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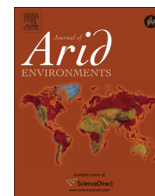


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The perfect storm: Land use change promotes *Opuntia stricta*'s invasion of pastoral rangelands in Kenya



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ABSTRACT

The process of alien plant invasion is complex and multidimensional. *Opuntia stricta* (var *stricta*), is one of the world's most invasive plants but evidence for the invasion process is limited to historical reconstruction and experiments. Here, we present data on the landscape spread of *O. stricta* into a high altitude dry savanna on the Laikipia Plateau of Kenya. Factors like species characteristics, ecosystem dynamics, habitat susceptibility, and system context are implicated. We propose that the current invasion, 50 years after the plant arrived in the area, is not the result of a "lag" phenomenon but instead is a response to recent changes in land use primarily sedentarization of pastoralists. Subsequent continuous heavy livestock grazing produced an ecological state transition to degraded rangeland which created the opportunity for the invasion. Thereafter, the special characteristics of *O. stricta*, the number of mammalian consumers, and additional anthropogenic changes fueled the process. These data strengthen existing evidence that change in land use provides opportunities for alien plant invasions. This Kenyan case illustrates the challenges posed by humanization of ecosystems and suggests why it is important to look at the underlying causes of alien plant invasions, not just deal with the symptoms.

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1. Introduction

Alien plant species pose a growing threat to biodiversity but the invasion process is complex, multifactorial, and multidimensional (Catford et al., 2012; Foxcroft et al., 2011; Thomsen et al., 2011; Witt and Nongogo, 2010). The study of alien plant invasions can be approached in various ways, for example by looking at the stages of invasion such as transport, colonization, establishment and landscape spread, (Theoharides and Dukes, 2007), in terms of species characteristics, system context and habitat susceptibility (Foxcroft et al., 2011), or in terms of specific hypotheses such as "enemy release" (Maron and Vilà, 2001), or the "intermediate disturbance hypothesis" (Catford et al., 2012).

Opuntia is one of the most diverse genera of cactus (Reyes-Agüero et al., 2006) and *Opuntia stricta* is one of the 100 of the world's worst plant and animal invaders (CABI, 2014; IUCN/SSG,

2009; Padrón et al., 2011). While *O. stricta* has been used as a model species in invasion ecology (Foxcroft et al., 2011), our understanding of *O. stricta* invasion is based primarily on historical reconstructions, experiments, or comparative interpretations of conditions in places where *O. stricta* has already invaded (e.g. Kruger National Park, South Africa: (Foxcroft and Rejmánek, 2007; Foxcroft et al., 2011, 2004); Australia: (Dodd, 1940; Hosking et al., 1994), St. Kitts and Nevia: (Pemberton and Liu, 2007), Spain, the Mediterranean region and Canary Islands: (Le Houérou, 2002; Padrón et al., 2011). Data on the actual process of *O. stricta* invasion is lacking.

Here we present the results of a real-time study of the process by which *O. stricta* spreads across the landscape of a high altitude semi-arid savanna on the Laikipia Plateau of Kenya. This opportunity was afforded by an ongoing and long-term baboon research project (Uaso Ngiro Baboon Project, UNBP; (Strum, 2005)) which has collected data since 1984 on the ecology of the area and on baboon diet and activity budgets (which have shifted dramatically during the course of the recent *O. stricta* invasion).

We ask two questions: why did *O. stricta* invade while other *Opuntia* species (*Opuntia ficus-indica*, *Opuntia monacantha*, and

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Austrocyllindropuntia subulata) also present did not, and why did the *O. stricta* invasion begin more than 50 years after the plant was brought to the area? Although these observations are specific to a place, a time, and a spatial scale, they offer insights about how newly created conditions of sustained livestock grazing generate settings for *O. stricta* to invade. The story illustrates the complexity of the invasion process and provides an improved understanding of why only 10% of nonindigenous plant species become naturalized (Theoharides and Dukes, 2007). The Mukogodo data further contribute to the literature on African plant invasions which is deficient compared to other regions of the world (Foxcroft et al., 2010; Pyšek et al., 2008).

2. Materials and methods

2.1. Study area

The study site lies in the northeastern Laikipia Plateau, Kenya and extends from below the Mukogodo Forest near Doldol (latitude 0.4040020; 0°24'14.41"N; longitude 37.1644840; 37°9'52.14"E), westward past the village of Il Polei including several adjacent large scale private ranches supporting both cattle and wildlife (Fig. 1).

The habitat is dry savanna with woodland and wooded/bushed grassland dominated by various species of acacia trees and interrupted by medium and large granitic inselbergs or “kopjes”. The soils are chiefly clay loams and gravelly clay loams, the result of a basement complex of metamorphic rock (granites, migmatites and gneise see Barton, 1990). There is a strong catena effect on both soils and vegetation (Mutua, 2001). Wildlife and livestock grazing, in addition to slope, contributes complexity to the local variation of erosion, soils, and vegetation.

Kenya experiences two rainy seasons and two dry seasons because of rainfall peaks produced by the Southeast Monsoon and the Northeast Monsoon. The study area has an annual average rainfall ranging from 350 to 400 mm (Strum, 2005). Maximum daily temperatures can exceed 36 °C in the short dry season and fall to below 10 °C at night when the skies are clear (UNBP unpublished records).

The Laikipia Plateau has the second largest wildlife concentration in Kenya (Kinnard et al., 2010). More than 40 mammalian species are present in the study area (Barton, 1990) ranging in size from elephants (*Loxodonta africanus*) to dik dik (*Rhynchotragus kirki*); some are permanent residents while others are seasonal visitors. Baboons are found throughout the area and sleep on rock kopjes for safety from predators such as leopard (*Panthera parus*), spotted hyena (*Crocuta crocuta*) and lion (*Panthera leo*). Wildlife densities on the communal land of the Ndorobo Reserve (now referred to as Mukogodo) are not as high as on the large private landholdings to the West but many species move between the private and communal lands daily (UNBP unpublished data).

Low rainfall and frequent droughts make the area unsuitable for crop production. It has been part of a migratory pastoralist system since at least the 1920's (Cronk, 2004). Communal land ownership is vested in “Group Ranches” and not in individuals (Kenya Government, 1970) although there are a few small unfenced parcels owned by individual Maasai scattered throughout the communal zone. The largest of these does not exceed 800 acres (324 ha).

The British colonial administration introduced at least four species of *Opuntia* cactus (*O. monacantha*, *O. ficus-indica*, *O. stricta*, and *A. subulata*) to the area in the 1950's. These were used as living fences around the local colonial government offices in the small administrative village of Doldol.

A process of rapid sedentarization began in the early 2000's and has continued to the present. Previously “bomas” (rough corrals with branch fencing and mud huts housing families and their livestock) were occupied seasonally but beginning with the high rainfall El Nino event of 1997–1998, the number of permanent bomas has steadily increased.

Droughts have also increase in frequency and intensity over the recent years (UNBP unpublished data; (Kaye-Zwiebel and King, 2014; Western et al., submitted).

2.2. *O. stricta*

Opuntia is the most diverse genus of *Cactaceae* with 202 species compared to an average of 20 species for other genera (Reyes-

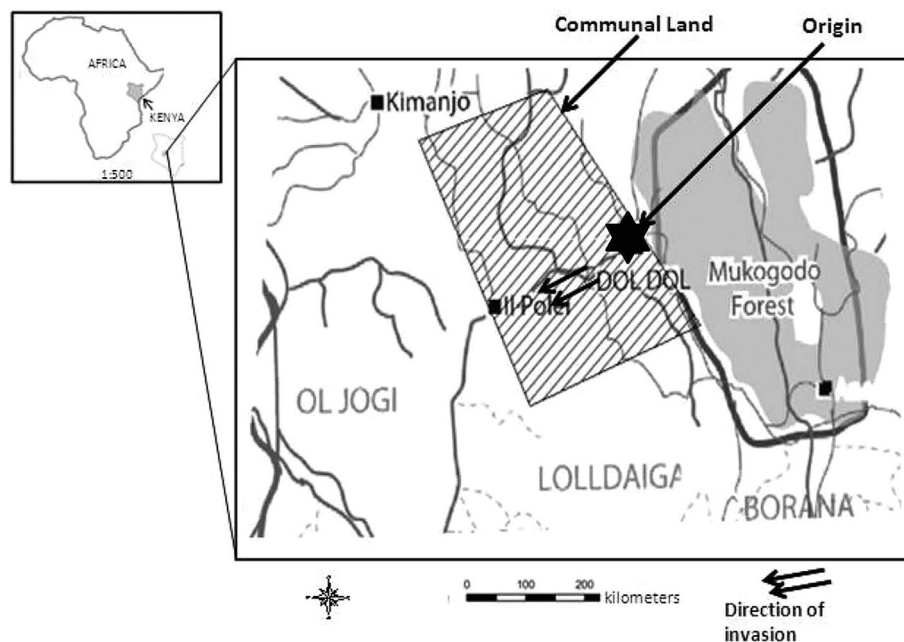


Fig. 1. Study site, origin of invasion, and direction of invasion.

Agüero et al., 2006). *Opuntia* species are succulent CAM plants with a highly efficient water use and are generally stress tolerant making semi-arid open rangelands particularly susceptible to invasion (Osmond et al., 2008). Their ability to reproduce either by vegetative propagation (multiplication) or seedling recruitment (reproduction), coupled with the now well documented role of propagule pressure means that large, locally dense patches can form quickly and new patches can be established through long distance seed dispersal in avian and mammalian fecal matter (Padrón et al., 2011). *Opuntia* was already established in Spain at the end of the 15th century (Le Houérou, 2002; Padrón et al., 2011). European colonial expansion, beginning in the 1600's, transplanted a variety of *Opuntia* species along with other alien plants and animals throughout a world-wide network of trade routes.

O. stricta taxonomy is controversial. For our purposes, we use the classification of the Invasive Species Compendium (CABI, 2014) which recognizes 2 varieties: *O. stricta* var *stricta* (Haworth) and *O. stricta* var *dillenii* (but see (Menkins, 2009). Unfortunately, the *Opuntia* literature is often not clear about these distinctions. Both variants are native to the New World where *O. stricta* var *stricta* has a much restricted distribution compared to *O. stricta* var *dillenii*. The plant identified in our study area is *O. stricta* var *stricta* (Fig. 2).

Today, notable invasions of the two *O. stricta* varieties are found throughout the world from Australia (Dodd, 1940; Hosking et al., 1994), to the Mediterranean region (Padrón et al., 2011) and from

South Africa (Hoffmann et al., 1998) to North Africa (CABI, 2014). *O. stricta*'s problematic status was recognized as long ago as 1940 when, according to Dodd (1940), it had already covered 24 million hectares in Australia, half of which was so dense that it was useless to humans.

2.3. Sampling

The research on *O. stricta* was incidental to Uaso Ngiro Baboon Project's (UNBP) long-term study of baboon socio-ecology dating from 1984 at this study site. The UNBP team ranged over the study area with the baboons, 12 h a day, 6 days a week. The baboon data include activity budgets and diet from a number of groups: the initial 2 study groups beginning in 1984, 3 troops beginning in 1987, and more recently up to 5 descendant study groups. This close and continuous natural history of the study area (and baboon diet data) provides the context for the period before the invasion study began. However, information on the changing context, before and during the *O. stricta* invasion, comes from quantitative data provided by monthly ecological monitoring. The context is compared between two baboon troops, in particular, one that ranges close to the point of origin for *O. stricta* near Doldol, and one that lives to the West (initially ahead of the invasion) where the plant was still absent when we began the *O. stricta* study. As well, in 2005, it was not yet obvious that this was an invasion. The placement of *O. stricta* plots



Fig. 2. *Opuntia stricta* var *stricta* medium sized plant with fruits and new pads.

and choice of variables were a best guess about how to document possible drivers of the plant's dispersal. We maintained these methods during the 10 year study for ease of comparison and simply added more *O. stricta* monitoring sites.

2.3.1. Herb layer biomass and grazing pressure

Information on herb layer biomass, grazing pressure, and impact of settlement on the rangeland comes from the Uaso Ngiro Baboon Project's (UNBP) monthly ecological monitoring (Strum, 2005). The twenty-two grassland monitoring plots are distributed through the study area (45 km²); they permit a fine grained assessment of herb layer biomass over a relatively small area compared to ecological monitoring of entire ecosystems (Western et al., submitted). UNBP grassland plots predate the *opuntia* monitoring and are distributed over the area in a representative fashion. This means that many are contiguous to the *opuntia* plots while others were still outside of the invaded area. Grassland biomass productivity is calculated monthly using data from a modified slanting pin-frame method (Groom and Western, 2013). For comparisons between plots, between months for the same plot, and to other studies that use the same method (Groom and Western, 2013; Western et al., submitted), raw data expressed as "hits per pin" can be converted into a measure of herb level biomass using the equation $y = 16.93H + 6.3$ where

$$H = \frac{\sum \text{Hits}}{\text{Total pins}} = \bar{X} \text{ Hits per pin}$$

These are combined into averages from 1984 until 2013.

Grazing pressure is assessed several ways. First total biomass per month from grassland plots is compared by two periods, before settlement (1984–1997) and after settlement (1999–2010), and their location, in the settled area and outside of it. The El Nino period (1998) was not included as it had exceptionally high rainfall and high biomass. Secondly, grazing pressure (measured at each grassland plot beginning in 2005 as % of blades with visible signs of grazing) is compared between plots located in the settled area and outside the settled area for the period 2005–2010. Finally, the ability of the herb layer to respond to rainfall is compared before and after settlement using rainfall data and total biomass data from grassland plots located in areas with and without settlement.

2.3.2. Maasai homesteads

Total counts of Maasai homesteads, bomas, were done in 2008 in the area closest to the point of origin (Doldol) and near Il Polei at the front of the *O. stricta* invasion in 2005 and 2008. Each homestead housed a related set of people, and since Maasai have patrilocal residence, this included a man, his wives and their descendants. The majority of the homesteads were built as permanent residences after 2000–2001 while a few had a longer history of seasonal occupancy, one dating back nearly 60 years and another 30 years.

2.3.3. *O. stricta* monitoring

Data on *O. stricta* was incorporated into monthly ecological monitoring in late 2005 at a time when the abundance of *O. stricta* had increased visibly near the origin.

We used several methods to monitor *O. stricta*. In 2006, an 11 km transect was surveyed and repeated in 2008 and 2011. This transect followed a gravel road from the point of origin of the invasion to Il Polei village (ahead of the invasion in 2006). Densities were initially recorded at 500 m intervals by measuring the diameter of plants within two, 2 m × 100 m quadrats each one perpendicular to the road on either side. Plant condition and state (flowers, fruits, and cladodes), plant location on slope (top of slope, middle of slope,

gully, plain), and other attributes like soil color and depth, rockiness, degree of shade, habitat and altitude were also recorded. Surveys were repeated in 2008 and 2011 but since *O. stricta* densities had visibly increased (see results below), monitoring sites were placed closer together, at 250 m rather than 500 m apart. For comparability in some analyses, we used only data from plots 500 m apart because that was the monitoring distance in 2006.

In 2006, PCQ transects (Cottam and Curtis, 1956) were added. These focused on a central point in the home ranges of the two main baboon study groups, one near the invasion origin (Doldol), where *O. stricta* was first established, and one that lived to the west and ahead of the invasion (Il Polei). In each area, transects extended 2 km in all four cardinal directions from a center point located in an area of highest *O. stricta* density near Doldol, and a topographically comparable area 11 km to the west near Il Polei. Monthly monitoring of *O. stricta* plants selected from these transects were matched for size and topographical location within and between the two baboon home ranges.

In 2008, additional data were collected on the density and distribution of *O. stricta* plants at baboon sleeping sites and at Maasai "bomas" using the same methodology as the road transect. The transects were placed either from the base of the rocky outcrop used as a baboon sleeping site and extended 600 m, or from the perimeter fence of a boma and extended 300 m. The distance of the transects reflected our initial best guess about the different dispersers' impact. The transects extended in a straight line in all four cardinal directions. Both the baboon sleeping sites and the eight boma sites were distributed from east to west following the direction of the *O. stricta* invasion. We eliminated one boma site (#2) in the analysis because its location in a gully generated a compound effect.

In 2008, a 10 km transect similar to the 11 km road transect was placed along an elephant corridor that crosses the study area going from the Mukogodo Forest in the SE to the Uaso Ngiro River to the NW. Monitoring sites were every 250 m starting from Windmill Gully (5 km west of Doldol) and included 5 km into private land, ahead of the invasion. In addition to the usual measurements, the presence of elephant dung and whether the elephants had been eating *O. stricta* (determined by remains of *O. stricta* in their dung—see Fig. 3) were recorded.

We could not repeat this transect because there were high levels of elephant activity along the corridor since 2010.

O. stricta density is calculated as the percent of the sampled area covered by *O. stricta* at each station. Fruit productivity is calculated as the number of fruits divided by the total number of flowers, buds, fruits which is then divided by the number of focal branches monitored on the plant.

Rainfall was recorded at several locations in the study area; these correlate well with each other (UNBP unpublished data) therefore we use the location with the most complete rainfall since 1984. Rainfall is used with monthly grassland biomass to calculate the herb layer "bounce back" for a specific amount of rainfall.

Analyses were performed using statistical programs **Statistica** (StatSoft, 2012), **Stata** (StataCorp, 2011), and **R** (R Development Core Team, 2013). One way Analysis of Variance, ANOVA, was used to determine differences in grassland and *O. stricta* plot data, for the impact of distance from origin on *O. stricta* plant density, and for ripe fruit analysis. Fixed effect ANOVA was used to evaluate the impact of plant size, position, and altitude on plant density and productivity while analysis of the effect of distance on *O. stricta* density at baboon sleeping sites employed main effects ANOVA. Linear regression was used for a number of data sets including the *O. stricta* road line transect and to examine plant distribution relative to topography and distance from origin, plant density and distance from bomas, and plant density along the elephant corridor. Correlation analysis was used on the relationship between plant



Fig. 3. *O. stricta* fruit and seeds in elephant dung.

density and distribution of baboon sleeping sites. Finally, independent t-tests were applied to the data on plant density and boma distance intervals.

3. Results

3.1. Grassland productivity and impact of changes in human land use

The migratory use of the area by pastoralists changed during the study period. As a result, the number of permanent bomas in the area ahead of the invasion increased 195%, from 137 bomas in 2005 to 267 bomas in 2008 (the same area had 12 temporary bomas in 1987). Those near the point of origin were not monitored in 2005 but numbered 143 in 2008.

The impact of settlement is reflected in the difference between mean herb layer biomass of pre-and post settlement data. There is no significant difference in mean biomass between the two periods for those plots outside of the settled area (ANOVA, *before settlement* $n = 113$, mean = 58.55 g/m²; *after settlement* $n = 159$, mean = 59.94 g/m²; $df = 1$, $F = 0.098$, $p = 0.75$) whereas there is a significant difference in biomass production between the two periods for those plots inside the settled area (ANOVA, *before* $n = 112$, mean = 40.32 g/m²; *after* $n = 161$, mean 34.47 g/m²; $df = 1$, $F = 4.98$, $p = 0.026$). Moreover, herb layer growth in response to rainfall (bounce back) is depressed in the settled area. This means that less biomass is produced per unit of rainfall in the area of settlement (*before* $n = 28$, *after* $n = 39$, ANOVA $df = 1$, $F = 3.752$, $p = 0.05$) but not in the area that wasn't settled (*before* $n = 28$; *after*, $n = 39$ ANOVA, $df = 1$, $F = 0.298$, $p = 0.59$).

3.2. Distance from origin

Distance from origin was a useful metric since we knew the exact location of the original imported *O. stricta* plants. The natural

history of the area and data from baboon diets showed a westward movement of the plant into the study area. In this way, distance from origin indicated the progress of the invasion, at least westward, in the area we were monitoring. This is obvious in the 2006 data, where *O. stricta* density decreased with distance from Doldol, the point of origin (Fig. 4; linear regression: 2006, $n = 23$, $df = 22$, $r = -0.481$, $p = 0.02$).

This invasion effect continued in subsequent years, in 2008 ($n = 23$, $df = 22$, $r = -0.40$, $p = 0.058$) and in 2011 ($n = 23$, $df = 22$, $r = -0.39$, $p = 0.065$). When the 11 km road transect is divided into 3 parts, from point of origin towards the front of the invasion (closest, intermediate distance, farthest) it confirms that mean *O. stricta* density declines significantly towards the front of the invasion (ANOVA, $n = 46$, $df = 2$, $F = 3.84$, $p = 0.014$). With time, *O. stricta* density also increased at each plot so that the plant's density at each site in 2008 was greater than in 2006 and in 2011 was greater than in 2008 (sign test: $n = 23$, $Z = 4.17$, $p < 0.001$).

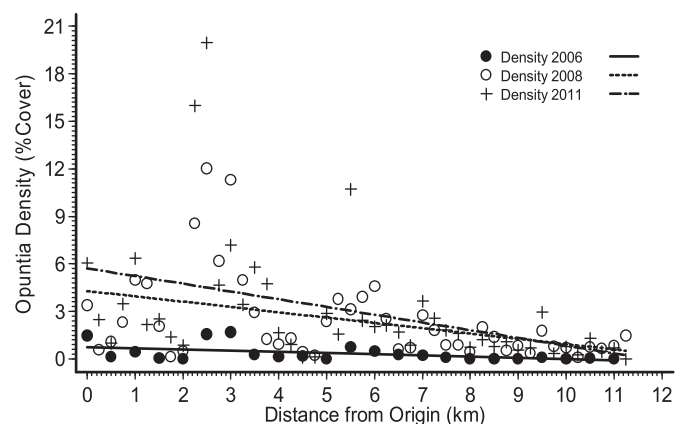


Fig. 4. *Opuntia* density in relation to distance from origin between 2006 and 2011.

3.3. Topography and distance from origin

The density of *O. stricta* was influenced by the plant's position on the landscape as well as the plant's distance from the point of origin. Natural gullies from drainage lines are more highly invaded by *O. stricta* than slopes. In 2008, the mean *O. stricta* density on slopes was 1.90% compared to a significantly higher 5.37% in gullies (one way ANOVA: $n = 40$, $df = 1$, $F = 12.02$, $p = 0.001$). When the 2008 and 2011 data are combined, *O. stricta* density in gullies and on slopes remains dissimilar (ANOVA: gully $n = 22$, slope $n = 51$, $df = 1$, $F = 19.63$, $p < 0.001$).

The declining plant density as distance from origin increased had an impact on *O. stricta* on slopes (2008: $n = 28$, $r = -0.37$, $p = 0.05$; for 2011: $n = 28$, $r = -0.28$, $p = 0.05$) and in gullies (2008: $n = 11$, $r = -0.64$, $p = 0.03$). However by 2011, the distance from origin effect in gullies was not significant ($n = 11$, $r = -0.283$, $p = 0.37$).

Therefore, *O. stricta* flourished more in gullies than on slopes but all parameters indicated that the plant was invading towards the West from its origin in the east, in Doldol.

3.4. Fruit productivity: rainfall, altitude, and plant size

Fruits and some ripe fruit were present throughout the year. The abundance did vary to some extent seasonally (Fig. 5). As expected, fruit productivity was higher in the area closer to the point of origin which had many more mature plants compared with the front of the invasion where the plants were younger (One way ANOVA: $n = 59$, $df = 1$, $F = 7.36$, $p = 0.009$). *O. stricta* plants have to reach a certain size/age before they produce fruits (Lotter and Hoffmann, 1998).

The relationship between altitude and distance from origin and fruit productivity was difficult to separate since they co-varied. The study area descends from a high of 1880 m, near Doldol village (the point of origin) to 1725 m at Il Polei village (to the west and at the front of the invasion). Despite their tight association, altitude and distance from origin each contributed significantly to the variation in ripe fruit but their interaction effect was not significant (univariate ANOVA: $n = 1066$, 13 distance categories each 500 m apart; altitude: $df = 7$, $F = 2.594$, $p = 0.012$; distance from origin: $df = 13$, $F = 4.268$, $p < 0.001$; interaction effect: $df = 3$, $F = 1.863$, $p = 0.098$). Treating them as one factor demonstrates a significant effect on fruit productivity caused by the size of plant and whether the plant was on a slope or in a gully (Table 1). Interaction effects

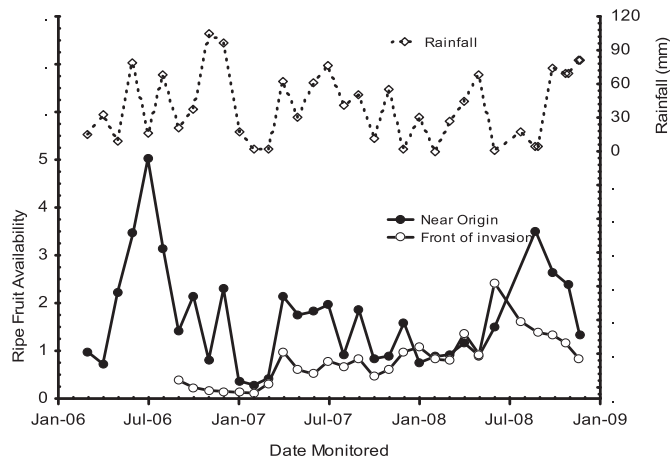


Fig. 5. Ripe Fruit Productivity in the two baboon home ranges, closest and farthest away from plant's point of origin.

Table 1
Opuntia stricta density, altitude, plant size, and position (slope or gully).

Fixed effects ANOVA:				
Source	N	DF	F	P
Altitude	853	1	69.788	<0.001
Size of Plant	853	2	11.663	<0.001
Position of Plant	853	4	2.183	0.069
Plant Position*Plant Size	853	5	8.649	<0.001
Plant position*Plant Size* Altitude	853	4	5.155	<0.001

occur between plant position and size, between plant position, plant size and altitude, but not between plant position and altitude, or size and altitude.

3.5. Agents of *O. stricta* dispersal

We monitored several possible dispersal agents for the spread of *O. stricta* including baboons, people, livestock, and elephants. *O. stricta* density data came from around baboon sleeping sites, Maasai bomas, and along an elephant corridor.

3.5.1. Baboons as dispersal agents

Baboon presence correlated with the *O. stricta* invasion; the density of *O. stricta* was highest nearest a sleeping site (Fig. 6: $n = 5$, $r = -0.849$, $p = 0.07$). Although we expected that baboons would spread *O. stricta* far, plant density declined rapidly beyond 100 m from the sleeping rocks.

This spatial effect applied not just to the sleeping rocks with the highest overall *O. stricta* density which were closest to the origin (main effects ANOVA; distance from sleeping rocks $n = 5$, $df = 4$, $F = 9.12$, $p < 0.001$), but the pattern also applied to all the other sleeping sites where the plant was present ($n = 9$, $df = 8$, $F = 3.51$, $p = 0.005$). However, as expected, sleeping sites closest to the point of origin had the greatest *O. stricta* density while those at the front of the invasion had no *O. stricta* at the time of monitoring ($n = 9$, $r = -0.859$, $p = 0.003$).

3.5.2. Pastoralists and livestock as dispersal agents

Pastoralists and their livestock also influenced *O. stricta* distribution. Maasai children regularly ate *O. stricta* fruit. Lacking formal toilets, children defecated around the settlements. The dung of cattle and goats corralled in the boma is also dumped outside of the

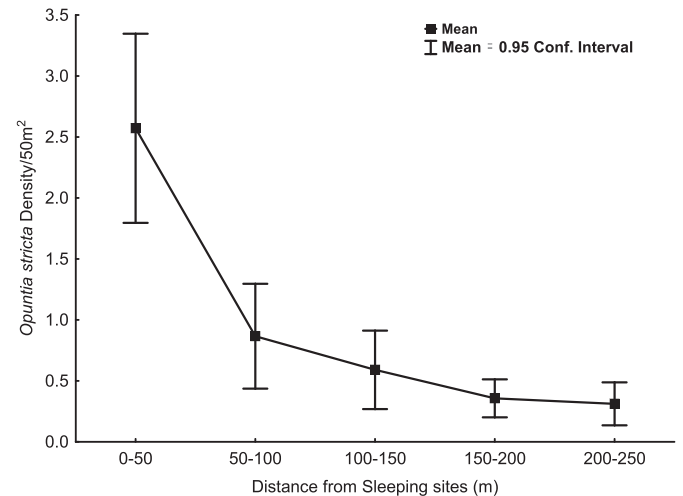


Fig. 6. *Opuntia* density from baboon sleeping sites.

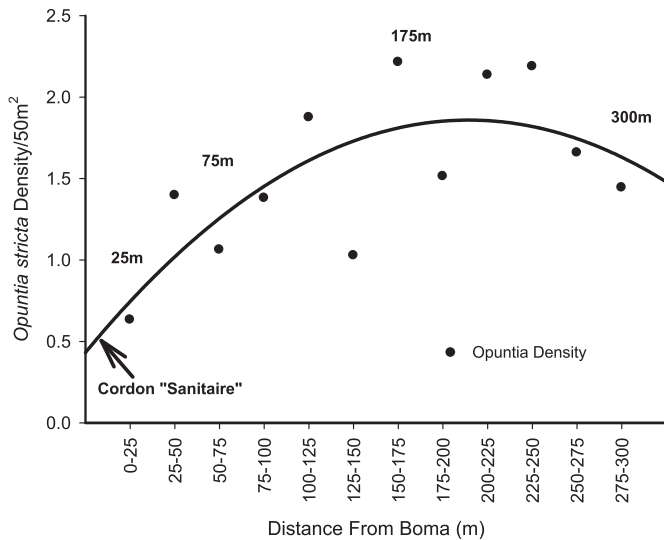


Fig. 7. *Opuntia stricta* density and distance from the boma.

boma periodically. Since cattle and goats eat *O. stricta* fruits, mainly in dry seasons, livestock excrete *O. stricta* seeds in their dung. The plant's density rose to a peak at 200 m from the boma and then declined (Fig. 7: $n = 12$, $r = 0.58$, $p = 0.046$; polynomial is $y = -0.0194x^2 + 0.3327x + 0.4318$).

There appears to be a "cordon sanitaire" within 25 m of bomas where *O. stricta* growth is significantly lower than in the rest of the transect, a pattern that is consistent across bomas regardless of their distance from the point of origin (independent t-test: 0–25 m $n = 6$, 25–125 m $n = 7$; $df = 7$, $t = -3.596$, $p < 0.004$).

3.5.3. Elephants as dispersal agents

Elephants also had an effect on *O. stricta* dispersal through fruits and seeds that remained in their dung. The 10 km elephant corridor transect (starting 5 km west of the point of origin) showed a strong negative correlation between *O. stricta* density and distance from the point of origin ($n = 101$, $r = -0.700$, $p < 0.001$). Plant density and visible signs of *O. stricta* in elephant dung were positively related ($n = 101$, $r = 0.61$, $p < 0.001$). However, this relationship changed in the last 5 km of the transect. Here, although there was no decline in the dung encounter rate (distance from origin $n = 101$, $r = 0.092$, $p = 0.360$), signs of *O. stricta* in the dung disappear west of the first 2 km in front of the invasion.

4. Discussion

The establishment and landscape spread of *O. stricta* in Mukogodo illustrates the complexity and multi-scale interactions of factors in alien plant invasions (Foxcroft et al., 2011; Theoharides and Dukes, 2007; Thomsen et al., 2011). Our real-time data show how species characteristics interact in a new ecological context shaping browsing patterns and subsequent propagule pressure and dispersal across the landscape. This lends support to reconstructions of the invasion process for *O. stricta* (and other alien plant) but also adds new dimensions.

4.1. Why did *O. stricta* and not the other alien *Opuntia* species invade Mukogodo?

There were at least 4 species of *Opuntia* that could have invaded: why *O. stricta* and not the others? We suggest that species characteristics were central (Foxcroft et al., 2011; Theoharides and

Dukes, 2007), most importantly the nearly continuous presence of ripe fruits. The amount and timing of rainfall affects the sexual reproduction of *Opuntia* species from the number of buds and fruiting success to the size of the fruit and the number of seeds (Reyes-Agüero et al., 2006). The double rainfall regime in Mukogodo (compared to single rainfall zones in other places) likely had an impact on *O. stricta* reproduction reducing its seasonality. Fruit abundance then influenced browser preferences for fruit over pads. However, *O. stricta* fruits also had nutritional advantages over pads (Kunyanga and Imungi, 2009) as well as over the fruits of native species (Foxcroft et al., 2011; Padrón et al., 2011; Rejmánek, 1996).

Next, because consumers only ate fruit, *O. stricta* plants were not destroyed. This is in contrast with both *O. ficus-indica* and *O. monacantha*. Browsers ate the seasonal fruit of these species but baboons and other mammals also ate the pads in the dry season. As a result, both species nearly disappeared from the study area in the late 1980s–1990's and also from the baboons' diet. The fourth major *Opuntia* species, *A. subulata*, has pads with a dense network of long spines, normally an effective defense against browsing. None-the-less, baboons ate *A. subulata* pads in the drought of 1992 when food was extremely sparse. *A. subulata* seeds are sterile outside of its native habitat (CABI, 2014) so as an alien plant, it disperses through vegetative growth. This is not a fast method; *A. subulata* living fences which predated the *O. stricta* invasion have grown very dense, but the plant hasn't spread far from each initial location.

The dispersal agents in the *O. stricta* invasion, elephants, baboons, people, and livestock, each had its own imprimatur. These vectors spread *O. stricta* over an area of 32 km² (3200 ha) in 2006, 48 km² (4800 ha) by 2008, and 662 km² (66,200 ha) by 2014. Elephants carried *O. stricta* the furthest using a corridor that traversed the area from the point of origin in the East, westward across communal and then private lands and ultimately across the Uaso Ngiri River, a distance of 53 km. This meant that elephants fed on *O. stricta* fruits in communal areas with highest plant density, then traveled 15 km in a day, depositing partially digested *O. stricta* fruits in their dung ahead of the invasion (see Fig. 3). In contrast, the pattern at baboon sleeping sites suggests that if *O. stricta* wasn't already in the baboons' home range, baboons couldn't and didn't play a role in dispersing the plant. Baboon impact on *O. stricta* density was highest within 100 m of the sleeping rocks, reflecting the baboon habit of defecating as they leave their sleeping site in the morning. People and their livestock also dispersed the fruit and seeds, foraging more widely than baboons but not as far as elephants. Within this area, Maasai homesteads (bomas) created hotspots of *O. stricta*. Density peaked at 200 m but there was a "cordon sanitaire" immediately around the settlement. Other human activity subsequent to the start of the study further influenced the spread of the plant. For example, local women began making charcoal from large indigenous acacia trees. Since there is no grass to cover the traditional kilns, the women now use *O. stricta* pads. Plants then grow on old charcoal making sites (Fig. 8).

4.2. Why did *O. stricta* invade now?

O. stricta was present in Doldol for more than 50 years before it invaded the surrounding landscape despite the same dispersal agents being present. Baboons, at least, were recorded to have eaten fruits from the few localized plants but nothing much happened during this 50 year period. A "lag" phase between establishment and spread of an invasive plant has been documented in other alien plant invasions (Theoharides and Dukes, 2007). However, in the case of Mukogodo, we proposed that the lag coincided with a specific ecological state transition, from savanna grassland to denuded landscape. Historically, Maasai and



Fig. 8. *O. stricta* growing out of abandoned charcoal kiln.

their livestock were only seasonally present in the study area. Beginning with the extreme rainfall of El Niño in 1998, pastoralists started to settle permanently. Our data demonstrate that this new grazing pressure reduced ground cover and suppressed herb layer growth in the settled areas but not elsewhere. A similar effect has been documented for other rangelands in Kenya (Groom and Western, 2013; Kaye-Zwiebel and King, 2014; Kioko et al., 2012; Western, 2009). The role of range degradation in invasibility is not surprising. Witt and Nongogo (2010) argue that CAM plants, including *Cactaceae*, have difficulty in savanna habitats because of the dominance of C_3 trees and C_3 and C_4 grasses. This would have been the case for Mukogodo for most of the 50 years. Latterly, increases in seasonal livestock grazing created “intermediate disturbance” (Catford et al., 2012; Theoharides and Dukes, 2007) which triggered the expansion of *Sansevieria intermedia*, an indigenous succulent that prefers disturbed areas. Local pastoralists commented on the loss of grazing to *Sansevieria* (see also (King and Franz, 2008)). Finally, settlement and year-round grazing sharply reduced ground cover. Destruction of a diverse native plant community released more of the captured organic matter stored in the above ground biomass and roots. *O. stricta* took advantage of this greater ecosystem invasibility (Bradley et al., 2010; Catford et al., 2012; Theoharides and Dukes, 2007).

The correlation between intense grazing by livestock and

increased invasibility of native plant communities (D’Antonio et al., 1999) has been documented in Australia and North America where native grassland communities suffered more damage from introduced ungulate grazers than from introduced annual plant species (Theoharides and Dukes, 2007). Data from Nevis and St. Kitts (Pemberton and Liu, 2007) also show a connection between the intensity of livestock grazing and the distribution of both native and non-native species of *Opuntia* on the islands. Janzen (1986) suggests that the historical introduction of livestock into the southwest US and northern Mexico was the precondition for the invasion of cacti and other large perennials into many habitats in that region. Further evidence from around the Mediterranean and the Canary Islands (Padrón et al., 2011) links *O. stricta* invasion with the elimination of all native plants in former croplands.

The removal of native competitors helps alien invasive plants to achieve higher growth rates despite being at initially low densities. Afterwards, propagule pressure is strongly correlated with the probability that an invasive species will become established (Leung et al., 2004). However, Britton-Simmons and colleagues (2008) demonstrate that propagule pressure alone was not enough to insure invasion success. They point to the newly released resource availability as critical to the timing of a successful invasion. In general, communities that were disturbed, and therefore had higher resource availability, were more likely to be invaded



Fig. 9. a: Inside and outside Twala enclosure under the same rainfall, 2014. b: Inside Twala enclosure 2014 with *O. stricta* being choked by native vegetation.

(reviewed in Theoharides and Dukes, 2007).

4.3. Comparison between Mukogodo and Kruger National Park: species, context, and habitat

A great deal of research has been done to reconstruct *O. stricta* invasion in Kruger National Park in South Africa (e.g. Foxcroft and Rejmánek, 2007; Foxcroft et al., 2011; Hoffmann et al., 1998). It is estimated that 30,000 ha of conserved habitat was invaded by *O. stricta* by 1998 (Foxcroft et al., 2004). The framework of Foxcroft et al. (2011) is useful for comparing Kruger National Park to Mukogodo. The similarities between the sites include species characteristics like the attraction of fleshy fruit to herbivores, the large number of viable seeds, suitable climate and the general success of CAM plants in invading semi-arid regions of the world. Both places have large herbivores with pathways for dispersal agents to travel, and propagule pressure. There are differences too. In Kruger, microhabitats were needed for *O. stricta* plant nurseries and baboons (*Papio ursinus*) were the long-distance seed dispersers whereas elephants were the short-distance vegetative disperser (Foxcroft and Rejmánek, 2007), the opposite of Mukogodo. Moreover, Kruger is a protected area where livestock and pastoralists are excluded whereas in Mukogodo, these have transformed and degraded the rangeland. The ecology also differs including the important role that fire plays in structuring the vegetation of Kruger National Park whereas there are no fires in Mukogodo. Witt and Nongogo (2010) emphasize that *O. stricta* is very fire sensitive and stress the complex interplay between heavy livestock grazing and suppressing *Opuntia* in South Africa rangelands and elsewhere.

The Mukogodo/Kruger comparison demonstrates the complexity of the invasion process. It clarifies why invasive species are best understood as part of ecosystem dynamics rather than isolated from them and as part of a complex system with many uncertainties and drivers operating at multiple scales.

4.4. Implications

Mukogodo provided a rare opportunity to study the invasion of *O. stricta* against a backdrop of a closely monitored environment in the course of transition from mobile pastoralism to sedentary herding. Enemy release and propagule pressure added to the opportunity for *O. stricta* to invade. If this interpretation is correct, then what is Mukogodo's future? The work in Kruger National Park is instructive. Over time, Kruger National Park developed an "integrated" management approach (Foxcroft et al., 2004; Hoffmann et al., 1998; Lotter and Hoffmann, 1998) that incorporated multiple control agents beginning with mechanical and chemical destruction and proceeding to biological control (Paterson et al., 2011).

An experimental introduction of a bio-control agent (*Dactylopius opuntiae*) in the study area has begun. Bio-control should limit the invasion, as it has in Kruger and elsewhere. But what will happen afterwards (Bradley et al., 2010)? Data from Nevis and St. Kitts (Pemberton and Liu, 2007), suggest that the effectiveness of bio-control varies according to plant species, location, and grazing pressure (Pemberton and Liu, 2007). Good pasture did not return after successful bio-control of *Opuntia* species on Nevis and St. Kitts because of continued overgrazing by goats (Pemberton and Liu, 2007). We suggest, therefore, that as long as *O. stricta* survives, facilitated by degraded habitat created by continued heavy livestock grazing, the fruit and seeds will continue to be dispersed by the same consumers. Perhaps, as Catford et al. recommend (2012), the focus should turn to the causes rather than the symptoms of invasion. For Mukogodo, this means an emphasis on better herding practices in the transition from subsistence to market economies

(Fratkin, 2001; King and Franz, 2008; Manzolillo-Nightingale and Western, 2006). A recent study of pastoralism conducted nearby concluded that it is no longer a viable livelihood because of land appropriation, increasingly limited opportunities for livestock mobility, growing livestock densities and over grazing, and growth of the human population (Kaye-Zwiebel and King, 2014). However, there is evidence from Mukogodo and elsewhere (Kioko et al., 2012; Western, 2009) that eliminating grazing quickly restores native rangeland. In 2012, a 16 ha fence was erected around the Twala Women's Group Cultural Manyatta to exclude all wild and domestic grazers and browsers. *O. stricta* was present throughout the parcel at the time. By the end of 2013, there was considerable grassland and tree regeneration (Fig. 9a). By 2014, native vegetation inside the enclosure was choking *O. stricta* (Fig. 9b). This suggests that restoration of natural herb layer and tree cover might stop the spread of *O. stricta* by reversing the degradation that facilitated its expansion in the first place.

Most ecosystems, including semi-arid and arid rangelands, are becoming human dominated (Vitousek et al., 1997) creating conditions and opportunities for invasive species (Catford et al., 2012). Bradley and colleagues state that "changes in land use or land cover could have a greater impact on invasion than other types of anthropogenic change" (Bradley et al., 2010: 314). In Mukogodo, *O. stricta* did not spread despite suitable climate and extensive rainfall and biomass variability until changed land use practices destroyed the native rangeland.

Humanization of landscapes is increasing throughout the world, from urban to rural and from forest to desert. Alien succulents are particularly suited to invading degraded rangelands and arid lands (Janzen, 1986; Osmond et al., 2008; Witt and Nongogo, 2010). The Mukogodo *O. stricta* invasion illustrates the challenges posed by alien plant species in human modified landscapes even before the effects of climate change (Bradley et al., 2010; Osmond et al., 2008; Theoharides and Dukes, 2007). This study suggests that it is important to look at the underlying causes of alien plant invasions to avoid exacerbating their impact on rangelands.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2015.02.015>.

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