

Current and potential economic costs of *Opuntia stricta* invasions in Africa

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Abstract

Cacti have been introduced to many parts of the world for food, fodder, and ornamental purposes. Many of these have become invasive, impacting negatively on human and animal health, biodiversity, and pasture production. *Opuntia stricta* is invasive in several countries in Africa. Studies in Laikipia County, Kenya, have shown that this invasive plant has significant negative impacts on livelihoods and biodiversity. We estimated the costs of current invasions to livestock production in Laikipia and regionally in eastern Africa. Using an eco-climatic model, we extrapolated potential costs to sub-Saharan Africa on the assumption that *O. stricta* is likely to at least partially invade all areas that are climatically suitable. Areas invaded by *O. stricta* in Laikipia prevented access by livestock and wildlife to an average of 408 g/m² of forage, valued at USD 0.12/m². Based on this finding, we estimate that the current cost of *O. stricta* invasions is over USD 5.67 and USD 168 million in Laikipia and in eastern Africa respectively. A conservatively estimated area of 682,000 km² (2.3% of sub-Saharan Africa) is at different levels of risk of invasion. Using plausible spread rates of 5–15% annually and scenarios of area at risk of invasion, we estimate that costs associated with the loss of forage in sub-Saharan Africa could grow to a mean present value of USD 77 billion over 50 years (range 10–300 billion assuming discount rates of 3 and 5%). The introduction of the biological control agent, *Dactylopius opuntiae* 'stricta' biotype, has already reduced these potential impacts significantly in South Africa and Kenya.

Introduction

A large number of species in the family Cactaceae have been introduced to various parts of the world where they have become invasive with significant negative impacts on agriculture, especially livestock production, and natural ecosystems (Ueckert et al. 1990; Beinart 2003; Larsson 2004; Novoa et al. 2017; Shackleton et al. 2017). In some situations, *Opuntia* species can even become problematic in their native range. For example, Captain Meriwether Lewis, commander of the famous Lewis and Clark expedition, was tasked to map and explore the Louisiana Purchase in North America in 1803. He recorded in his journal that “the prickly pear is now in full blume (sic) and forms one of the beauties as well as the greatest pests of the plains” (Bergon 1989 in Defelice 2004). Lewis later wrote that “the prickly pears are so abundant that we could scarcely find room to lye (sic).” Even today, *Opuntia* spp. are considered to be problematic in the USA, including Texas, where the prickly pear occupies about 10.3 million ha of rangeland (Lundgren et al. 1981).

Of the cactus species that have been introduced outside of their native range, 57 have become naturalised and problematic, particularly in arid rangelands (Novoa et al. 2015). Currently there are three invasion hotspots with 35, 26 and 24 invasive cactus species recorded in South Africa, Australia, and Spain, respectively (Novoa et al. 2015). The most widespread of the invasive cactus species is *O. ficus-indica* (22 countries), with other species invasive in 15 or fewer countries (Novoa et al. 2015). Of the invasive cactus species in eastern Africa such as *Opuntia stricta* (Haw.), *O. ficus-indica* (L.) Mill., *O. monacantha* Haw., *O. engelmannii* Salm-Dyck ex Engelm., *O. elatior* Mill. Gard., *Austrocylindropuntia subalata* (Maehlenpf.) Backeb., and *Cereus jamacaru* DC., only *O. ficus-indica* is actively utilized for its

fruit and occasionally for fodder, while most of the others are seen as being largely problematic, impacting negatively on livelihoods and/or biodiversity (Witt and Luke 2017; Shackleton et al. 2017; Witt et al. 2018).

Once established, cactus species can rapidly invade a large area, especially in arid and semi-arid regions. For example, the Australian pest pear, *O. stricta*, which was first introduced to pastoral areas in Australia in the 1840s, covered over 4 million hectares in Queensland and New South Wales by the early 1900s, and by 1925 had invaded over 24 million hectares, resulting in the abandonment of large tracts of agricultural land (Dodd 1940; Mann 1969; Raghu and Walton 2007). Land abandonment was also reported in Kenya (Shackleton et al. 2017). In Laikipia County, Kenya, two-thirds of respondents to a questionnaire survey undertaken in 2014 estimated that 50–75% of valuable grazing land had been invaded by *O. stricta* (Shackleton et al. 2017). This can have a serious impact on livestock carrying capacities. Livestock will not graze grasses growing around, or amongst, cactus plants to avoid being injured by the spines, leaving a band of grass around each stand (Fig. 1). This ungrazed portion may actually comprise twice the area of that covered by the cactus plants themselves (Taylor and Whitson 1999). In Madagascar, *O. stricta* has invaded crop fields and rangelands, and has encroached on villages and roads, impeding human movement (Larsson 2004). In Madagascan rangelands it has had a negative impact on native grasses and herbs, and according to communities is affecting trees by inhibiting their growth and regeneration (Larsson, 2004). The majority of respondents to a survey in Laikipia, said that *O. stricta* also had a negative impact on grass and wildlife (Shackleton et al. 2017).

Respondents to the survey in Kenya also said that *O. stricta* also had a negative impact on livestock health (Shackleton et al. 2017). This finding was supported by earlier research that reported that fruit consumption resulted in bacterial infections, while the hard seeds may cause rumen impaction, which can be fatal (Ueckert *et al.* 1990). According to Beinart (2003) the glochids on the fruit often diminish an animal's capacity to eat and sometimes result in death. The consumption of large amounts of cactus cladodes can also cause cattle to scour and may even cause bloat, especially in cases where cattle are not accustomed to it as a feed. Some cattle have even been reported to die from accumulation of cactus fibre in the stomach (Griffiths 1905). A more recent study by Ncebere et al. (2021) found that goats affected by *O. stricta*, especially those that consumed large numbers of cactus fruit, had poor body condition, wounds on various body parts, and diarrhea. The pathological effects resulted in “emaciated goats due to pain, inability to masticate and assimilate food, and stress, resulting in poor carcass and organ quality and possible condemnation and death” (Ncebere et al. 2021).

Consumption of the fruit can also have negative impacts on human health (Larsson 2004) and in some instances cacti can cause both an allergic response and a nonimmunologic irritant reaction in people (Paulsen et al 1997; Andersen et al 1999). Invasive alien plants such as cacti can also enhance the survival of disease-carrying organisms (Manda et al. 2007; Müller et al. 2010; Junnila et al. 2011; Nyasembe et al. 2012; Stone et al. 2012; Müller et al. 2017; Stone et al. 2018). Junnila et al. (2011) found that one of the most attractive fruits to sand flies in Israel were those from *O. ficus-indica*. Phlebotomine sand flies are known to transmit leishmaniasis which affects some of the poorest people on earth, and is

associated with malnutrition, poor housing, a weak immune system and population displacement. Leishmaniasis affects 700,000 to 1 million people, causing 26,000 to 65,000 deaths annually (WHO 2023). The proliferation of invasive cacti may therefore contribute to the increased incidence of malaria and leishmaniasis.

Taylor and Whitson (1999) found that grasses growing adjacent to cactus plants are also not grazed because animals are wary of the spines. This is known as “associational resistance”, whereby spiny or unpalatable plant species effectively protect other plant species from herbivorous animals (Callaway et al. 2000, 2005; Smit et al. 2005, 2006; Barbosa et al. 2009). Toxic and well-defended nurse plants, like those with spines, provide associated recruits with significant protection (Smit et al. 2007). For example, survival and growth of *Quercus robur* seedlings was inhibited by the presence of cattle and rabbits, but survival was significantly enhanced when they were planted near young, thorny *Prunus spinosa* shrubs (Bakker et al. 2004). In Laikipia County, Kenya, 50% of survey respondents mentioned that *O. stricta* increased the presence of trees and shrubs in the landscape (Shackleton et al. 2017), because the spines on cactus plants protect native seedlings and saplings from livestock consumption. Cacti therefore reduce livestock carrying capacities by directly or indirectly reducing access to forage.

Despite the serious negative impacts of invasive cacti, the potential economic costs of cactus invasions have never been estimated at a local, national or continental scale. In this study we estimate the amount of grass forage rendered inaccessible to livestock due to the presence of the invasive cactus, *O. stricta*. Our study is based on the potential loss of grazing alone, and other costs are not considered. Based on the results of an eco-climatic model, and assuming that *O. stricta* will invade a conservatively estimated proportion of climatically suitable areas, we extrapolate those costs to the rest of the continent under plausible scenarios of rate of spread and area likely to be invaded over the next 50 years.

Materials and Methods

Study sites

This study was undertaken at local, regional and continental scales. The local impact of invasions by *O. stricta* on grass biomass was examined at two sites (Dol Dol and Ol Jogi) in Laikipia County, Kenya. Laikipia County lies on the equator, north of Nairobi. It has a temperate climate with mean annual rainfall of between 200 and 600 mm and mean annual temperatures of 16–26 °C. The natural vegetation is a mixture of grasslands and savannas dominated by tree species in the genera *Vachellia* and *Commiphora*. Dol Dol, a town in Laikipia County, is surrounded by smaller villages and settlements occupied mainly by Mukogodo Maasai pastoralists who have recently adopted a semi-sedentary lifestyle. The area is relatively under-developed, with most households relying on livestock and natural resources for sustenance. Much of the land is severely overgrazed and degraded. In contrast, the neighbouring Wildlife Conservancy of Ol Jogi is in a much better condition but like much of the surrounding community rangelands is also heavily invaded by *O. stricta*. The distribution and cover of *O. stricta* at a regional scale was based largely on roadside surveys in Ethiopia, Kenya, and Tanzania, and in

more detailed surveys in Laikipia County. At a continental scale, the potential for invasion was extrapolated based on climatic modelling (see below) to cover all sub-Saharan countries in Africa.

Impact of *Opuntia stricta* on grass production

We attempted to determine the amount of the inaccessible forage by measuring the amount of grass growing amongst, and adjacent to *O. stricta* plants. Clipped pasture sampling is the most accurate and commonly used method for determining phytomass (Sharrow 1984; Harmoney et al. 1997), but clipping is laborious and destroys a portion of the sward sampled. To address this a disc pasture meter (DPM) was developed to determine forage phytomass (Bransby and Tainton 1977). The DPM integrates sward height and density into one measure and provides a practical and efficient method to determine grass biomass (Joubert and Myburgh 2014). Initially we used the clipped pasture method, and later the DPM which allowed us to take multiple measures in and around each cactus plant. The DPM provides a measure of dry mass in the field, which was used for estimating the financial value of the grass (see below).

For clipped pasture sampling we established ten transects, each 50 m in length, in two landscapes, one in communal grazing lands near Dol Dol, and the other in Ol Jogi Wildlife Conservancy. Transects were established every 50 m along the road, perpendicular to the edge of the road. We placed 1x1 m quadrats at 10 m intervals along each line transect. Measures were taken at the starting point at 0 m, which allowed for six samples per transect. All grass within the quadrat was removed at ground level and placed in a bag and weighed. If the quadrat fell on a cactus plant, all cladodes were removed and the grass under the plant was removed and weighed. In this way we were able to determine the wet (field) biomass of grass in quadrats occupied, or partially occupied, by cactus, for comparison to quadrats where there was no cactus.

We then estimated dry grass biomass using a DPM. Fifteen *O. stricta* plants were randomly selected in each of the two landscapes, the communal lands near Dol Dol, and on Ol Jogi Conservancy. All cactus cladodes, and stems, in the centre of each plant were carefully removed to ground level. The DPM was then used to estimate grass biomass growing below each cactus plant. Similar measurements were made at each of the four compass points immediately adjacent to each plant, and another four 1 m away. In this way we obtained nine measurements for each of the 15 *O. stricta* plants. The height at which the disc settled was then converted to kg of dry matter/ha using the regression equation developed by Botha (1999) in Lewa Wildlife Conservancy, Kenya, approximately 100 km east of Ol Jogi.

Current distribution and cover of *Opuntia stricta*

At a local scale, the distribution of *O. stricta* in Laikipia County was obtained from Witt (2017) who mapped the distribution of *O. stricta* in grid cells of 1/16 degree of longitude and latitude (~ 11 x 11 km). At each locality within the grid cell, the status of *O. stricta* was recorded as either present, naturalised, or invasive and spreading. The cover of *O. stricta* in Ol Jogi Conservancy and Dol Dol was also determined by establishing five 100 x 100 m plots at random in each of these two landscapes. Ten 10x10 m sub-

plots were then randomly located within each of the plots, and the percentage cactus cover for each of the 50 sub-plots was estimated visually.

Information on the distribution of *O. stricta* at a regional scale was estimated in three eastern African countries (Ethiopia, Kenya, and Tanzania) using data from Witt and Luke (2017). These data recorded the presence of *O. stricta* within grid cells of half a degree of longitude and latitude (~ 55 x 55 km), with status noted as either present, naturalised, or invasive and spreading, as above.

Estimates of cactus cover at a wider landscape level was also obtained from an unpublished report compiled by the United States Department of Agriculture Forest Service (USFS) who used remote sensing to determine cactus cover in 2018 over an area of 160,000 ha in Naibungu Conservancy, Laikipia. The USFS recorded *O. stricta* as absent or rare (< 5% cover) on 88% of the landscape, and present with higher cover (> 5%) on 12% of the landscape. Overall cover values ranged from 0–29% over the whole surveyed area.

We combined the data from Witt and Luke (2017) with that of the USFS to estimate the cover of *O. stricta* in Ethiopia, Kenya and Tanzania. We only included grid cells in which *O. stricta* was recorded as invasive and spreading by Witt and Luke (2017). Within these cells, we assumed that 88% of the grid cell had no cactus cover (more conservative than the USFS data), and that the remaining 12% had cover values of 5, 10, 15, 20, 25 and 29% in equal proportions, based on USFS data (i.e. a mean cover of 17.33% over 12% of the invaded area). At a regional level these estimates are assumed to be conservative, as the survey of Witt and Luke (2017) only covered 35, 64 and 39% of the grid cells in Ethiopia, Kenya and Tanzania respectively (Witt et al. 2018).

Area suitable for invasion

Distribution data recorded by Witt and Luke (2017) and Witt (2017), or acquired from other databases such as the Global Biodiversity Information Facility (GBIF) were used to develop a CLIMEX eco-climatic model (Kriticos and Randall, 2001). CLIMEX is used to fit eco-climatic niche models that estimate the potential distribution or phenology of organisms based on distribution data for the target organism, and additional information about the response of the organism to weather variables drawn from experiments or phenological observations (Kriticos et al. 2015; Sutherst and Maywald 1985).

To determine how much of Africa is at risk of invasion based on its eco-climatic suitability index (EI) we converted the CLIMEX model output to a shapefile. The model was then cut to African country boundaries (Natural Earth data) and the major African lakes were removed. The cells were then grouped by EI value with 0 = not suitable; 1–30 = low suitability; 31–60 = medium suitability; and 61–100 = high suitability. The area of cells within each suitability category was then calculated for each country.

Value of forage displaced by invasions

Natural forage is not a resource that is regularly traded on the open market, but is used directly as fodder for free-ranging livestock. We therefore used shadow pricing to assign a monetary value by using the

price of straw bales, based on the assumption that the loss of this pasture would need to be replaced. Overgrazing, as well as invasion by *O.stricta*, has led to the loss of grass forage which must be replaced by purchased fodder in straw bales if livestock numbers are to be retained, especially in arid areas. This provided a shadow price of the financial value of forage that could no longer be accessed by livestock because of the presence of *O. stricta*. To this end we purchased and weighed 15 straw bales and calculated a mean cost per kg for each bale.

The current value of forage displaced by *O. stricta* invasions locally in Laikipia and regionally in Ethiopia, Kenya, Tanzania was determined by multiplying the area covered by the value of displaced grass per unit area.

Future growth of *Opuntia stricta*

Climatic modelling provided an estimate of the area at risk of future invasion over the next 50 years assuming that the climate remains unchanged over that period. A 50-year time horizon was used as this reflects the time taken for *O. stricta* invasions to gradually establish a population before spreading exponentially over available suitable areas. Climate is only one of several factors that influence the ability of an invasive species to colonise new areas, albeit a very important one. To address this uncertainty, we examined three scenarios to illustrate possible future states, in which the proportion of each CLIMEX suitability class differed in terms of the proportion that would become invaded (Table 1). In each scenario, we assumed that the area that becomes invaded would be in the same proportion to the range of coverage reported by the USFS (i.e. only 12% of the climatically suitable area would be covered by *Opuntia stricta* with a mean cover of 17.33%, see above). The rates at which populations of *O. stricta* could plausibly spread are uncertain and can vary over space and time. To account for this uncertainty and variability, we simulated the potential spread of *O. stricta* using a logistic function calibrated and run using three values for the average annual rate of spread (5, 10 and 15%). These rates of spread were chosen based on published estimates recorded for a range of invasive species in different settings (van Wilgen and Le Maitre 2013). The logistic function was:

$$dP/dt = kP(1 - P/L)$$

where

P = population at time t ;

L = limiting or carrying capacity (maximum size of population); and

k = constant of proportionality (i.e. rate of spread)

Table 1
Three scenarios depicting the percentage of an area that could become invaded by *Opuntia stricta* in four categories of climatic suitability

Scenarios of possible cover achieved	Suitability based on climate modelling			
	Not suitable	Low	Moderate	High
High	0	5	20	50
Moderate (base case)	0	2	10	30
Low	0	1	2.5	15

Potential future value of lost forage

We used the estimated area invaded annually and the value of grass forage that would not be accessible for consumption to derive future costs of invasion over 50 years for each country under the three scenarios of cover achieved (Table 1). The estimated annual future costs were discounted at rates of 3% and 5% that reflect the time preference of individuals to value the present over the future. Discounting of future to present values is necessary because options are available to invest money and receive a positive rate of return, depending on the market interest rate. Most countries in Africa have interest rates between 2 and 10% with 11 countries experience rates of between 15 and 25%. We have used a lower rate than the official interest rates of most African countries because of inter-generational equity issues associated with the longer time horizons over which environmental and social costs manifest, the possibility of significant (non-marginal) threshold effects associated with invasive species infestations, and the high levels of uncertainty (DeMartino et al. 2024; Stern et al. 2022; Weitzman et al. 1998).

Results

Impact of *Opuntia stricta* on grass production

Estimates using both the clipped quadrat and disc pasture meter (DPM) revealed 2–5 times more grass biomass under or adjacent to *O. stricta* plants than where *O. stricta* was absent. At Ol Jogi, five of the 60 clipped quadrats were bare ground with no grass or *O. stricta* cover, 11 were fully or partially occupied by *O. stricta*, and the remainder (44) mainly had grass cover. Quadrats occupied by *O. stricta* supported an average ($\pm$ SE) of 217 ± 34 g/m² ($n = 11$; range 53–444 g/m²) of grass (wet mass), compared to 105 ± 14 g/m² ($n = 49$; range 0–410 g/m²) where *O. stricta* was absent, a significant difference ($P = 0.001$) (Fig. 2). At Dol Dol, 31 of the 60 clipped quadrats had no grass cover, although four of these supported small cactus plants. Quadrats occupied by *O. stricta* supported an average of 154 ± 28 g/m² ($n = 22$; range 0–418 g/m²) of grass (wet mass), compared to 32 ± 11 g/m² ($n = 38$; range 0–254 g/m²) where *O. stricta* was absent (Fig. 2), a significant difference ($P < 0.001$).

Estimates using the DPM indicated that dry grass biomass was always higher under cactus plants than in areas adjacent to plants, and 1 m away (Fig. 3). Dry grass biomass was significantly ($P < 0.001$) higher

under *O. stricta* plants in Ol Jogi ($558 \pm 52 \text{ g/m}^2$) than in Dol Dol ($257 \pm 33 \text{ g/m}^2$). There was also more grass biomass adjacent to and 1 m away from plants at Ol Jogi than Dol Dol. At Ol Jogi, on average, there was 45% less grass biomass immediately adjacent to cactus plants than under plants, with 48% less grass biomass 1 m away from plants than immediately adjacent to plants. The pattern was similar in Dol Dol, where there was, on average, 69% less grass biomass in areas adjacent to cactus plants than directly under plants.

Value of forage displaced by invasion

The straw bales had a mean ($\pm$ SE) mass of $9.24 \pm 0.48 \text{ kg}$ per bale, and cost between USD 2 and 3.5 (2016 values of USD) depending on season and availability, so 1 kg of dry grass had an average value of USD 0.295/kg. Because bales are dry biomass, we used the data collected with the DPM which estimated dry biomass (clip plots provided estimates of wet biomass as sampled in the field). We combined the data from Dol Dol and Ol Jogi to get an average dry biomass of $408 \pm 41 \text{ g/m}^2$ on sites that were invaded by *O. stricta* plants ($n = 30$). The average value of this dry biomass growing under *O. stricta* was USD 0.12/ m^2 (USD 120,000 per km^2). This excludes the amount of forage that was not fully utilised adjacent to cactus plants, which in reality would push this figure up considerably (Fig. 3).

Current distribution and cover of *Opuntia stricta*

Opuntia stricta was recorded as invasive in 5.1% of grid cells ($\sim 55 \times 55 \text{ km}$) surveyed in eastern Africa (Witt et al. 2018). *O. stricta* was recorded as invasive in six grid squares in Ethiopia, so it was present in an area of approximately 15,000 km^2 , and present, naturalized or invasive in 27 grid squares in Kenya, an area of about 67,000 km^2 (Witt and Luke 2017). The most significant invasions in Kenya were in Laikipia County and Tsavo East National Park. In Laikipia County, where more thorough surveys were undertaken *O. stricta* was found within 34 1/16 degree grid cells ($\sim 11 \times 11 \text{ km}$); present in five, naturalized in ten and invasive in 19 (Witt 2017).

The mean percentage cover of *O. stricta* in 10 x 10 m sub-plots was 8.82 ± 2.08 (range 0–70%) in Ol Jogi and 13.7 ± 2.62 (range 0–90%) in Dol Dol, giving a mean percentage cover of 11.26 ± 1.68 ($n = 100$). Using these cover estimates and with dry grass estimates of 558 g/m^2 and 257 g/m^2 under *O. stricta* in Ol Jogi and Dol Dol respectively means that 492 kg/ha and 352 kg/ha of dry grass is inaccessible to herbivores in each invaded hectare in each of these areas respectively. However, extrapolating these figures to invasions across the larger Laikipia County, and regionally to eastern Africa, has to be approached with caution, so we used the cover data from the USFS study which was estimated over a much larger area (160,000 ha). This gave an estimated area in which *O. stricta* was present of 1,800, 4,200, and 2,100 km^2 at a mean cover of 17.33% in Ethiopia, Kenya and Tanzania, respectively, giving a total estimated cover of 1,404 km^2 (Table 2).

Table 2

Estimated area invaded by *Opuntia stricta* in three eastern African countries and Laikipia County (Kenya) and the estimated value of forage inaccessible to herbivores as a result of the invasion. Grid cells were approximately 2500 km² in the three countries and 121 km² in Laikipia. Invasions occurred over 12% of the area of grid cells where *O. stricta* was recorded as invasive, with a mean cover of 17.33%

Country or county	Number of grid cells where <i>O. stricta</i> recorded as invasive	Area of grid cells where <i>O. stricta</i> recorded as invasive (km ²)	Area invaded at > 5% cover (km ²)	Estimated area covered by <i>O. stricta</i> (km ²)	Value of inaccessible forage (USD)
Ethiopia	6	15 000	1,800	312	37,440,000
Kenya	13	32,500	4,200	728	87,360,000
Tanzania	7	17,500	2,100	364	43,680,000
Total	26	65,000	8100	1,404	168,480,000
Laikipia County	19	2,299	276	48	5,760,000

Area suitable for invasion

The CLIMEX model indicated that large parts of sub-Saharan Africa have a climate which is suitable for the establishment of *O. stricta* (Fig. 4). There were 14 countries where the risk of invasion was > 10, 000 ha, accounting for between 1.4 and 10.7% of those countries (Table 3). In some smaller countries the proportion at risk of invasion was much greater (e.g. 51% in Malawi, 16% in Rwanda, 14.6% in Benin and 11.4% in Eswatini). For estimates for all countries, see Online Resource 1.

Table 3

The estimated area of selected sub-Saharan countries at risk of invasion by *Opuntia stricta*. The list includes those countries that have > 10 000 ha at risk of invasion under the base case scenario (Table 1). An asterisk (*) indicates that *O. stricta* has been recorded as present in the country

Country	Total area of country (km ²)	Predicted area at risk of invasion (km ²)	Proportion of country at risk of invasion (%)
Angola*	1,244,652	51,448	4.1
Botswana*	578,952	11,448	2.0
Central African Republic	617,984	10,979	1.8
Democratic Republic of the Congo	2,301,012	60,313	2.6
Ethiopia*	1,121,052	70,480	6.3
Kenya*	574,195	41,464	7.2
Mozambique*	779,801	41,335	5.3
Namibia*	822,714	14,347	1.7
Nigeria	906,266	12,282	1.4
South Africa*	1,218,420	99,717	8.2
Tanzania*	885,539	59,508	6.7
Uganda*	206,755	22,123	10.7
Zambia*	742,629	15,133	2.0
Zimbabwe	386,699	19,453	5.0
Sub-Saharan Africa	29,693,104	682,719	2.3

Future growth of *Opuntia stricta*

The proportions of the area suitable for invasion by *O. stricta* that could be covered within 50 years was 19%, 73% and 97% under the spread rates of 5, 10 and 15% per year respectively for the base case scenario. The spread becomes exponential after about 20 years for a growth rate of 15% per year and after about 35 years for a growth rate of 10% per year. The area occupied by *O. stricta* would only reach the full extent of suitable habitat after 50 years in the case of the base scenario if the spread rate is 15% (Fig. 5).

Potential future value of lost forage

The average annual discounted value of displaced forage ranged from USD 512 to 2751 million per year for the base case scenario at different rates of spread, assuming a 3% discount rate (Table 4). The

estimated present value of annual losses at the scale of sub-Saharan Africa grows as the invasion spreads, and when the area becomes more invaded the present value decreases as spread slows (or no further spread is possible) and discounting results in a decline for years further into the future (Fig. 6). The estimated present value of of annual losses displaced forage over 50 years ranged from USD 9.9 to 299.5 billion, with an estimate of 77.1 billion USD for the base case scenario of moderate cover, 10% annual spread and a 3% discount rate (Table 4). The estimated values for all scenarios of area covered, spread rates and discount rates are provided in Online Resource 2.

Table 4

The present value, and average annual discounted value, of displaced forage in parts of sub-Saharan Africa that are climatically suitable for invasion by *Opuntia stricta*. Values are estimated over 50 years for high, moderate (base case) and low levels of cover achieved, assuming annual spread rates of 5, 10 and 15%, and discount rates of 3 and 5%

Assumed annual rate of spread (%)	Discount rate (%)	High cover achieved		Base case		Low cover achieved	
		Present value (billions of USD)	Average annual discounted value (millions of USD)	Present value (billions of USD)	Average annual discounted value (millions of USD)	Present value (billions of USD)	Average annual discounted value (millions of USD)
5	3	55.7	1,092.6	26.1	512.0	9.9	194.8
10		164.5	3,226.3	77.1	1,511.7	29.3	575.2
15		299.5	5,872.6	140.3	2,751.7	53.4	1,047.1
5	5	33.6	658.7	13.4	431.5	5.1	164.2
10		89.8	1,760.7	28.4	917.7	10.8	349.2
15		164.5	3,225.9	56.1	1,809.8	21.3	688.6

Discussion

Impacts associated with cactus invasions

The fact that cactus invasions can reduce the carrying capacity of rangelands has been shown in a number of studies. According to Price et al. (1985) *Opuntia* species invasions reduce grazing potential, a finding supported by Hanselka and Paschal (1991) who found that forage production was two to three times greater in the absence of *Opuntia* species. In Laikipia, Kenya, 91% of respondents to a questionnaire survey reported that cactus invasions reduced access to grasses (Shackleton et al. 2017). Oduor et al. (2018) found that stands of the invasive cactus *Opuntia ficus-indica* in Nairobi National Park, Kenya, harboured more native species than adjacent uninvaded plots. They concluded that the invasive cactus was deterring herbivory of native plant species growing adjacent to it. In this study we have been able to support these findings and demonstrated that there is more grass growing in and among, and immediately adjacent to *O. stricta* plants than in areas 1 m or more away from cactus plants. This is

supported by Taylor and Whitson (1999) who found that the spines of cactus discouraged livestock and wildlife from foraging in or near plants. Cactus plants therefore support the theory of “associational resistance”, whereby spiny or unpalatable plant species effectively protect other plant species from browsing animals (Smit et al. 2005, 2006; Barbosa et al. 2009).

Taylor and Whitson (1999) found that an area 15–20 cm around each cactus plant was not grazed, which is comparable to twice the area of the cactus plant itself. A pasture of 10 ha producing 450 kg of forage would thus lose 160 kg of potentially utilisable forage if invaded. Sheep generally consume 2.5–3% of their body weight per day (~ 3 kg of forage, Taylor and Whitson 1999). This amount of forage could potentially feed one sheep for 53 days. It is assumed that cattle generally consume, on average, about 2.6% of their body weight per day based on the globally accepted norm of a 1,000 pound (~ 454 kg) cow consuming 26 pounds (~ 12 kg) of dry forage daily (Society for Range Management Rangeland Assessment and Monitoring Committee 2016). The carrying capacity of rangelands is thus substantially reduced by rendering a large proportion of forage inaccessible to livestock or wildlife.

The lack of forage is not compensated for by the presence of *O. stricta* in the landscape, despite livestock readily eating the fruit, especially goats. Fruit consumption is known to have a negative impact on livestock health, and the lack of other forage probably leads to an increase in consumption of cactus fruits. Attempts to access grass growing in and around cactus plants, especially during drought when forage is scarce, probably also leads to an increase in injuries caused by the spines. These impacts contribute to estimated losses of between USD 100 and 1000 per household for 78% of survey respondents in Laikipia, Kenya (Shackleton et al. 2017). Considering that the heads of 200 households were interviewed by Shackleton et al. (2017) this amounts to losses in excess of USD 54,000 to 126,000 for the community at large. Fruit consumption results in the lodging of glochids in the lips, mouth and gastro-intestinal tracts of livestock, leading to weight loss and a reduction in milk production, often followed by death (Shackleton et al. 2017). According to Ncebere et al. (2021) internal lesions were observed in subcutaneous tissues (100%), together with stomatitis, cheilitis, gingivitis, glossitis, abomasitis (100%), rumen, reticulum, omasum thinning and loss of papillae (72.2%), esophagitis, and duodenitis (5.6%) in goats that were exposed to *O. stricta* in Laikipia. The spines caused cataracts and blindness in goats and were present on many parts of the body where they elicited pain, swelling and ulcerative wounds (Ncebere et al. 2021). No studies have demonstrated negative impacts on wildlife although Walters et al. (2011) report that spines and glochids are damaging to small wildlife that have not coevolved with cacti.

Many other invasive alien plant species also have negative impacts on livestock carrying capacities (van Wilgen et al. 2008; Witt and Luke 2017; Witt 2017; O'Connor and van Wilgen 2020). For example, the unpalatable invasive plant *Chromolaena odorata* (L.) King & Rob (Asteraceae) is known to reduce pasture carrying capacities from about six hectares per large livestock unit (LSU) to more than 15 ha/LSU (Goodall and Morley 1995). The invasive herb *Parthenium hysterophorus* L. (Asteraceae) has reduced pasture carrying capacities by as much as 90% in Karnataka, India (Jayachandra 1971) while *Cryptostegia grandiflora* Roxb. Ex R.Br. (Asclepiadaceae), once described as the single biggest threat to

natural ecosystems in tropical Australia (McFadyen and Harvey 1990) can reduce carrying capacities by as much as 100%. In South Africa the invasive jointed cactus *Opuntia aurantiaca* Lindl. reduced grazing capacity by up to 90% (van Wilgen et al. 2004). In Ethiopia, *Neltuma juliflora* (Sw.) Raf. (Fabaceae) (previously *Prosopis juliflora*) has reduced understorey basal cover for perennial grasses from 68–2%, and has reduced the number of grass species from seven to two (Kebede and Coppock 2015). In the Nama Karoo, South Africa, moderate prosopis invasions (approximately 15% canopy cover) in a heavily grazed rangeland reduced grazing capacity by 34% from 3.87 to 2.56 LSU per 100 ha (Ndhlovu et al. 2011). Yapi et al. (2018) found a 72% reduction in grazing capacity in sites densely invaded by another invasive tree *Acacia mearnsii* De Wild (Fabaceae). In these dense stands the basal cover of grasses was reduced by up to 42%, resulting in a reduction in grazing capacity of 75%, from 50 to 12.5 LSU units per 100 ha in uninvaded and densely invaded sites, respectively. Without management of these and other invasive alien plants natural grazing capacity in, for example South Africa, would be reduced by 71% (van Wilgen et al. 2008). It is estimated that invasive alien plants currently reduce the value of livestock production in South Africa by ZAR 340 million (USD 19 million at 2025 exchange rates) annually. We are of the opinion that this is a serious underestimate considering that we estimated that *O. stricta* alone could reduce access to forage valued at more than USD 37, 87 and 43 million in Ethiopia, Kenya and Tanzania respectively.

An issue that is often not considered when evaluating the impacts of invasive alien plants is that the lack or absence of forage in invaded areas leads to overgrazing in uninvaded areas, a key driver of landscape degradation, leading to a reduction in plant cover and causing soil erosion. The global economic impact of landscape degradation is highly uncertain, ranging from USD 40 to 490 billion (Nkonya et al. 2016). It is estimated that soil erosion by water could result in economic losses of up to USD 625 billion by 2070 (Satori et al. 2024). In parts of Sub-Saharan Africa, soil erosion is already reaching levels of up to 100 tonnes per hectare annually. According to the Global Assessment of Soil Degradation (GLASOD) (Oldeman et al. 1991, commissioned by the UN Environment Program), the only global assessment of land degradation, 65% of African agricultural land, 31% of permanent pastureland, and 19% of forest and woodland is degraded. The main drivers of soil degradation in Africa are overgrazing (49%), agricultural mismanagement (28%), and deforestation (14%) (Soil Atlas 2024). What is often overlooked is that soils store more carbon than vegetation and the atmosphere combined. At a global level the top 30 cm of soil holds about 694 gigatonnes of carbon (Soil Atlas 2024). Soil erosion therefore contributes significantly to climate change. Invasive alien plants in rangelands are therefore contributing to climate change by reducing available forage, leading to overgrazing and associated soil loss.

Potential savings through management

Biological invasions come at a high cost to Africa. A recent review (Diagne et al. 2021) estimated that the costs of invasions in Africa were between USD 18.2 billion and USD 78.9 billion between 1970 and 2020, and noted that these costs were “highly underestimated” and “increasing exponentially over time”. The impacts of invasive Cactaceae have frequently been negated through the effective use of biological control. For example, in South Africa and Kenya, the deployment of the cochineal insect *Dactylopius*

opuntiae 'stricta' biotype has effectively brought *O. stricta* under substantial control (Witt et al. 2020; Paterson et al. 2021; Zachariades 2021). Although the identification and screening of biological control agents does carry some costs, these are more than offset by the avoided impacts. For example, De Lange and van Wilgen (2010) estimated a benefit-cost ratio of 2,731:1 for all biological control efforts against Cactaceae species in South Africa. Biological control is also comparatively inexpensive and more effective than other control methods. McCulloch-Jones et al. (2024) estimated that spending on the control of biological invasions in South Africa amounted to ZAR 9.6 billion (adjusted to 2022 values) between 1960 and 2023 (although this was clearly a substantial underestimate due to the scarcity of records on spending). Of this, only ZAR 120 million (1.25%) was spent on biological control. However, despite substantially more being spent on physical and chemical control, alien plants continued to increase, and it was only in the plant species where biological control was included in the control program that spread rates were retarded or range contractions were noted (Henderson and Wilson 2017; Kotze et al. 2025). The widespread use of biological control against *O. stricta* across Africa would therefore go a long way to preventing the reduction of forage for livestock and wildlife on which we have placed a present value of USD 77 billion. The cost of preventing this loss would be trivial in comparison, because (1) an effective biological control agent, *Dactylopius opuntiae*, has already been identified, screened, and found to be safe and effective, and (2) the agent is likely to spread naturally from release sites in South Africa and Kenya at no real cost to neighbouring countries. The only cost may be a need to physically introduce the cochineal to countries or regions with isolated *O. stricta* invasions, areas that the cochineal is unlikely to reach through natural dispersal. To speed up the spread within cactus invasions there may also be a need for deliberate breeding and release. The challenge is that those that will benefit from control are unlikely to have the financial resources to introduce, rear, release and disseminate the cochineal. This points to the need for governments or international development or environmental agencies to fund such projects for significant livelihood and environmental benefits.

Declarations

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Author contributions

ABRW conceived the study. ABRW and WN were responsible for data collection in the field. TB curated observation data and performed spatial analysis. JB did some statistical analysis and developed the graphs. RMW conducted the spread and economic analyses. Data analysis and interpretation was done jointly by ABRW and BWvW, and the paper was jointly written by ABRW and BWvW. All authors approved the final copy of the paper.

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Data availability

Data on the distribution of *Opuntia stricta* in Africa are available at <https://www.gbif.org/dataset/23ec2d04-c0eb-4ca4-afb8-a8710e38f641>

Conflict of interest

The authors declare no conflicts or competing interests.

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Figures



Figure 1

Opuntia stricta showing the abundance of grass which is inaccessible to livestock in an otherwise overgrazed area, near Dol Dol, (left) and with the cactus plant removed in Ol Jogi Conservancy (right), both in Laikipia County, Kenya

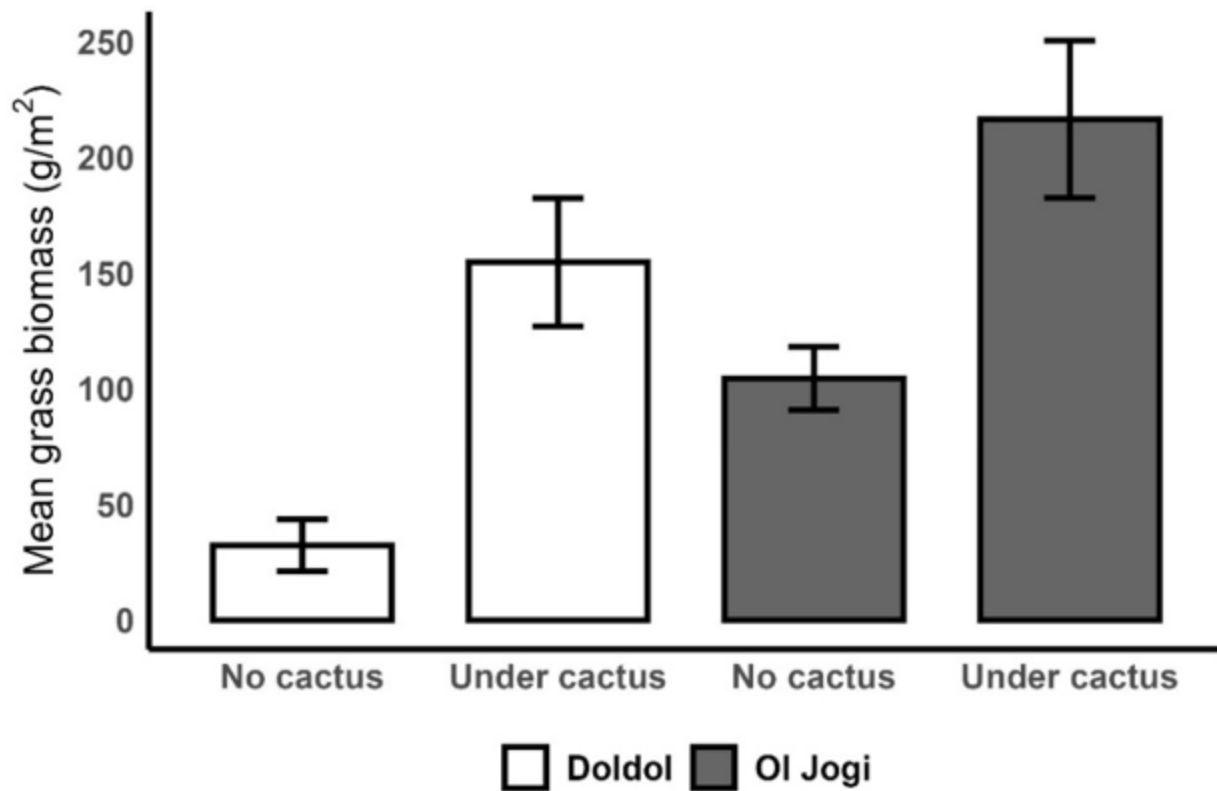


Figure 2

The mean field (wet) biomass of grass in quadrats under *Opuntia strictacactus* plants and on quadrats with no cactus in Dol Dol and Ol Jogi Wildlife Conservancy in Liakipia County, Kenya. Bars show the standard error of the mean

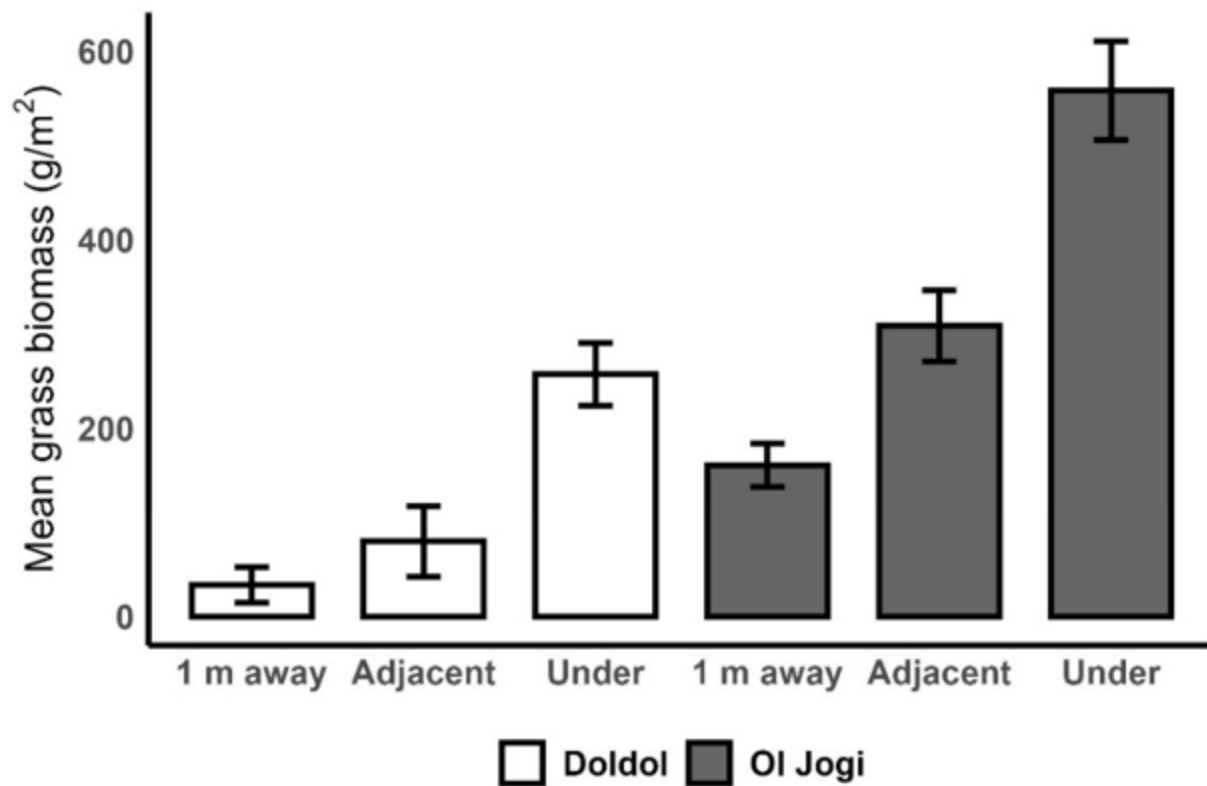


Figure 3

The mean dry biomass of grass under, immediately adjacent to, and 1 m away from the edge of *Opuntia stricta* plants as estimated by a Disc Pasture Meter in Dol Dol and Ol Jogi Wildlife Conservancy, Laikipia County, Kenya. Bars show the standard error of the mean

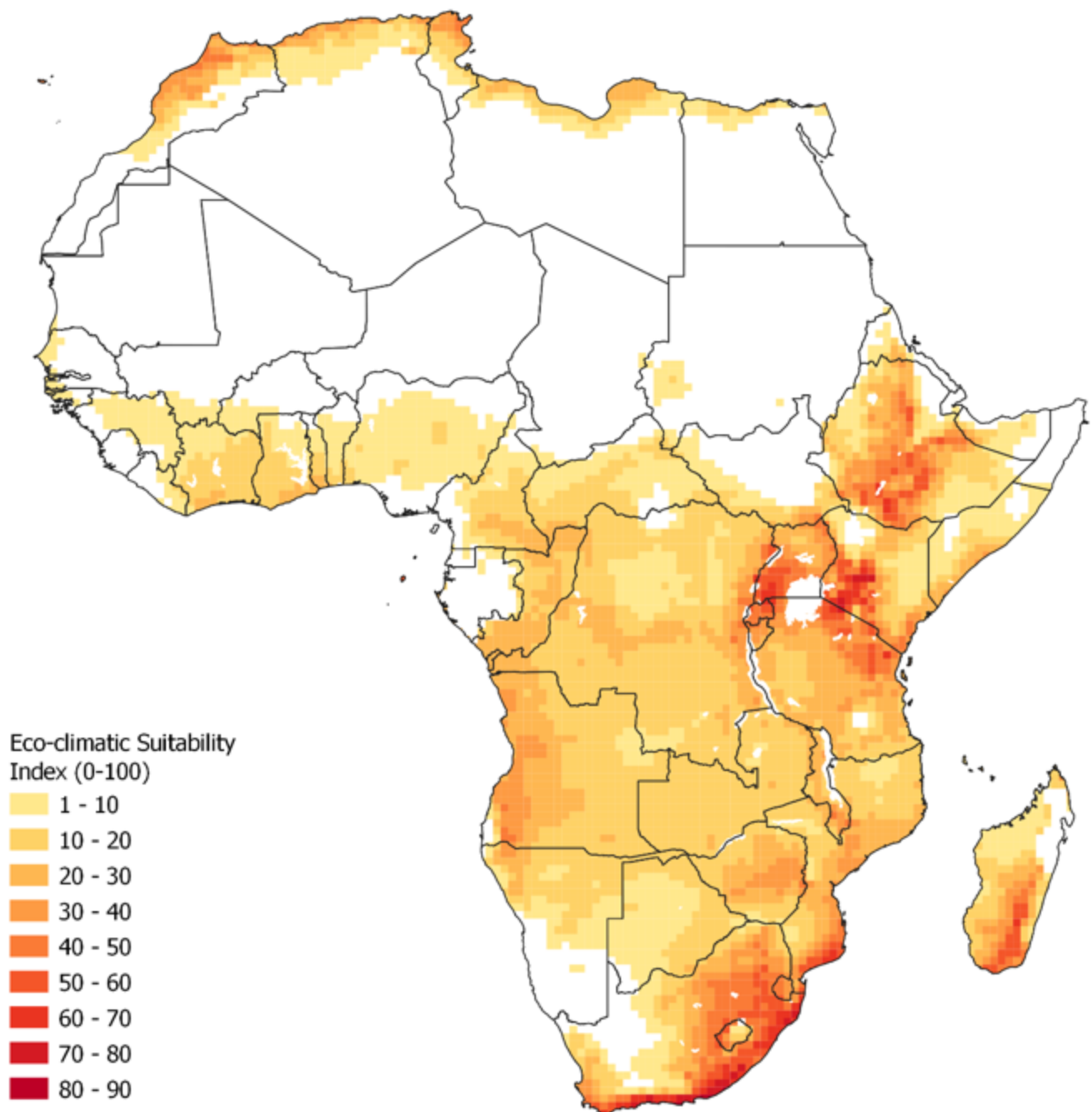


Figure 4

Areas in Africa that are climatically suitable for the establishment of *Opuntia stricta* based on a CLIMEX eco-climatic model developed by Kriticos (unpublished); the darker the shade of orange, the better the match

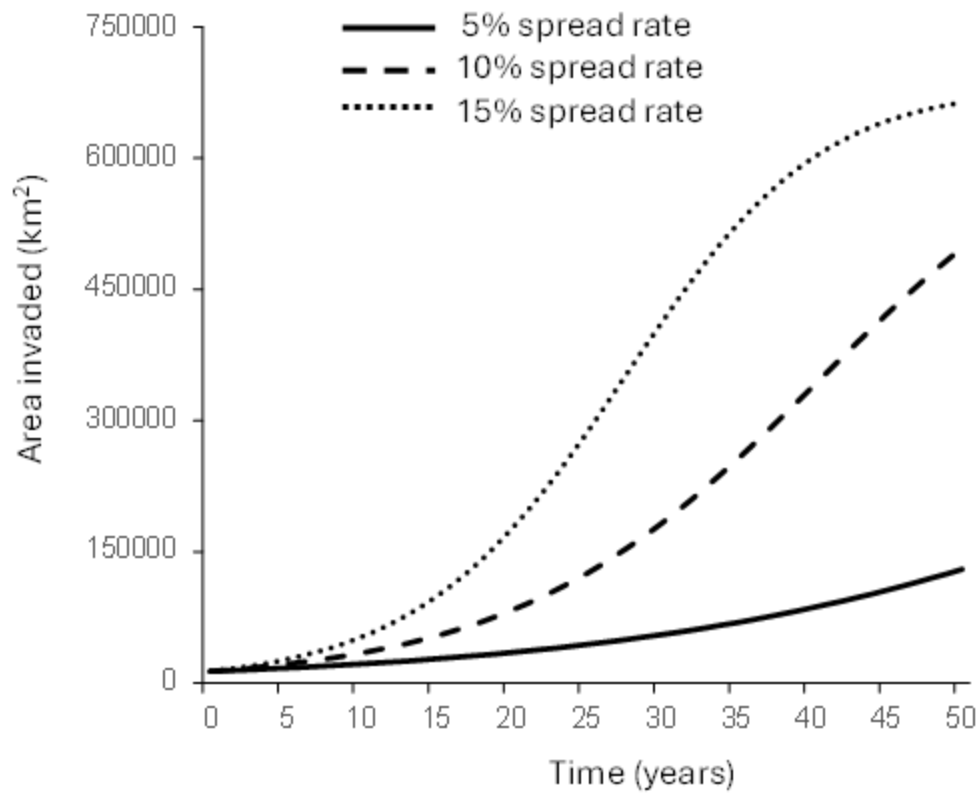


Figure 5

The estimated area invaded by *Opuntia stricta* in sub-Saharan Africa over 50 years, assuming that the mid-level (base case) cover is achieved at spread rates of 5, 10 and 15%

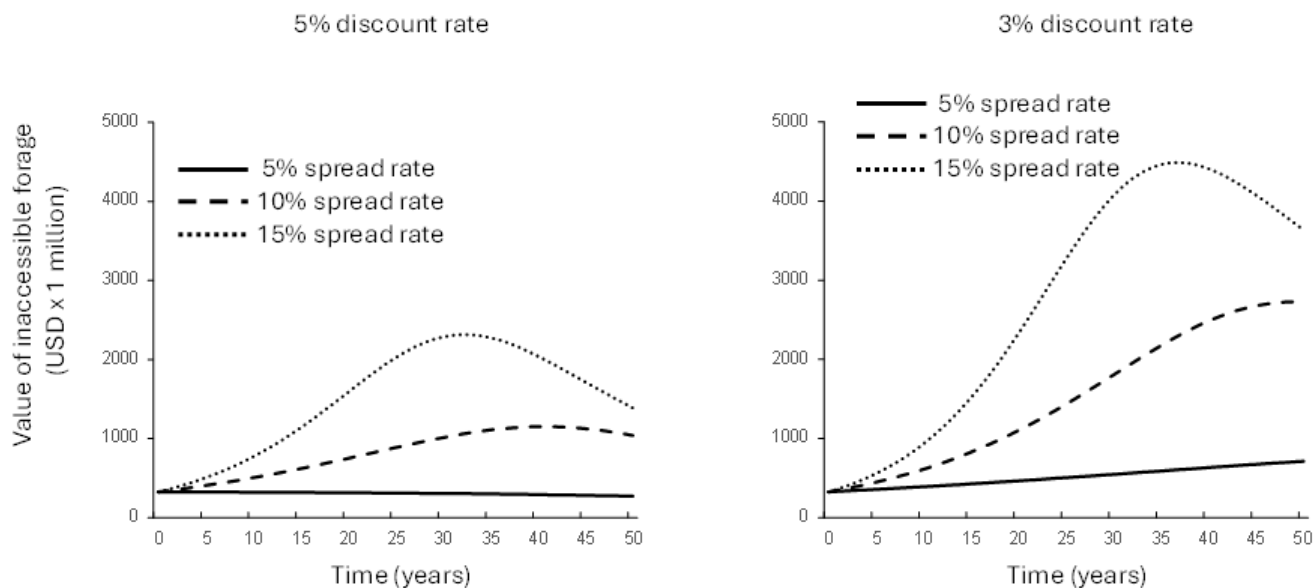


Figure 6

The present value of fodder displaced by *Opuntia stricta* each year in sub-Saharan Africa over 50 years at discount rates of 3 and 5%, assuming that the mid-level (base case) cover is achieved at spread rates of 5, 10 and 15%

Supplementary Files

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