = 0.003$) or there were more shrubs ($p = 0.039$). Species richness on such soils can be predicted by: species richness = 0.844(0.097) + 0.105(0.023) × habitat diversity + 0.00279(0.001) × dryness + 0.00727(0.003) × shrub cover. On shallow sandy soils ($R^2 = 0.39$, $F_{4,51} = 8.14$, $p < 0.0001$), there were more species on older than on younger settlements ($p = 0.004$). On sandy soils, there were more species closer to settlements ($p = 0.039$) and where there was less dung ($p = 0.003$). Topographic position of the settlement also affected species richness on shallow sandy soils. Hilltops on sands were less diverse compared to lower areas ($p < 0.001$): species richness = 1.46(0.053) − 0.0455 (0.011) × landscape position + 0.00851(0.003) × settlement age − 0.000159(0.001) × amount of dung − 0.000412(0.001) × distance from settlement.

Although the number of species was about the same on top of and far from the settlements, species composition was very different in these two locations. We calculated the Jaccard similarity index to quantify and assess changes in species composition with distance from settlements relative to the species composition on the settlement site. The similarity index dropped faster with increasing distance on shallow sandy soils, and reached background levels at a distance of 100 m, than on the deep clayey soils on which the index dropped uniformly and more gently with increasing distance. The drop in the similarity index with distance was more marked on the shallow sandy soils than on the deep clayey soils (Fig. 4).

The number of hits per pin is a measure of plant abundance and often of plant biomass. Soil type, vegetation cover and height were the most important factors (multiple

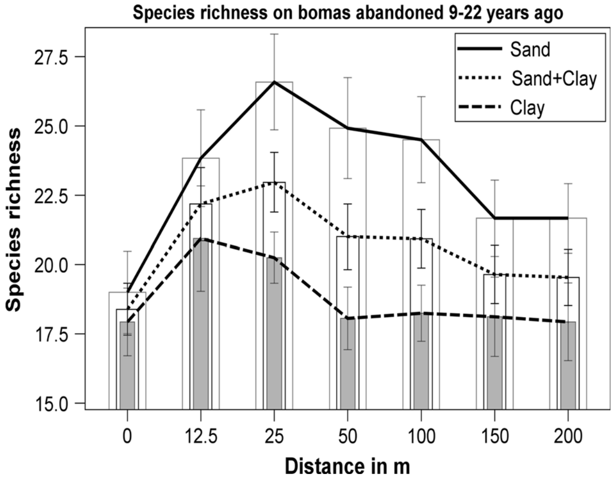

Fig. 2 Species richness along the transect from the settlements abandoned 9–22 years ago

regression, $p < 0.001$) affecting plant abundance. Plant abundance was greater on deep clay than on shallow sandy soils, and on sites with more plant cover and taller plants.

At the species level, we found the following six different patterns of response to old settlements.

1. Species least abundant on settlements. Settlement disturbance depressed the abundance of some species like the grass, *T. triandra* (Fig. 5a). The cover of *T. triandra* was significantly lower on top of the settlements than on all the other plots off the settlements (Mann–Whitney *U* test, $p < 0.001$). Other species that responded to and also grew best away from settlements were *Botriochloa insculpta*, *Chrysochloa orientalis*, *E. tenuifolia*, *Sporobolus stapfianus* and *Aristida adoensis* (the latter species responded this way only on shallow sandy soils).
2. Species least abundant on and at the edge of settlements. *Fimbristylis ovata* was less abundant on and at the edge of the settlement than at 100 ($p = 0.004$), 150 ($p < 0.001$) and 200 ($p < 0.001$) m based on the Mann–Whitney *U* test (Fig. 5b). Abundance of *Dyschoriste radicans* increased farther from the settlement, levelling off at 50 m but at 100 m for *Panicum repens*, *Pennisetum mezianum* showed the same response but levelled off farther from the settlement at 100 m (but only on deep clay soils). *Chloris gayana*, *Sporobolus pyramidalis* and species in the Cyperaceae family were more sensitive to boma disturbance, reaching non-settlement levels only at 150 m from the settlement.
3. Species most abundant on the settlement itself. *Cynodon dactylon* (Fig. 5c) exemplified species strongly dependent on settlements with much higher abundance on than off-settlements (Mann–Whitney *U* test, $p < 0.001$). This species, along with *Cynodon nlemfuensis* Vanderyst, dominated settlements and are often called “manyatta” or “boma” grass. *Justicia calyculata*, *Achyranthes aspera* (on shallow sandy soils) and *Sida alba* (on deep clay soils only) showed similar patterns. On medium-aged settlements on both soils, *Sida ovata*, *Portulaga quadrifida* and *Digitaria abyssinica* were also most abundant on settlements.

Table 4 Comparison of mean species richness between the two soil types at each of seven distance classes from abandoned settlements

Species	Effect	Distance	Soil type	Soil type	Difference	SE	DF	T	P > |T|
All species	Soil × distance	0	Clay	Sand	−0.058	0.089	182	−0.649	0.5174
	Soil × distance	12.5	Clay	Sand	−0.130	0.081	182	−1.609	0.1093
	Soil × distance	25	Clay	Sand	−0.272	0.079	182	−3.450	0.0007
	Soil × distance	50	Clay	Sand	−0.322	0.082	182	−3.900	0.0001
	Soil × distance	100	Clay	Sand	−0.295	0.083	182	−3.565	0.0005
	Soil × distance	150	Clay	Sand	−0.178	0.085	182	−2.090	0.0380
	Soil × distance	200	Clay	Sand	−0.189	0.086	182	−2.206	0.0286
Grasses	Soil × distance	0	Clay	Sand	0.008	0.167	133	0.048	0.9621
	Soil × distance	12.5	Clay	Sand	−0.165	0.138	133	−1.192	0.2355
	Soil × distance	25	Clay	Sand	−0.272	0.134	133	−2.035	0.0438
	Soil × distance	50	Clay	Sand	−0.303	0.135	133	−2.239	0.0268
	Soil × distance	100	Clay	Sand	−0.158	0.136	133	−1.164	0.2466
	Soil × distance	150	Clay	Sand	−0.096	0.141	133	−0.680	0.4979
	Soil × distance	200	Clay	Sand	−0.084	0.147	133	−0.573	0.5676
Shrubs	Soil × distance	0	Clay	Sand	0.613	0.385	133	1.593	0.1136
	Soil × distance	12.5	Clay	Sand	−0.023	0.310	133	−0.074	0.9412
	Soil × distance	25	Clay	Sand	0.125	0.285	133	0.440	0.6606
	Soil × distance	50	Clay	Sand	−0.532	0.305	133	−1.744	0.0835
	Soil × distance	100	Clay	Sand	−0.486	0.302	133	−1.610	0.1097
	Soil × distance	150	Clay	Sand	−0.693	0.373	133	−1.856	0.0656
	Soil × distance	200	Clay	Sand	0.208	0.369	133	0.562	0.5749

4. Species most abundant on or at the edge of settlements. The abundance of *D. abyssinica* (Fig. 5d) decreased slowly away from settlements, levelling off at a distance of 50 m from the edge of abandoned settlements (Mann–Whitney *U* test, *p* value in the range 0.016–0.002) on medium-aged settlements on both soil types. *Dactyloctenium aegyptium* exhibited the same kind of pattern on shallow sandy soils.
5. *Species most abundant at intermediate distances from settlements Commelina* (Fig. 5e) were more abundant at 25 m than at any other distance on shallow sandy soils. Weaker responses to intermediate disturbance, although not always statistically significant, were found for *Digitaria macroblephara*, *Tephrosia pumila* and *B. insculpta* on shallow sands. On deep clay, similar responses were found for *Craterostigma plantagineum*, *D. aegyptium*, *Harpachne schimperi*, *Sida massaica*, *Rhynchosia minima* and *A. aspera* (the latter only on medium-aged settlements).
6. Species not responsive to settlement impacts. *D. macroblephara* on deep clay and *D. abyssinica* on shallow sandy soils did not respond to settlement disturbance (Fig. 5f).

There were three distinct patterns of soil type effect on species response to settlements (Table 5). First: *A. aspera*, *D. abyssinica* and *Oxygonum siniatum* were more abundant on settlements or in their vicinity on sandy soils, as was *S. pyramidalis* on clay soils. Second: *Eragrostis exasperata*, *C. dactylon* and *Indigofera tanganyikensis* were more abundant at intermediate distances. For the third pattern, *A. adoensis*, *D. macroblephara*, *F. ovate*, *Eragrostis braunii* and *H. schimberi* were more abundant farther away from the abandoned

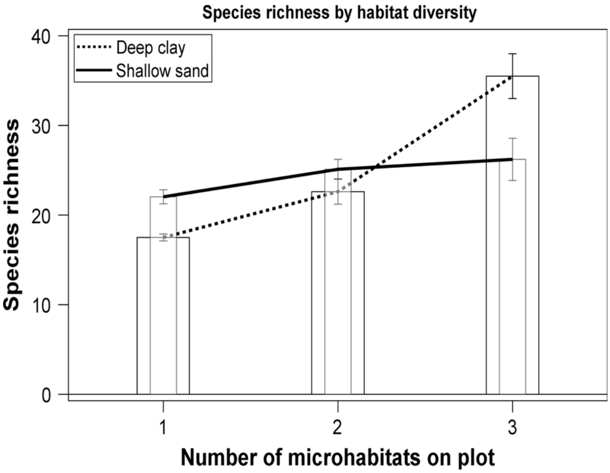

Fig. 3 Species richness by habitat diversity

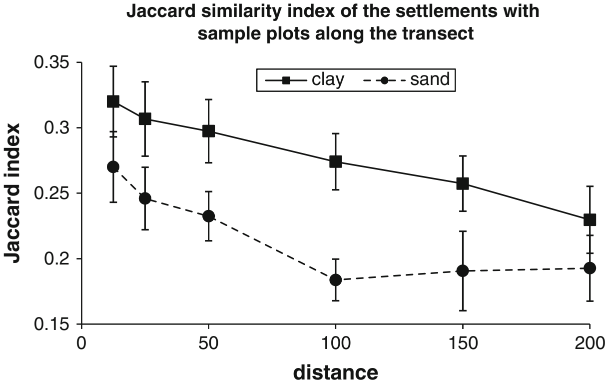

Fig. 4 Jaccard similarity index of the settlements with sample plots along the transect

settlements. Shrubs rarely responded to soil type with the exception of *Ormocarpum trichocarpum* that had higher cover on settlements on deep clay soils than on shallow sandy soils (Mann–Whitney *U* test, $p = 0.037$).

As settlements recovered from human use over time, plant species composition changed. Recently abandoned bomas were initially dominated by the boma-dependent *Cynodon* species. They dominated abandoned settlements for about 25 years. When *Cynodon* species began to disappear, they were principally replaced by *T. triandra*. On settlements 20–24 years old *T. traindra* constituted 2.1 % (±0.021) of the plant abundance, but increased to 45.8 % (±0.029) on the two oldest settlements that were about 40 years old *E. tenuifolia* also increased threefold over time in abundance from 5.6 % (±0.021) on 25-year-old to 17.7 % (±0.080) on 40-year-old settlements. Abundance of sedges in the Cyperaceae family increased by an order of magnitude from 0.1 ± 0.001 on abandoned settlements to 3.8 ± 0.002 on the oldest (>25 years) settlements. On or at the edge

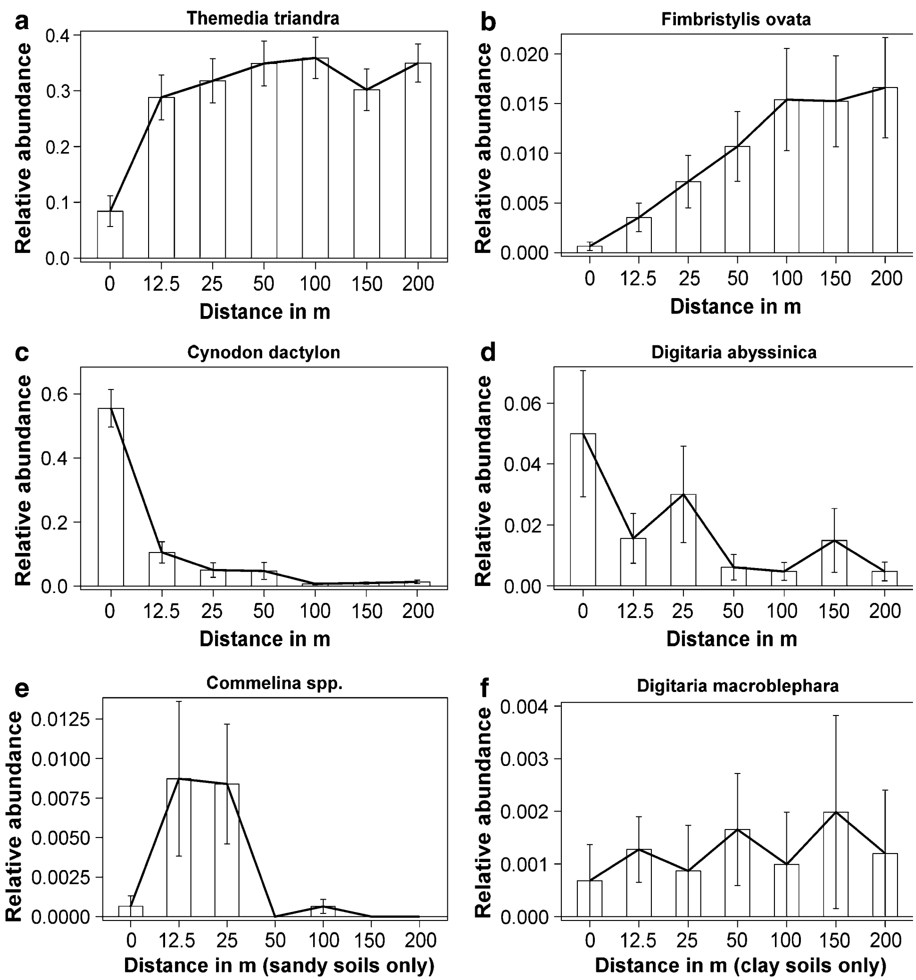

Fig. 5 Relative abundances of **a** *T. triandra*, **b** *F. ovata*, **c** *C. dactylon*, **d** *D. abyssinica*, **e** *Commelina* and **f** *D. macroblephara* along the transect from the settlements

(12.5 m) of settlements, *Cynodon* was less abundant where many other grass species were also abundant (Fig. 6, Poisson regression $F_{1,54} = 21.128$, $p = 2.6253 \times 10^{-5}$).

Abandoned settlements seem to be important in shrub regeneration especially on deep clay soils. Shrubs strongly colonised settlement sites over time (Fig. 7, regression analysis, adj. $R^2 = 0.506$, standardized coef: 8.38 ± 2.07, $p = 0.001$).

TWINSPAN analysis placed all the plots into five clusters (Fig. 8), each representing a specific plant community distinguished by soil type and distance from old settlements. The first division was between settlement and non-settlement sites (Mann–Whitney *U* test, $p < 0.001$). The second was by soil types and location of the plots, on and outside settlements. On the settlements (Mann–Whitney *U* test, $p = 0.003$). *C. dactylon* and *E. tenuifolia* were on shallow sandy soils (group D) and *C. nlemfuensis* and *Sporobolus confinis* on deep clay soils (group E). Outside the settlements, also based on soil type, *F. ovata* species emerged as an indicator of deep clay soils (group C). The third division separated intermediate (group A) and far distances (group B) from each other, but only on

Table 5 Differences in species abundance by soil type and distance

Species	Soil type	Distance class from settlement in m						
		0	12.5	25	50	100	150	200
Achyranthes aspera	Sandy soil	0.020						
Digitaria abyssinica	Sandy soil	0.042						
Oxygonum siniatum	Sandy soil	0.038						
Sporobolus pyramidalis	Clay soil	0.067	0.060					
Eragrostis exasperata	Clay soil		0.020	0.010				
Cynodon dactylon	Sandy soil		0.007	0.028	0.019			
Indigofera tanganyigensis	Sandy soil		0.038	0.038	0.038			
Aristida adoensis	Sandy soil		0.003	0.002	0.000	0.024	0.076	0.016
Digitaria macroblephara	Sandy soil			0.000	0.003	0.000	0.012	0.002
Fimbristylis ovata	Clay soil			0.065	0.013	0.085	0.053	0.011
Eragrostis braunii	Sandy soil				0.058	0.052	0.007	0.005
Harpachne schimperi	Sandy soil				0.007	0.023	0.001	0.067

p values are for Mann–Whitney *U* test for each distance class. Statistical significance of all hypothesis tests was assessed at $p = 0.05$

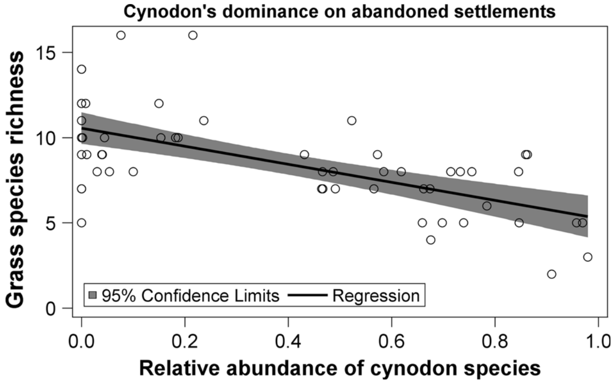

Fig. 6 *Cynodon*'s dominance on abandoned settlements

sandy soils. Ten of the 210 plant species sampled were generalists and occurred in all the community clusters: *Heteropogon contortus*, *S. stapfianus*, *F. ovata*, *T. triandra*, *D. radicans*, *E. tenuifolia*, *B. insculpta*, *C. dactylon*, *Eragrostis racemosa* and *S. confinis.*

CCA analysis for all the plots together (Fig. S1 in Supplementary materials), showed that the amount of dung deposited was the most influential environmental factor along the first axis, but distance from the settlement was also correlated strongly with the first axis. The amount of dung separated the settlements (plots labelled ‘A’), together with distances 12.5 (‘B’) and 25 (‘C’) m clearly, which were placed on the right side of the figure. Species attracted to high concentrations of dung were *Kyllinga nervosa*, *Athroisma psyllioides*, *Amaranthus graecizans* L. subsp. *thellungianus* and *C. dactylon*. Grass height was the most important environmental factor along the second axis. Along this axis were settlements not heavily grazed by livestock and thus having high grass (at the bottom of the figure). High grass plots were characterised by *Commelina benghalensis*, *Cyperus kilimandscharicus*, *C.*

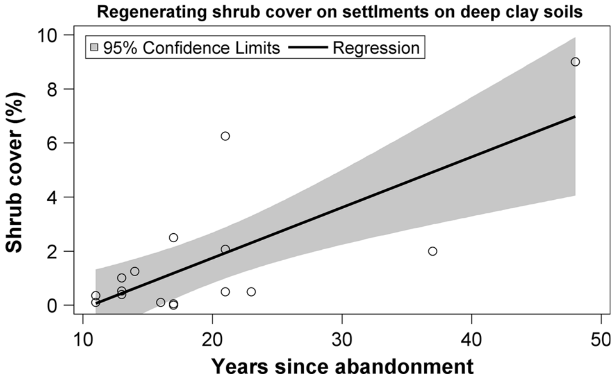

Fig. 7 Regenerating shrub cover on settlements on deep clay soils

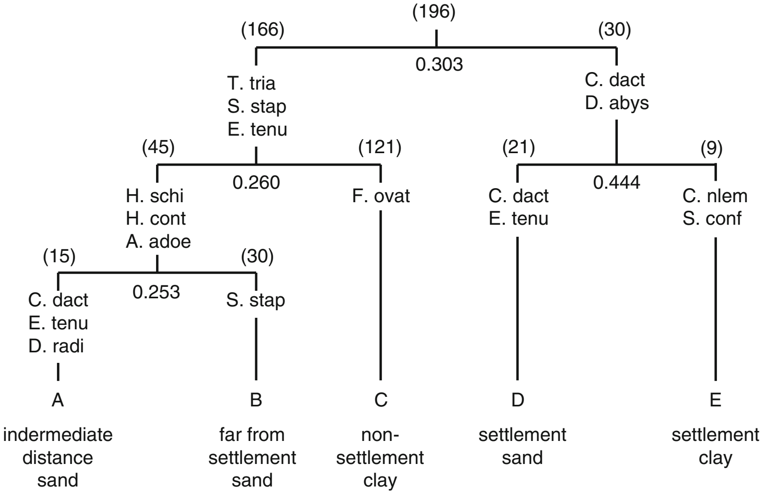

Fig. 8 TWINSPAN-classification of the settlements

nlemfuensis and *Panicum merkeri*. Landscape position also emerged as an important variable along the second axis. Landscape position had its highest value when the settlement was situated on a hilltop (at the top of the figure) and lowest value when it was close to rivers in bottomlands. Hilltops supported shorter grasses, were typically drier, more eroded and located on shallow sandy soils with high cover of *Crabbea velutina*, *Tragus berteronianus*, *Cissus rotundifolia* and *Blepharis maderaspatensis*. Soil types were scattered equally throughout the figure, though all the plots on hilltops were located on shallow sandy soils. The time since abandonment was not an important factor when all the plots were included.

The CCA, for plots on shallow sands only (Fig. S2 in supplementary materials), again indicated that the amount of dung explained most of the variation along the first axis. Plots with lots of dung were close to the origin of the figure and were characterised by species like *C. nlemfuensis*, which occurred only once on shallow sandy soils on a very recently abandoned and larger settlement, and also by *A. psyllioides*, *S. ovata*, *Ipomoea sinensis* and *C. dactylon*. Settlement age and grass height were nearly equally important along the second axis; young plots had taller grasses than old plots. At the top of the figure, there is a cluster of plots on old settlements characterized by short grass and species like *Cucumis ficifolius*, *S. massaica*, *Sporobolus discosporus* and *C. velutina*. Other important environmental variables on shallow sands were landscape position, distance to settlement and vegetation cover.

Plots on deep clay soils responded to environmental gradients less strongly than they did on shallow sands, as indicated by the more compact cluster of plots (Fig. S3 in supplementary materials). Grass height was the most important environmental variable along the first axis. It separated the tall grass plots to the left with species like *Asystasia mysorensis*, *I. sinensis*, *C. benghalensis*, *Teramnus labialis* and *C. nlemfuensis*. The amount of dung was the most important variable along the second axis. The plots on settlements were located farthest from the centroid at the top of the figure and were characterized by species like *K. nervosa*, *A. graecizans* and *J. calyculata*.

Discussion

Pastoral settlements and biodiversity patterns in wet and dry savannas

One of the aims of this study was to get a broader understanding of how pastoralists and their settlements influence biodiversity patterns over a broad range of East African savannas. We thus intentionally chose our study location to contrast with those studied previously on much drier locations with 250–550 mm rainfall (Augustine 2003; Muchiru et al. 2009, 2008; Reid and Ellis 1995; Stelfox 1986; Veblen and Young 2010; Young et al. 1995) and on relatively poor soils. Our study site receives 1,000–1,341 mm of rainfall annually, and is principally on nutrient-rich soils. We were also able to compare two soil types that have been shown to have different levels of nutrients within our study site (McNaughton 1985). To our knowledge this is the first analysis of the relative influence of different soil types and rainfall on pastoral settlement impacts on biodiversity.

Previous studies have shown that bomas can leave a visible legacy in the soils, animals and plants for a long time in regions receiving less than 500 mm of rainfall. In South Turkana (200–400 mm rainfall) the N, C and P values of livestock corral soil remained twice those of background soils for at least 20 years in a sandy soil environment (Reid and Ellis 1995). These same settlements appear to enhance establishment of most of the large *Acacia* trees in the Turkana landscape. Such large trees are critically important as centres of biodiversity in another dry landscape in southern Africa (Dean et al. 1999???). In Amboseli (350 mm rainfall), vegetation on settlements located on sandy soils and more than a century old are visibly different from the surrounding landscape to the human eye and still contain elevated levels of nutrients 140 years after abandonment (Muchiru et al. 2009). On sandy, nutrient-poor soils of Laikipia, central Kenya (500 mm rainfall), settlements at least 39 years old also have higher levels of P than non-settled areas (Augustine 2003). In Laikipia, long term glades, which are thought to be sites of pre-colonial Maasai bomas, that are more than 70 years old, had higher values of nitrogen, carbon, sodium, calcium and potassium inside than outside the glades. These glades supported up to 10 times more dung of wild and domestic large mammals compared to sites far from glades. Glades also supported plant species that are rare or absent elsewhere (Young et al. 1995). In the Athi-Kaputiei Plains (500 mm rainfall), Kenya, Stelfox (1986) found that bomas had higher values of wildlife dung, nitrate, phosphate, sulphate, calcium, salts and organic matter compared to background levels. Grasses growing inside the Athi-Kaputiei bomas were richer in proteins and lower in fibre content compared to control areas.

The evidence from vegetation cover and changes in species composition as bomas age suggests that the "signature" of settlements does not last as long in the moist and nutrient-rich Mara as it does in these drier savannas, which may support our 'nutrient disappearance' hypothesis. 25 years after abandonment, species composition on the settlement very much resembles that far away from the settlements in the Mara, in contrast to the patterns documented for the drier savannas.

Why do the effects of settlements on plants disappear faster in the Mara? In relation to rainfall, dung decomposition rates are probably higher in areas, like the Mara, where soils remain wet for longer periods of time than in areas where soils dry out quickly. For example, dung disintegrates rapidly due to the activities of numerous coprophagous insects, especially in the rainy season. In African savannas the occurrence of dung beetles is primarily dependent on the rains (Cambefort 1991). During the dry season the dung dries out quickly and attracts only a few dung beetles. In addition, there are fewer species and lower populations of dung beetles in drier than wetter systems (Cambefort 1991). Also, improved soil fertility leads to higher production (Breman and Dewit 1983) and thus faster use of available nutrients.

How settlements affect plant richness and composition

Abandoned settlements clearly both depressed and elevated plant richness in this conservation system. Bomas create a disturbance in savannas, opening up opportunities for early successional, pioneer species to thrive; they also create nutrient hotspots where nutrient-loving plants also thrive. The TWINSPAN analysis nicely captured plots on the settlements, with indicator species being disturbance and nutrient-favouring, open area pioneering, native rhizomatous grasses (Boonman 1993; Ibrahim and Kabuye 1987; Skerman and Riveros 1990) *C. dactylon* and *D. abyssinica.* Thus settlements may increase the plant species richness in savannas.

Species richness, however, tells us nothing about the types of species in a place or if these species have biodiversity value (Reid 2012). In our study, composition shifted strongly with distance from settlement and many of the species close to the settlement were weedy and some were introduced. The replacement of native species by aliens is typical of fertilized herbaceous vegetation (Burke and Grime 1996; Huenneke et al. 1990; Lauenroth et al. 1978; Wilson and Tilman 2002). For example, there were 10 plant species found only on the settlements (boma specifics), 21 others within 12.5 m and 44 within 25 m of the edge of the settlement. About 25 % of the species on and near settlements are weeds, and several, like *Alternanthera pungens*, *Tagetes minuta*, *Ageratum conyzoides*, were introduced from North America. Many of the species near the settlements also have broad distributions in different types of grasslands (Boonman 1993; Ibrahim and Kabuye 1987; Skerman and Riveros 1990). Others often grow on termite mounds, like *Cadaba farinosa*, *Pavetta subcana*, *Capparis erythrocarpos*, *Capparis tomentosa*, *C. rotundifolia* and *Flueggea virosa*. For these species, bomas may provide a similar disturbed environment. Nearly half the species on or near settlements favoured disturbed places (Boonman 1993; Ibrahim and Kabuye 1987; Skerman and Riveros 1990). There were a few species on or near settlements that are classified as locally common or uncommon, including four herbs: *Dyschoriste nagchana*, *Cucumis figarei*, *Caralluma dicapuae*, *Hibiscus cannabinus* and two shrubs: *Solanum arundo*, *Phyllanthus sepialis*. Thus, settlements supported species that otherwise would not have existed in the area, but only a few of these have biodiversity value. Settlements are, nevertheless, important places for shrub regeneration, replenishing shrubs harvested by the Maasai.

While the settlements themselves had the most powerful effect on plant species, soils, dung and grazing also influenced species richness and composition. For example, different soil types supported different kinds of species composition and diversity. For example, *A. adoensis*, *D. macroblephara*, *E. braunii* and *H. schimperi* were more abundant on shallow sandy soils than on clay soils.

Plants responded more strongly to settlement impacts on shallow sandy soils than on deep clay soils, which suggests support for our 'context matters' hypothesis. We did not measure soil nutrients, but we suspect that this is the cause of this difference (although water infiltration rates could also be important). We know from other studies that settlements create nutrient hotspots in savannas. In sandy soils, these hotspots should be much more nutrient-rich than soils far from settlements. By contrast, settlements on nutrient-rich clay vertisols will not contrast as sharply with soils far from settlements, because these soils are already nutrient rich. In addition to nutrients, dung likely alters the water holding capacity of settlement soils, more so on sandy soils than on clayey soils.

High concentrations of nutrients, represented by the presence of dung, also depressed species richness, similar to other studies. There were fewer species within the settlement sites, for example, where dung concentrations were very high, than anywhere else we sampled. We also noted that even the smallest amounts of dung were sufficient to change species composition, even far from settlements. Proulx and Mazumder (1998) showed that plant richness declines when a limiting resource increases in an environment with high concentrations of resources. Also, Wilson and Tilman (2002) tested the effects of nutrients and disturbance on plant species richness. They found that richness declined as nitrogen increased, regardless of disturbance level, caused by declines in species colonization and turnover and increases in species extirpation. Our settlement sites had high concentrations of resources favouring species that tend to out-compete and dominate others in the ecosystem (Grime 1973b), like *Cynodon*.

We also found support for the intermediate disturbance hypothesis (Connell 1978; Grime 1973a), which suggests that species richness should be greatest at intermediate levels of disturbance and lower at both high and low disturbance. In our case, there were 50 % more plant species just outside but within 50 m of the edge of the settlement than anywhere else we sampled. This is where livestock trampling and dung were at moderate levels rather than at low or high levels. The increased richness at intermediate distances from settlements can be explained by the fact that the competitive dominants in the unsettled savanna, (*T. triandra* and *E. tenuifolia*) were strongly affected by pastoral settlements (Wilson and Tilman 2002). Disturbance can increase soil resource heterogeneity which may increase diversity by creating establishment sites (Grime 1986), altering resource ratios (Tilman 1988) or changing the relative importance of root and shoot competition (Wilson 2000). Richness is controlled ultimately by disturbance and productivity, and proximately by colonization and extirpation (Grace and Pugesek 1997; Rydin and Borgegard 1988), with disturbance increasing both colonization and extirpation rates (McIntyre and Lavorel 1994; Montalvo et al. 1993).

Some species were more sensitive to pastoral settlements than others. For example *A. adoensis* was quite insensitive to settlement disturbance, reaching its background abundance level just outside the settlement. *E. braunii* and *H. schimperi* were more sensitive to settlement disturbance, only reaching their background level 50 m from the edge of the settlement.

Consequences of expanded permanent settlements and new wildlife conservancies

Due to recent land demarcation in the Mara pastoral ranches, the Maasai are starting to settle down more permanently. This means a major change in their traditional pastoral lifestyle. Sedentarization stops further creation of abandoned settlements. As a result, one important characteristic and special habitat type is disappearing; a habitat that has existed in the area for at least 2,000 years (Marshall 1990). It also represents a loss of a unique interaction between the Maasai, their livestock, vegetation dynamics and wildlife.

Land privatisation and more permanent settlement may deplete savanna biodiversity. Settlements create spatially focused animal activity sites (Andrew 1988; Muchiru et al. 2008; Young et al. 1995); they are important local habitats for large mammals, due to enhanced food quality and greater ability to detect predators (Reid et al. 2003). In particular, small and medium ungulates concentrate in the pastoral ranches of the Mara in the wet season to feed on the short, actively growing and hence nutritious forage and to benefit from the higher visibility of predators than in the adjoining Mara Reserve created by intense livestock grazing (Bhola et al. 2012a, b). Reid et al. (2003) surmised, based on their extensive wildlife counts in the Mara in 1999 and 2002, that land privatisation could have strong negative impacts on wildlife. If all the pastoral land outside the reserve were privatized, 40 % of the wildlife or 45,000 animals could be lost, and perhaps all the elephants and most carnivores. In addition, were these settlement habitats to disappear, we would expect a number of plant species to disappear, although only a few of these species have high biodiversity value.

Interestingly, the recent establishment of wildlife conservancies will also cause these abandoned settlement sites to disappear, because the vast majority of the Maasai are no longer living in the conservancy areas. For example, our study site, which was full of Maasai settlements during our study period, is now a wildlife conservancy with no Maasai settlements. Conservation goals in these savannas are relatively new inventions, creating new habitats where people are not allowed to settle in parks and conservancies. They may have unintended consequences for biodiversity, and some of these consequences may be negative (Western and Gichohi 1993). However, given the rapid expansion of settlements in the Mara over the last 40 years (Lamprey and Reid 2004; Norton-Griffiths et al. 2009; Ogutu et al. 2009), conservancies will keep towns from expanding into the open savannas, which should be a net gain for wildlife, despite the loss of traditional settlements.

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