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ARTICLE

Socio-Ecological Systems

Cascading effects of elephant–human interactions and the role of space and mobility in sustaining biodiversity

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Abstract

Our study monitored the changes in elephant numbers, distribution, and ecological impacts over a 50-year period. During this period, the free-ranging intermingled movements of wildlife and traditional subsistence pastoralists across the Amboseli ecosystem were disrupted by a national park, livestock ranches, farms, settlements, and changing lifestyles and economies. Elephants compressed into the national park by poaching and settlement turned woodlands to grassland and shrublands, and swamps into short grazing lawns, causing a reduction of plant and herbivore diversity and resilience to extreme events. The results echo the ecological findings of high-density elephant populations in protected areas across eastern and southern Africa. The impact has led to the view of elephants in parks as being incompatible with biodiversity and to population control measures. In contrast to Amboseli National Park, we found woody vegetation grew and plant diversity fell in areas abandoned by elephants. We therefore used naturalistic and exclosure experiments to determine the density-dependent response of vegetation to elephants. We found plant richness to peak at the park boundary where elephants and livestock jostled spatially, setting up a creative browsing-grazing tension that caused a patchwork of habitats and peak of plant richness. Prehistorical and historical literature reviews lend support to the Amboseli findings that elephants and people, the two dominant keystone species in the savannas, have been intimately entangled and coexisted prior to the global ivory trade and colonialism. The findings point to the need to view specific elephant populations in historical perspective and, as far as possible, create connectivity beyond protected areas to allow mobility on an ecosystem and landscape scale. The Amboseli study underscores the significance of space and mobility in the keystone role of elephants, and community-based conservation as a way to foster coexistence at an ecosystem and landscape scale. Space and mobility also alleviate the ecological disruption of compressed populations, and minimizes population management.

KEYWORDS
biodiversity, compression-impact, elephants and humans, keystone role, mobility, space

INTRODUCTION

After decades of physical forces being viewed as bottom-up drivers of ecosystem processes (Lindeman, 1942; Odum, 1957; Whittaker & Likens, 1975), the role of carnivores and herbivores in governing community dynamics from the top-down has been well established in both ecological theory (Curtin & Allen, 2018; Holt et al., 2010; Oksanen et al., 1981; Paine, 1969; Schoener & Spiller, 1987) and conservation policy and management (Eisenberg, 2013; Seip, 1992; Sinclair & Norton-Griffiths, 1979). The extermination, reintroduction, displacement, and compression of keystone large herbivores, and carnivores can all have long-term repercussions on ecosystems and landscapes (Bakker et al., 2016; Owen-Smith, 1988).

Given the growing impact humans have on wildlife (Grooten & Almond, 2018), population disruptions offer naturalistic experiments for testing the role of mega mammals as keystone species precipitating trophic cascades through ecosystems (Holt et al., 2010). The impact of megafaunal disruptions will, however, differ between biogeographic regions depending on their histories. The heavily depleted faunal assemblages of North America during the Pleistocene period (Grayson, 1989) and Madagascar during the Holocene (Burney et al., 2003), for instance, will respond differently to disruptions of East Africa megafauna, which has remained relatively intact since the late Pleistocene (Reid, 2012; Sinclair & Norton-Griffiths, 1979). Whereas the reintroduction of the wolf into Yellowstone's Pleistocene-depleted predator fauna caused large ripple effects on the plant and animal communities (Eisenberg, 2013), the recolonization of wild dogs on the Laikipia Plateau in Kenya (Woodroffe et al., 2005) caused little change. In Africa, the biotic impact of large herbivores is far greater than that of carnivores. The large impact of elephants on the structure and dynamics of African forests and savannas, for example, has been well documented (Fritz et al., 2002; Guldemond et al., 2017; Laws, 1970; Toit & Moe, 2015). How much greater then would be impact of reintroducing megaherbivores, such as elephants and rhinos, into North America biomes after 11,000 years of faunal depletion and weakened plant defenses than the reintroduction of the wolf into Yellowstone?

Most studies of elephants, the world's largest terrestrial herbivore, have been conducted in protected areas where their impact is intensified by compressed populations and by curtailed seasonal movements. Wall et al. (2021) showed the distribution of elephants to occupy only 17% of their potential range due to the level of the human disturbance and safety in protected areas. Normalized for rainfall, censuses of 34 populations showed elephant densities in East Africa to be five times higher in protected than nonprotected areas (Western, 1989).

Discussions on the keystone role of elephants have centered on their impact on woody vegetation and whether the findings support equilibrium, nonequilibrium, or alternative multistate theories of ecosystem dynamics (Caughley, 1981; Dublin et al., 1990; Walker, 1981). Here again, the focus on the impact of protected area elephant populations on woody vegetation and biodiversity has deflected attention from the larger keystone role they play when free-ranging at an ecosystem and landscape level. The lack of studies prior to the establishment of protected areas masks the complex and shifting interplay that likely shaped African ecosystems for millennia (Laws, 1981).

ELEPHANT–HUMAN INTERACTIONS

Paleo records and historical accounts point to the ancient links and changing relationship between hominins and elephants since the Lower and Middle Stone Ages. In the Olorgesailie formation in the Rift Valley of Kenya one million BP, fossilized remains of *Elephas recki* were surrounded by discarded stone tools and show multiple cut marks on the bones (Potts et al., 2018). Whether the disappearance of *E. recki*, together with a 75% turnover of the large mammal fauna between 500,000 and 350,000 BP, was due to climatic changes or human impact, is yet to be resolved. It does, however, suggestively coincide with the emergence of sophisticated weaponry and hunting techniques (Potts et al., 2020).

In historical times, lateen-rigged sailing vessels transported large quantities of ivory from Africa to the Arabian Peninsula and India from 500 AD onward. Evidence points to the depletion of elephant populations across eastern and southern Africa by the late 19th century (Coutu et al., 2016; Håkansson, 2004), resulting in the growth of woody vegetation (Leuthold, 1996).

Historical accounts of Amboseli mirror the continental picture. The writings of Joseph Thomson and Count von Hoehnel, the first European explorers to pass through Amboseli in the 1880s, make no mention of seeing elephants (Thomson, 1887; von Höhnel, 1894). Photographs by Schillings (1906) in the early 1900s show an abundance of regenerating fever trees (*Acacia xanthophloea*) but no mature woodlands. A repeat photographic survey of photos taken by Martin and Osa Johnson in 1921 (Johnson, 1935) shows thick, regenerating groves of fever trees and a dearth of elephant dung or tree damage. In the years following, the trees matured and elephant damage intensified, leading to the replacement of woodlands by grasslands across much of the Amboseli basin from the 1950s onward (Western, 2010).

Given that elephants have contracted to a fifth of their available habitat due to human displacement (Wall et al., 2021), how has displacement and compression of elephant populations by human activity distorted the ecological impact of elephants on vegetation and large mammal populations? Laws (1970) suggested that elephants, free to move in response to human activity, created a large-scale mosaic of habitats due to the differential impact of browsing and grazing intensity. Western and Maitumo (2004) similarly hypothesized that free-ranging elephants and livestock populations shifting in response to each other set up a creative tension causing a dynamic mosaic of habitats.

The Amboseli Conservation Program (ACP) was set up in 1967 to track seasonal and long-term trends in wildlife and human activity and to monitor the causes and consequences of change. The ACP program has run continuously since then. The 55-year study spans the period of free-ranging movements of elephants in the 1960s, the responses to heavy poaching and the creation of Amboseli National Park in the 1970s, and, in the following decades, the spread of farming, sedentism, and land subdivision among pastoral communities. Our aim in this paper is to look at the demographic and ranging responses of elephants to human activity, track the cascading effects on vegetation and large herbivores, and use naturalistic and exclusion experiments to detect the impact of intensified browsing. We review the literature to look at the importance of space and mobility in sustaining free-ranging elephant populations, theories of the keystone role of elephants, and the ecological disruptions caused by our growing human impact.

STUDY AREA

The 8500 km^2 Amboseli ecosystem (Figure 1) is defined by the seasonal movements of the large wild herbivore and pastoral livestock populations lying in the rain shadow of Kilimanjaro along the Kenya–Tanzania border.

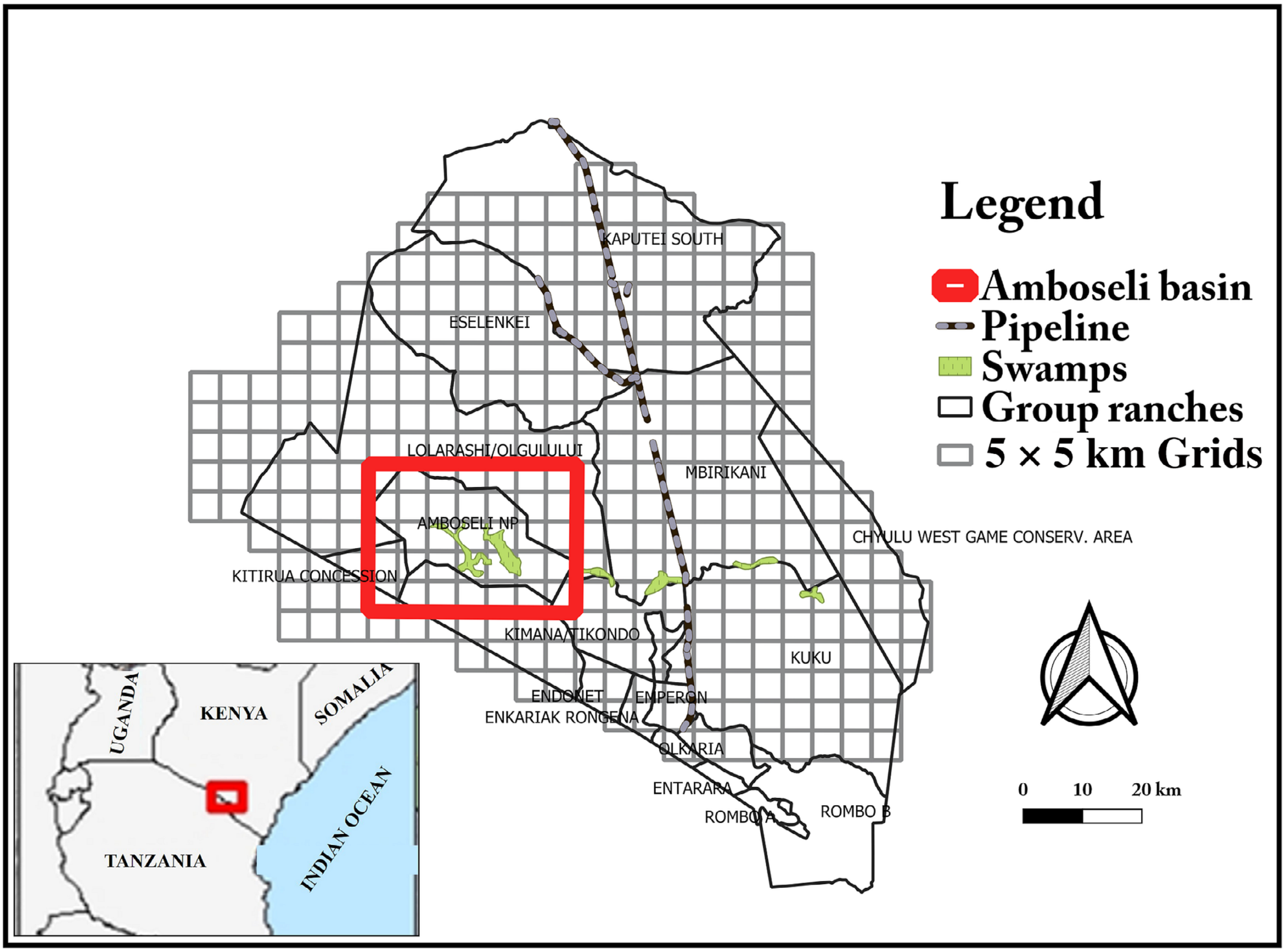

FIGURE 1 A map of the study area showing Amboseli National Park, the surrounding group ranches, and the 5 × 5 km grid overlay used in flying flight lines and spatially plotting wildlife and livestock population estimates.

The wild herbivore migrants, including elephants, zebra, wildebeest, hartebeest, eland, and buffalo, move seasonally between the wet season and the dry season range concentrated around the permanent swamps of the Amboseli basin. The ecosystem has been detailed in several publications (Moss et al., 2011; Western, 1973, 2007). The vegetation is dominated by bushed grassland falling within ecological Zone V of Pratt, Greenway, and Gwynne (Pratt et al., 1966). Aquifers emanating in the northern forests of Kilimanjaro drain into the dry Pleistocene lakebed of the Amboseli basin, creating a series of permanent swamps and a shallow water table (Figure 1), which support hydrophilic vegetation dominated by *A. xanthophloea* woodlands. Maximum temperatures range from 26 to 44°C, and minimum temperatures range from 6 to 14°C. The twice-yearly rainy seasons fall between October to December and March to May, averaging 350 mm annually (Altmann et al., 2002).

In the 1960s, elephants, along with other wildlife and livestock, migrated seasonally during the rains to the surrounding bushed grasslands and returned to the Amboseli basin as the dry season progressed (Western, 1975). Western and Lindsay (1984) documented the subsequent changes in elephant populations and seasonal movements in the Amboseli basin from 1973 to 1980. The habitat changes in Amboseli since the 1950s have been described in detail (Croze & Lindsay, 2011; Western, 2007). From 1950 to 2017, grassland habitats expanded from 28% to 40% of the basin in inverse proportion to the contraction of woodlands from 25% to 5%. The major habitat changes have been shown to correspond to increasing browsing intensity (Western & Mose, 2021).

Despite the abundance of wildlife, the herbivore biomass is dominated by the cattle, sheep, and goats of the pastoral Maasai, who followed the same seasonal migratory patterns as wildlife until the late 1970s. In 1978, livestock were excluded from the 388 km^2 Amboseli National Park to protect the rich wildlife concentrations of the Amboseli Basin and secure their late-season forage against settlement and farming. The Maasai in the surrounding communal lands were given title deeds to seven group ranches, each managed separately by elected representatives (Kimani & Pickard, 1998). The higher rainfall slopes of Kilimanjaro were divided into small farms that spread downslope toward the permanent swamps from the 1960s onward. Beginning in the 1970s, the permanent swamps Namelog and Kimana lying east of Amboseli National Park were subdivided into private holdings supporting irrigated farming. Subdivision of the group ranches, which began in the northern Kaputei section of eastern Kajiado District in the 1970s and displaced wildlife, including elephants (Kimani & Pickard, 1998), is currently underway in the group ranches surrounding Amboseli National Park.

METHODS

Herbivore monitoring

Counts of the 704 km^2 dry season concentration area of the Amboseli basin, which included all herbivores larger than 25 kg, were conducted using sample aerial counts between 1967 and 1971 (Pennycuick & Western, 1972; Western, 1973). From 1975 onward, aerial counts of the Amboseli basin were flown to give a total count of elephants within a 1 km^2 UTM grid (Western & Lindsay, 1984). From 1974 onward, aerial sample counts of all large wild and domestic herbivores were flown across the 8500 km^2 eastern Kajiado County one to several times most years (Western et al., 2021). The area was divided on a UTM map projection into 5×5 km grids (Figure 1). Flight lines were flown through the center of each grid in a north-south direction, 90 m above ground. All wildlife and livestock within a strip width averaging 170–200 m were counted on either side of the aircraft by two back-seat observers. Herds too large to count by eye were photographed and later counted under a binocular microscope. Population estimates (PE) and standard deviations were derived from the 8% to 10% sample counts using the Jolly II equation (Jolly, 1969). The global PE and the standard error (SE) for each species were calculated as follows:

$$\mathrm{PE} = N\bar{y} \text{ and } \mathrm{SE} = \sqrt{\frac{N(N-n)}{n}S^2}, \tag{1}$$

where N is the number of samples needed to give a complete coverage of the study area, $\bar{y}$ is the sample mean, n is the sample size, and S^2 the sample variance.

Elephant carcasses were added to the live animal counts when a surge in poaching was detected in 1974. Carcasses counted included freshly killed animals with tusks removed, skin still intact or bones undispersed. Carcasses in bush country are likely to be undercounted, but using the narrow counting strips of the ACP monitoring, carcass-to-live ratios have been shown to give good minimum estimates of poaching levels (Douglas-Hamilton & Burrill, 1991). A summary description of the elephant datasets is provided in Table 1.

Vegetation measurements

The woodland changes in the Amboseli basin were measured by tree density in 30 18-ha plots randomly distributed on aerial photos dated 1950, 1961, 1967, and 1980. We used the photo set to detect how woodland density had changed across the length of the Amboseli basin in response to a protected area in the center of the basin

TABLE 1 Items descriptions of the elephant and carcass data, as well as the tree and herbaceous biomass data, used in this paper.

Data item	Area sampled	Size in km^2	Timespan (sampling/analysis period)	Type (aerial/ground)	Frequency	Associated figure/analysis
Elephant no. in the Amboseli basin area.	Amboseli basin area.	704 km^2	1968 to 2020	Aerial survey	Monthly	Figures 3 and 4
Elephant no. in the Amboseli ecosystem.	Amboseli ecosystem.	8500 km^2	1974 to 2020	Aerial survey	Annually	Figure 3
Poached no.	Amboseli ecosystem.	8500 km^2	1974 to 2020	Aerial survey	Annually	Figure 3
Elephant density from the centre of the park.	Amboseli basin area experiment conducted in the 1988.	704 km^2	Averages from 1975 to 1988	Aerial survey	N/A	Figure 5
Tree species no. from the centre of the park.	Amboseli basin area experiment conducted in the 1988.	704 km^2	1988	Ground transects east and west from the centre of the park	N/A	Figure 6
Elephant and herbaceous biomass at heightened poaching period.	Amboseli basin.	704 km^2	Data analyzed from 1978 to 1985	Ground herbaceous biomass data sampled following Western et al. (2021).	1978–1985 monthly analysis	Analysis reported in the *Results*

and pastoral livestock activity in the periphery. For lack of later aerial photography, we conducted a similar count of tree density updated to 2020 using 2020 Google Earth Pro satellite imagery (CNES/Airbus, 2020). The satellite imagery gave good resolution of mature trees but a minimum estimate in densely packed regenerating groves. We conducted a separate study in 1988 to determine how tree density, shrub cover, and herbaceous cover related to elephant density from the centrally protected area of the Amboseli basin to the peripheral basin areas outside used by Maasai herders and farmers. Tree cover and bush density by species were measured by the point-center-quarter method (Cottam & Curtis, 1956). Herb layer composition and biomass inside the park were measured by the slanting pin frame method (Jonasson, 1988; Western et al., 2021). Sample plots were spaced 0.75 km apart along the transect. To derive elephant densities along the transects between 1975 and 1988, the period of maximum tree loss, we averaged monthly total aerial counts of the basin area using a 1 km^2 grid.

The ACP set up a controlled experiment to determine the impact on woodland and swamp vegetation of removing elephant impacts from a 250-ha exclosure (Appendix S1: Figure S1). Elephants were excluded by two electrified wires extending 2 m and above from the ground, allowing smaller herbivores, including buffalo, wildebeest, and waterbuck, to use the plot (Appendix S1: Figure S1). The Ilmarishari site selected was, until the late 1960s, an area of dense woodlands enclosing a small swamp. Heavily destroyed by elephants in the 1970s and 1980s, the woodlands gave way to *Suaeda monoica*, *Salvadora persica*, and *Azima tetracantha* shrubland by 2000 (Western, 2007). The swamp, dominated by the 2–3 m sedges *Cyperus papyrus* and *C. immensus*, was gradually grazed down to a short sward with *Cynodon dactylon* and *Digitaria* grasses invading the edges. The experimental and adjacent unfenced control plots were monitored for changes in plant biomass and composition between September 2002 and July 2005 (Sarkar, 2006).

We used other high-level electric fence exclosures to measure tree recovery with elephant exclusion. These included two constructed by Kenya Wildlife Service (KWS) at Simek (≈2 ha) and Ol Tukai Orok (≈0.5 ha) in 2010, and two outside the park at Soito Nado, constructed at a Ker and Downey Safaris campsite (each ≈0.2 ha) between 2000 and 2010.

Statistical analysis and modeling

To delineate where elephants spent their time in the ecosystem in the 1970s, 1980s, 1990s, and 2000s, we used a kernel density estimation (Figure 2), and contour percentages (Gibin et al., 2007) categorizing the band isopleths probability as 50% (core area), 75% (migration area), and 95% (home range).

We used a lag correlation analysis to compare elephant population numbers to poaching rate measured by carcass to live ratio (Figure 3). The shifting seasonal elephant population numbers in the Amboseli basin were compared using the Wilcoxon sign rank test (Rosner et al., 2006) for the periods 1968–1978, 1980–1983, and 1984–2005, derived from visual inspection of the time series shown in Figure 4. The association between tree survivorship and elephant density was tested using the nonparametric Spearman rank correlation (Astivia & Zumbo, 2017).

We used both naturalistic and exclusion experiments to test whether elephant compression was a primary cause of the habitat and species compositional changes. In the naturalistic experiment, we used the 1988 combined ground transects running east and west from the park center to basin periphery (Figure 5) to test whether grass and shrub biomass increased with declining elephant density along the transects. Here, a multivariate multiple regression (Nkurunziza & Ejaz Ahmed, 2011) was used to model the ratio of grasses and shrubs to tree biomass as a function of distance from the center of the park.

The model is given by

$$Y_s = \beta_0 + \beta_1 X + \varepsilon \quad s = 1, 2, \tag{2}$$

where Y_s are the ratios of grass and shrubs to tree biomass, respectively, X is the distance, β_0 and β_1 are model parameters, and ε is the error term.

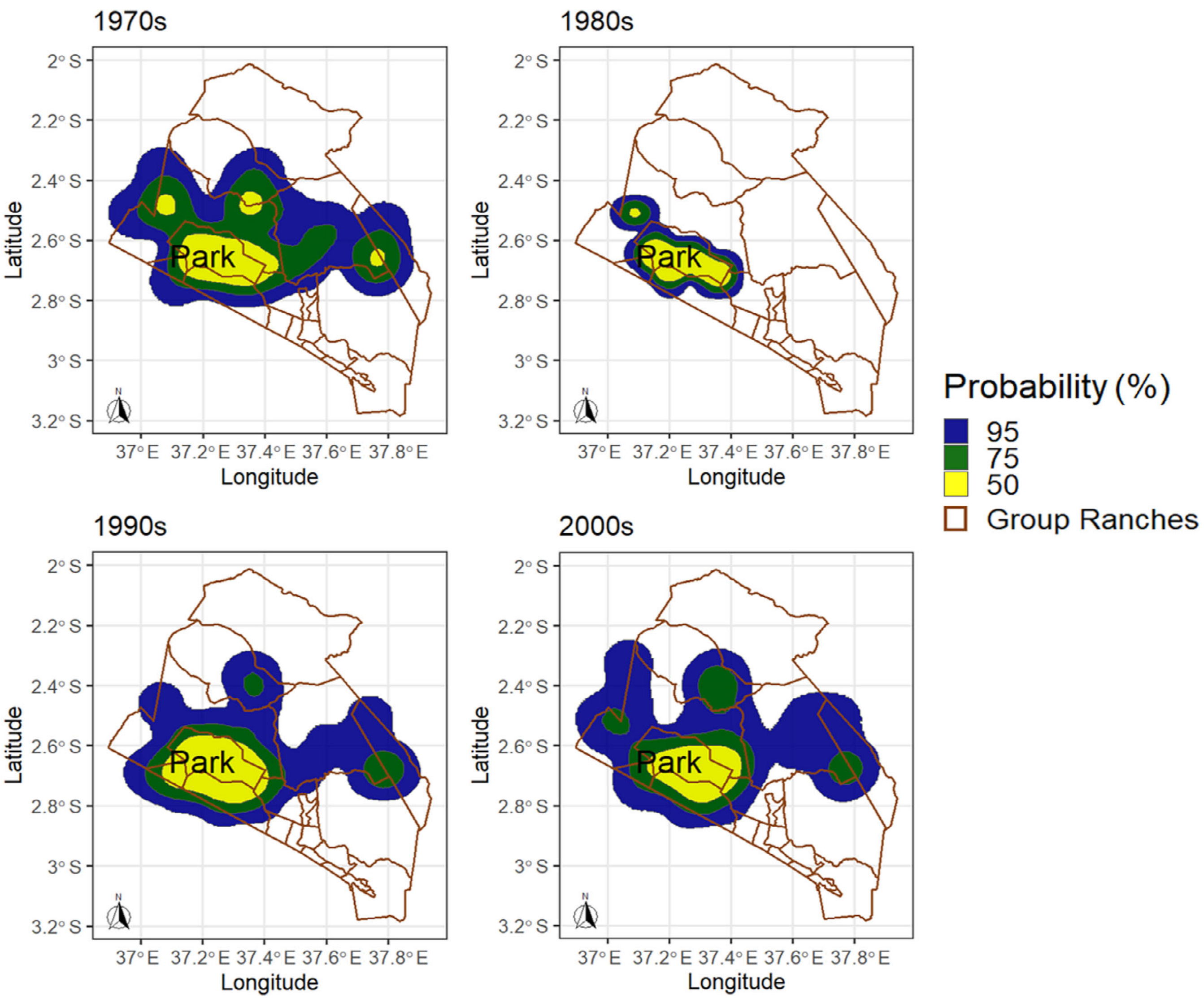

FIGURE 2 Kernel Density Distributions of Elephants in Amboseli Ecosystem 1974 to 2016.

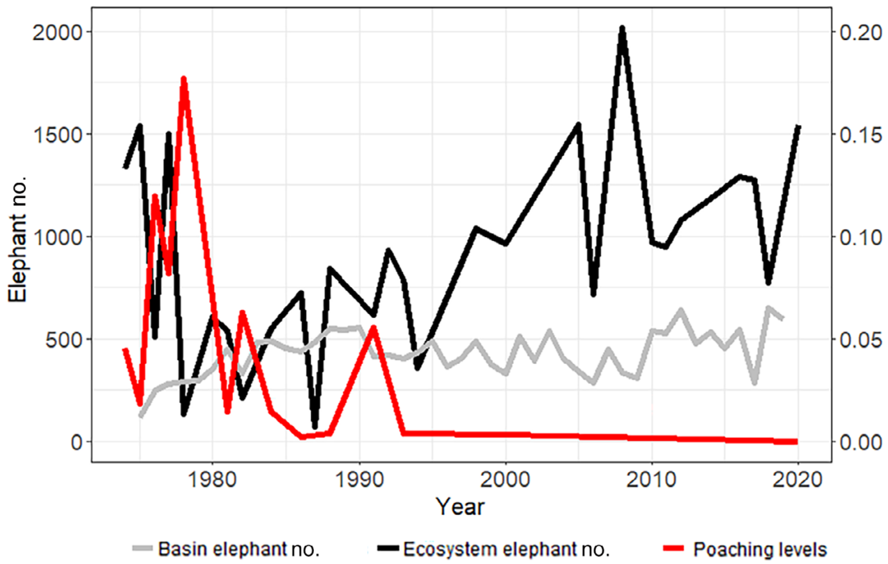

FIGURE 3 Elephant numbers in the 8500 km^2 of eastern Kajiado spanning the Amboseli ecosystem (black) and 704 km^2 dry season range (gray) are plotted against carcass ratios as a measure of poaching levels (red).

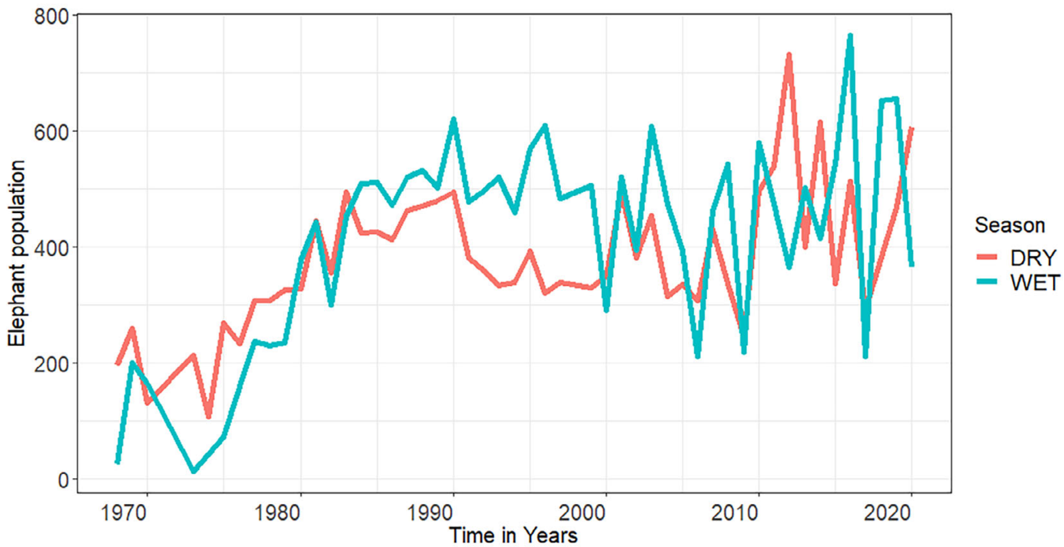

FIGURE 4 Mean annual wet and dry season population counts of the Amboseli basin show a drop in migrations in the late 1970s and early 1980s in response to a surge in poaching outside the national park, followed by a reversal of migrations through to 2006, when movements became more erratic in response to wet and dry years.

In a controlled experimental manipulation of elephant impact using high-wire exclosures in the former woodland areas (Appendix S1: Figure S1), we tested whether elephant exclusion would revert the *Suaeda*-dominated shrublands to fever tree woodlands. Model (2) was applied with the independent variable X taken as time in years.

We used the elephant density gradient from the center to periphery of the national park (Figure 6) to test whether elephant density accounts for the changes in species richness, including trees, shrubs, herbs, and grasses. We fitted a power function given by:

$$D = \gamma E^{\alpha} \quad \gamma > 0, \ \alpha \neq 0. \tag{3}$$

The above equation shows that the estimated species richness D vary with elephant density E (number per square kilometers).

Calculation of the variance explained (R^2) was made after model linearization (Khalil, 2002).

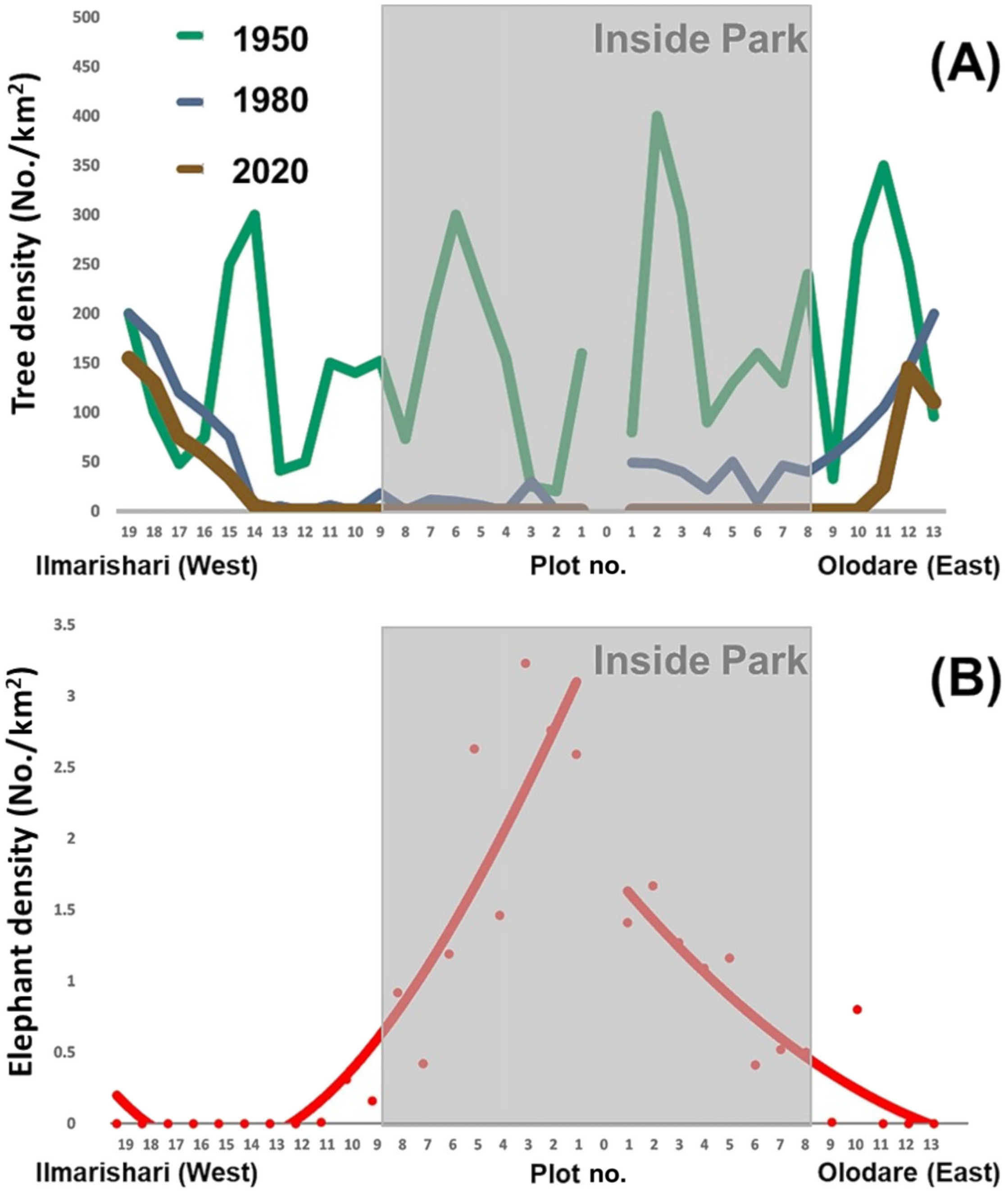

FIGURE 5 The density of fever trees was measured along the Amboseli basin on aerial and satellite imagery for the years 1950, 1980, and 2020 (A). Woodland density, fairly uniform along the basin in the 1950s when elephant numbers were low, declined steeply with the influx of elephants into the national park (shaded region) in the 1970s. Woodland density was found to be a density-dependent function of elephant density averaged from total counts of the basin between 1975 and 1988 (B). The woodlands declined in an outward wave from center to periphery of the park, where human activity restricted elephant movements and protected the remaining groves. The Ilmarishari elephant exclusion plot established in 2001 saw a rapid recovery of fever trees (Appendix S1: Figure S1) in the center of the park.

To test whether pasture abundance, measured by herbaceous biomass at the height of the poaching period (1978–1985), influenced the rise in elephant numbers inside the protected Amboseli National Park, we fitted a generalized least squares model (Kariya & Kurata, 2004) to account for possible temporal autocorrelation in the data. We utilized the nlme package in R for analysis and modeling (Pinheiro et al., 2018).

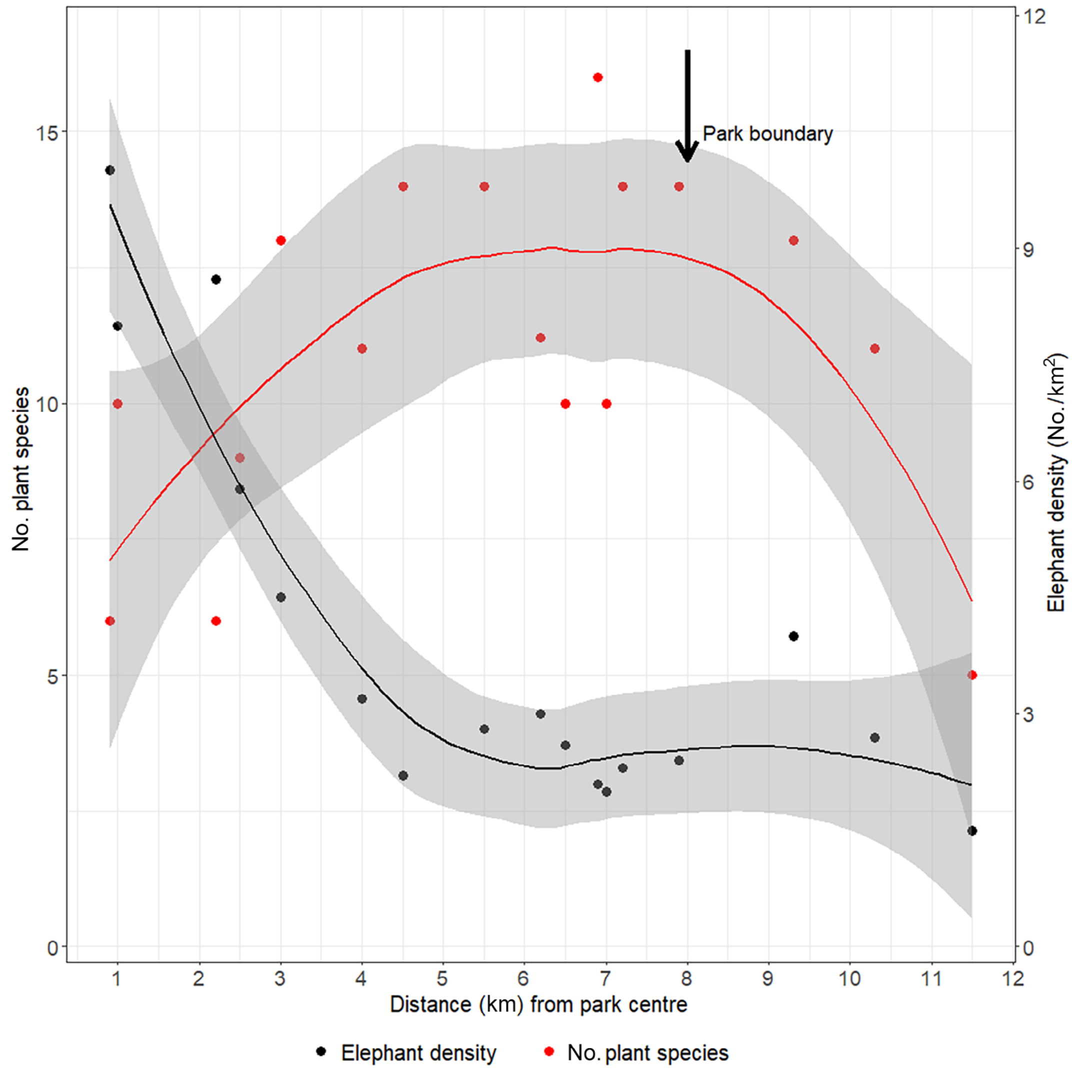

FIGURE 6 Plant species richness in relation to elephant densities along combined east and west transects from the center to periphery of the Amboseli basin. Plant richness increases linearly with declining elephant density to the national park boundary, then declines sharply at increasing distances. The shaded bands are pointwise 95% confidence bounds derived from a generalized additive model smooth function fit.

RESULTS

Changes in elephant migrations and population size

Aerial counts of the ecosystem from 1974 onward show elephant numbers in the ecosystem fell from well over 1000 to under 500 between 1974 and 1978 (Figure 3). At the onset of the counts, large numbers of recently poached elephants with their tusks hacked out were sited across the ecosystem outside Amboseli National Park, often in clusters, including youngsters. The population decline was inversely proportional to the poaching rate measured by the carcass:live ratio over the previous year ($r = -0.37$, $p = 0.0453$). Allowing for the undercounting bias, the estimated 536 ± 102 carcasses accounted for the losses. A recovery in the elephant numbers coincides with the remaining population concentrating within the safety of the national park (Figure 1) and a cessation of poaching in the early 1980s (Figure 2). The elephants began to recolonize their ecosystem range through the 1990s and 2000s when poaching across the region had dropped to low levels (Figure 4).

We found a statistically significant negative association between elephant numbers in the protected national park and herbaceous biomass over the heightened poaching period of 1978–1985 ($t = -2.094$, $p < 0.0396$) after accounting for the temporal correlation present in the errors of the generalized least squares regression model relating the two variables. During this period, herbaceous biomass decreased by 38% for each unit increase in elephant population. This shows the elephant concentration into Amboseli National Park occurred despite a sharp decline in herbaceous biomass.

The change in numbers and movements of elephants after the 1970s points to a response to human activity, namely a population reduction and range contraction due to poaching, and a concentration in the Amboseli basin due to the protection afforded by the national park. With the cessation of poaching and safety in the park, elephant numbers rose steadily through recruitment (Moss et al., 2011) to over 1200 in the early 2000s (Figure 3) in line with the increase documented by the Amboseli Elephant Program (Croze & Lindsay, 2011).

By the 1990s, the herds had resumed seasonal migrations, but in a reversal of the earlier wet season migrations (Figure 4). Whereas wet season counts of the basin were significantly lower than dry season counts between 1968 and 1978, dry season counts showed no significant difference between 1980 and 1984 ($W=4$, $p=0.3429$). From 1984 to 2005 the dry season numbers were significantly lower than the wet season ($W=42$, $p<0.0001$). During these two decades, the basin population fell from a yearly average of 500 to under 300 (Figure 4). A sharp decline in elephant numbers was recorded in the basin in the 2009 drought (Figure 4) when over 400 elephants died (Moss, personal communication) Elephant numbers in the park subsequently rebounded but became more erratic (Figure 4).

The dislocation of the elephant migrations in the late 1970s compressed elephant habitat use and had large knock-on effects on the plant community, which we explore next.

The impact of elephant compression on the Amboseli basin

The concentration of elephants in Amboseli National Park in response to poaching created a knock-on effect along the plant biomass gradient shown to be used seasonally (Lindsay, 1982, 1994). The rising numbers initially built up in the woodlands, then shifted to the swamp habitats (Mose & Western, 2015). The shifting concentration of use from woodland to swamps correlates inversely with the depletion of total woody biomass in the Amboseli basin between 1975 and 1995 ($r=-0.49$, $p=0.01$), pointing to rising elephant numbers intensifying the herbaceous biomass gradient of seasonal use.

The close correlation between elephant density, tree damage, and tree death found by Western and Van Praet (1973) makes the fever tree a useful indicator species for tracking the ecological impact of elephants in the Amboseli basin over the last 70 years. The results of the aerial photo and Google Earth Pro counts (Figure 5) show fever woodlands in 1950 to be dense and relatively uniform across the basin. By 1980, tree density had declined steeply in the national park, corresponding to the rising elephant numbers in the basin (Figure 4). Tree survivorship increased with distance from the park center to periphery ($r_s=0.67$, $p=0.0064$). A repeat measure correlation analysis shows the declining woodland loss from the park center to basin periphery to correlate significantly with declining elephant density ($r_{rm}=0.62$, $p=0.0298$), supporting the density-dependent tree damage findings of Western and Van Praet (1973).

The results of the combined 1988 vegetation transect running east and west from the park center to basin periphery (Figure 5) show grass and shrub biomass to have increased with declining elephant density (Model 2). We found both the ratio of grass ($y=-0.6x+9.3$, $R^2=0.54$, $p=0.0061$) and shrubs ($y_1=-0.28x+2.6$, $R^2=0.49$, $p=0.0118$) to decline along a distance gradient in proportion to tree biomass density.

We used the results of the experimental removal of elephants from the Ilmarishari high-wire exclosure (Appendix S1: Figure S1) to determine if fever tree woodlands would recover with the exclusion of elephants and reverse tree replacement by *Suaeda*, *Salvadora*, and *Azima* shrubland. By 2015, the fever trees had regenerated and formed a dense canopy of mature trees. The ratio of both shrub ($y_s=-0.9x_e+1795$, $R^2=0.41$, $p=0.0341$) and herbaceous biomass ($y_g=-7.42x_e+14881$, $R^2=0.38$, $p=0.0158$) fell sharply with the regeneration of trees after the exclusion of elephants (Appendix S1: Figure S1). The shade-intolerant *Suaeda* had disappeared from the maturing woodland plots by 2015.

We used the same exclosure to determine if the grazed-down swamp in the center of the plot would reestablish the former tall sedges which had been grazed to a short sward by elephants (Appendix S1: Figure S1). Despite no recovery in the control swamp, the residual *Cyperus papyrus* and *Cyperus immensus* sedges in the experimental exclosure showed strong recovery within a year (Sarkar, 2006). The visual evidence in Appendix S1: Figure S1 shows a full recovery of 3-m-tall sedges within five years of elephant exclusion.

Finally, we used the 1988 transects from the center to periphery of the national park to determine whether plant species richness, including trees, shrubs, herbs, and grasses, changed along the elephant density gradient. The results show a density-dependent correspondence in which species richness increased inversely with elephant density from the park center to a peak at the park boundary before declining sharply with increasing distances beyond the park boundary. The parameter estimates from model (3) were highly significant ($\gamma=17.75$, $p<0.0001$)

and ($\alpha = -0.36$, $p < 0.0034$), showing that elephant density accounts for 53% of the decline in species richness.

DISCUSSION

The Amboseli ecological changes

The year-round concentration of elephants in the basin is best explained by the combination of poaching outside and the safety of herds inside the national park, where tourist vehicles and ranger forces offered protection (Moss et al., 2011). The safety factor was also evident in the relaxed behavior of herds in the park, their clumped and agitated formations outside the park (Western & Lindsay, 1984), and their flight into the park when disturbed (Kangwana, 1993). Most movements out of the park were under the safety of night, a pattern common to other protected area populations in response to human threats (Wall et al., 2021).

The greatest impact of the elephant range compression was on the woodlands. We have shown the loss of woodlands to be a density-dependent function of elephant numbers and distribution across the Amboseli basin. The experimental removal of elephants using high-level electric fences showed woodlands to recover when the browsing pressure is removed. Fifteen other exclosures across basin established by KWS and tourist lodges since 1990 show strong tree regrowth against the continuing loss of woodlands and woody vegetation in the park. The recovery of woodlands in the exclosures reinforces the findings of a 20-year exclusion experiment showing elephant browsing pressure to be the main cause of woodland loss (Western & Maitumo, 2004).

The results of our study are consistent with the changes in vegetation previously described due to intensified elephant browsing with range compression (Sarkar, 2006; Western, 2007). The changes include a contraction of woodland and bushland habitats, a proliferation of *Suaeda*, *Azima*, and *Salvadora* shrubland, and an expansion of swamp-edge and swamp habitats. The most significant ecological changes are a reduction in habitat diversity, convergence in plant species composition among habitats, species downsizing, a sharp decline in vegetation biomass, increased turnover rate, and a greater dominance of herbivore-resilient species of shrubs and grasses (Western & Mose, 2021).

The heterogeneity in woodland structure and species composition converged over the period from the 1970s to 2017, due largely to woody mass declining across the Amboseli basin from 600 to 200 $g\ m^{-2}$ (Western et al., 2021). The permanent swamps increased by twofold, switching from tall to short sedges and banks of floating weed and large stretches of open water (Sarkar, 2006).

Changes in the vegetation and large herbivore community in Amboseli over the last five decades show the ecological role of elephants to be heavily determined by their interactions with humans. The interaction can cause positive or negative cascading changes depending on whether elephant populations are compressed or move freely in response to shifting human activity.

We attribute the compressed elephant populations in the Amboseli basin to heavy poaching in the 1970s. The exclusion of livestock in 1978 following the creation of Amboseli National Park may have temporarily contributed to the influx of elephants (Croze & Lindsay, 2011), but considering herders resumed using the park within three years, this would not explain the continuing concentration of elephants (Figure 4). The compression into a tenth of the elephant's 1960s range transformed woodlands into shrublands and expanded the area of grasslands and swamps. The collapse of the migrations and compression of elephants following heavy poaching caused a cascade of vegetation changes, including a convergence in composition typified by smaller browse-tolerant species, reduced primary production, an accelerated turnover rate, and reduced resilience (Western & Mose, 2021).

Changes in the swamp vegetation, in contrast, highlight the role of elephants as ecological engineers in opening up wetlands to a range of smaller herbivores. The effects of elephant trampling, fecal deposits, water aeration, and sediment churning on swamp vegetation provide a good example extensively documented by Sarkar (2006). The post-1980s decline in the basin elephant population is explained by the depletion of forage, culminating in the heavy elephant and ungulate mortality in the 2009 drought (Western et al., 2021). The impact of elephants on the Amboseli swamps mirrors the account of the grazing succession in Lake Rukwa in southern Tanzania (Vesey-FitzGerald, 1960). Here, elephants trample and graze down tall sedges, creating a succession of smaller herbivores onto the newly created grazing lawns as the dry season progresses.

Changes in Amboseli large herbivore community over the last half century track the changing habitat and species composition. The changes in the composition and structure of the herbivore community have been monitored since the late 1960s using both the surface bone assemblage and live counts across the Amboseli basin. The results show the composition of the fifteen large herbivore species to track habitat changes, with the relative abundance of grazers growing and browsers declining with the loss of woodland and expansion of grasslands and swamp-edge vegetation (Western et al., 2021; Western & Behrensmeyer, 2009).

General discussion

A review of 238 studies and a meta-analysis of 21 research sites across Africa (Guldemond & Van Aarde, 2008) found high densities, amplified by low rainfall and fencing, to reduce woody vegetation. The compressed elephant population in Amboseli National Park has also caused a heavy loss of woody vegetation across the ecosystem, but this paints a more nuanced picture. Transects across the Amboseli park boundary show a loss of plant species richness at low as well as high elephant densities due to dense woodland cover suppressing understory plants. Poulsen et al. (2017) also found elephant extirpation to result in plant species loss and ecosystem simplification in African forests. Based on the density-dependent responses of plant species richness (Figure 6), we deduce that protected area populations mask the larger shifting patchwork effect of elephants as landscape agents (Davies et al., 2018).

Although Guldemond et al. (2017) and Cook and Henley (2019) found that high-density elephant populations generally cause tree loss and habitat simplification, we suggest that elephants can promote habitat and species diversity when free to move, and play an ecological engineering role in denser habitats and wetlands by facilitating grazing successions. Skarpe and Ringrose (2014), for example, in a multispecies study of Chobe National Park in Botswana, showed elephants to cause a wide range of cascade effects as a function of distance from water. Heavy concentrations of elephants along water courses and waterholes caused an expansion of grasslands and increase in meso-herbivores, large carnivores, small mammals, and gallinaceous birds. Lower elephant densities farther from water resulted in heavy bush and woodland cover. Their study also found elephant impact to be moderated by bottom-up geomorphology, soils, and hydrology.

Fritz et al. (2002) in investigating the impact of megaherbivores on the guild structure across 31 African ecosystems found elephants to compete with meso-browsers and mixed feeders but not grazers, a finding echoed in our study. In a yet broader review of the role of megaherbivores, Bakker et al. (2016) combined paleo-data and exclosure studies to show that megaherbivore extinctions and exclusions can cause large ecological cascades no less than high-density populations, in this case through an expansion of woodlands and an increase in species dominance.

The focus on protected areas and a lack of studies on free-ranging populations interacting with humans at a landscape scale have fostered a view of park elephants as being incompatible with biodiversity conservation and the need for elephant reduction programs to alleviate the biotic impact. Hoare and Du Toit (1999), in contrast, found elephants and humans to coexist across a wide range of settings below a threshold of disturbance. They noted the lack of studies on the ecological interaction of elephants and people moving freely in response to each other. Their findings, along with those from Amboseli, signal the need for context-specific studies to decipher the ecological role of unrestricted elephant populations.

Elephants, we suggest, need large spaces and the creative tension of human disturbances lacking in parks to play a positive keystone role in African savannas and forests. Contemporary elephant populations studies tell us little about the ecological role of free-ranging elephants prior to colonialism, parks, and the rapid human population growth in Africa over the last century (Caughley, 1988; Laws, 1981). The Amboseli study supports the suggestion that elephants in precolonial days shifted with the loci of human activity, creating a large-scale mosaic of habitats with local differentiation due to browsing, grazing, and human activity (Laws, 1981). The findings also support the hypothesis based on the multivariate 20-year elephant exclusion study in Amboseli that elephants and livestock interactions can, through a creative tension, cause a shifting mosaic of habitats (Western & Maitumo, 2004). We suggest that the continuous "jostling" of livestock and elephants at the park boundary in Amboseli explains the peak of plant species richness (Figure 6). The hump-back curve of species richness along the Amboseli elephant density gradient fits the Intermediate Disturbance Hypothesis (Roxburgh et al., 2004), as modified by the Milchunas-Sala-Lauenroth (MSL) models (Gao & Carmel, 2020) looking at the impact of disturbance along a productivity gradient.

The context-specific impact of elephants points to the futility of separating the ecological role of elephants from people, treating parks as natural ecological systems, and ignoring the importance of mobility and scale in ecological cascades (Curtin & Allen, 2018; Holt et al., 2010). The million years or more of human-elephant coevolution have shaped ecological, behavioral, and cultural adaptations in elephants and people in relation to each other. Elephants readily distinguish human responses by, for example, foraging beyond park boundaries at night to avoid people (Wall et al., 2021), yet acting benignly around safari vehicles, lodges, and campsites in parks (Moss et al., 2011).

Other factors bearing on how elephants and people shape ecosystems include physical factors such as rainfall (Fritz et al., 2002), landscape heterogeneity (du Toit, 2003), the size of parks, distance from water (Skarpe & Ringrose, 2014), rainfall seasonality, and the scale and pattern of migrations.

The loss of elephant mobility and range and the rising conflict with people have reduced the scope for coexistence. The loss of coexistence has shifted the human–elephant interactions from increasing both plant and large herbivore diversity to greater ecological disruption and uniformity. Caughley (1988), in reviewing the causes and consequences of local overabundance in mammals, further suggested that the exceptions to the reversion of vegetation from temporary overabundance are due to the loss of mobility in livestock and elephants. O'Connor et al. (2007) go further in suggesting elephants are predominantly grazers based on their digestive physiology but increasingly become browsers when compressed into protected areas.

We propose that prior to the ivory trade, the creative tension of free-ranging elephants in response to humans created a patchwork of habitats and a shifting mosaic of vegetation consistent with the view of elephants as a keystone species and ecosystem engineer. The impact of the ivory trade over the last few centuries (Coutu et al., 2016; Håkansson, 2004), a breakdown in traditional lifestyles and cultures, the growth and expansion of human activities, and protected areas, have since compressed elephant ranges and caused a growing ecological dislocation by disrupting the interactions of the two keystone species (Power et al., 1996).

The widening ambit of conservation in the last few decades has begun to scale up space for large mammals through community-based conservation and other land management initiatives (Anderson & Grove, 1987; Western & Wright, 1994). Examples include the cross-border Kruger link between South Africa and Mozambique (Mabunda et al., 2003), the greater Amboseli ecosystem in Kenya (KWS, 2020), and the Greater Yellowstone Coalition in the United States (Keiter, 2020). Yet wider regional linkages include the Paseo Pantera landscape in Central and South America (Lambert & Carr, 1998), the Yellowstone-to-Yukon landscape across the US–Canadian border (Chester, 2015), and the four-border Kavanga-Zambezi (KAZA) landscape in southern Africa (Stoldt et al., 2020). The theoretical framework for widening conservation from protected areas to regional and continental levels in the face of human impact and climate change has been highlighted by Soulé and Terborgh (1999), Allen and Singh (2016), and Curtin (2015). Such examples hold out hope of finding the space and mobility elephants and other large herbivores and carnivores need to play as keystone species in sustaining biodiversity in an increasingly human-dominated world, in alleviating the ecological disruption of compressed populations in parks, and in minimizing the need for intense species population management.

CONCLUSIONS

Our study tracked a half century of change in elephant numbers, distribution, and a cascade of ecological impacts in response to human activity, including poaching, the creation of a national park, and settlement across the Amboseli ecosystem.

Elephants compressed into the national park turned woodlands to grasslands and shrublands and swamps into short grazing lawns, causing a sharp increase in the proportion of large herbivore grazers relative to browsers. The results match the findings of high-density elephant populations in protected areas across Africa. In contrast, biodiversity fell as woody vegetation came to dominate grasslands in areas abandoned by elephants in Amboseli. We used naturalistic and exclosure experiments to show plant richness peaks where elephants and livestock overlapped and jostled spatially, setting up a creative tension that caused a patchwork of habitats and a peak in species richness.

A literature review adds to the Amboseli findings that the interactions of elephants and people, the two dominant keystone species in the savannas, created a shifting patchwork of habitats prior to the global ivory trade and colonialism. The shifting mosaic has since been disrupted by growing human activity and land fragmentation.

The Amboseli study points to the importance of space and mobility in enabling the interacting keystone roles of elephants and people to create and sustain habitat heterogeneity at an ecosystem and landscape scale. Space, mobility, and coexistence, rather than fragmentation and insularization of elephant populations, alleviate the ecological disruption of compressed population and minimizes the need for population management.

AUTHOR CONTRIBUTIONS

David Western has designed, planned, and directed the field programs of the Amboseli Conservation Program since its inception in 1967. Victor N. Mose has been responsible for data management, statistical analysis, and graphical presentations of the data used in this paper. Both authors contributed to the conceptualization and presentation of the paper and divided writing assignments. David Western was largely responsible for the literature review and final manuscript writing, and Victor N. Mose for the preparation for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Mose & Western, 2022) are available from Figshare: https://figshare.com/articles/dataset/Elephant_cascades_in_the_savannas/21383715.

ETHICS STATEMENT

Kenya Wildlife Service (KWS) issued permits to conduct fieldwork inside the protected Amboseli National Park (latitude: −2.626610; longitude: 37.2544060). For study sites located in the park and surrounding group ranches (Figure 1), no endangered plant species were involved. Aerial sample surveys of large herbivores were conducted in line with the Kenya Government, Department of Resource Surveys and Remote Sensing (DRSRS) methodology.

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REFERENCES

Allen, A. M., and N. J. Singh. 2016. "Linking Movement Ecology with Wildlife Management and Conservation." *Frontiers in Ecology and Evolution* 3: 155–68.

Altmann, J., S. C. Alberts, S. A. Altmann, and S. B. Roy. 2002. "Dramatic Change in Local Climate Patterns in the Amboseli Basin, Kenya." *African Journal of Ecology* 40: 248–51.

Anderson, D., and R. Grove. 1987. "The Scramble for Eden: Past, Present and Future in African Conservation." In *Conservation in Africa: People, Policies and Practice*, edited by D. Anderson and R. Grove, 1–13. Cambridge: Cambridge University Press.

Astivia, O. L. O., and B. D. Zumbo. 2017. "Population Models and Simulation Methods: The Case of the Spearman Rank Correlation." *British Journal of Mathematical and Statistical Psychology* 70: 347–67.

Bakker, E. S., J. L. Gill, C. N. Johnson, F. W. M. Vera, C. J. Sandom, G. P. Asner, and J.-C. Svenning. 2016. "Combining Paleo-Data and Modern Exclosure Experiments to Assess the Impact of Megafauna Extinctions on Woody Vegetation." *Proceedings of the National Academy of Sciences of the United States of America* 113: 847–55.

Burney, D. A., G. S. Robinson, and L. P. Burney. 2003. "*Sporormiella* and the Late Holocene Extinctions in Madagascar." *Proceedings of the National Academy of Sciences of the United States of America* 100(10800–10): 805.

Caughley, G. 1981. "Overpopulation." In *Problems in Management of Locally Abundant Wild Mammals*, edited by P. A. Jewell, S. Holt, and D. Hart, 7–19. New York: Academic Press.

Caughley, G. 1988. *A Projection of Ivory Production and Its Implications for the Conservation of African Elephants*. Melbourne: CSIRO, Division of Wildlife and Ecology.

Chester, C. C. 2015. "Yellowstone to Yukon: Transborder Conservation across a Vast International Landscape." *Environmental Science & Policy* 49: 75–84.

CNES/Airbus. 2020. "Google Earth Pro Image." https://www.google.com/maps/@-2.6542265,37.2306966,6830m/data=!3m1!1e3?authuser=0.

Cook, R. M., and M. D. Henley. 2019. "The Management Dilemma: Removing Elephants to Save Large Trees." *Koedoe: African Protected Area Conservation and Science* 61: 1–12.

Cottam, G., and J. T. Curtis. 1956. "The Use of Distance Measures in Phytosociological Sampling." *Ecology* 37: 451–60.

Coutu, A. N., J. Lee-Thorp, M. J. Collins, and P. J. Lane. 2016. "Mapping the Elephants of the 19th Century East African Ivory Trade with a Multi-Isotope Approach." *PLoS One* 11: e0163606.

Croze, H., and W. K. Lindsay. 2011. "Amboseli Ecosystem Context: Past and Present." In *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*, edited by C. J. Moss, H. Croze, and P. C. Lee, 11–28. Chicago, IL: University of Chicago Press.

Curtin, C. G. 2015. *The Science of Open Spaces: Theory and Practice for Conserving Large, Complex Systems*. Washington, DC: Island Press.

Curtin, C. G., and T. F. H. Allen. 2018. *Complex Ecology: Foundational Perspectives on Dynamic Approaches to Ecology and Conservation*. Cambridge: Cambridge University Press.

Davies, A. B., A. Gaylard, and G. P. Asner. 2018. "Megafaunal Effects on Vegetation Structure throughout a Densely Wooded African Landscape." *Ecological Applications* 28: 398–408.

Douglas-Hamilton, I., and A. Burrill. 1991. "Using Elephant Carcass Ratios to Determine Population Trends." *African Wildlife: Research and Management* 80: 98–105.

du Toit, J. T. 2003. "Large Herbivores and Savanna Heterogeneity." In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, edited by J. T. du Toit, K. H. Rogers, and H. C. Biggs, 292–309. Washington, DC: Island Press.

Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. "Elephants and Fire as Causes of Multiple Stable States in the Serengeti-Mara Woodlands." *The Journal of Animal Ecology* 59: 1147–64.

Eisenberg, C. 2013. *The Wolf's Tooth: Keystone Predators, Trophic Cascades, and Biodiversity*. London: Island Press.

Fritz, H., P. Duncan, I. J. Gordon, and A. W. Illius. 2002. "Megaherbivores Influence Trophic Guilds Structure in African Ungulate Communities." *Oecologia* 131: 620–5.

Gao, J., and Y. Carmel. 2020. "Can the Intermediate Disturbance Hypothesis Explain Grazing–Diversity Relations at a Global Scale?" *Oikos* 129: 493–502.

Gibin, M., P. Longley, and P. Atkinson. 2007. "Kernel Density Estimation and Percent Volume Contours in General Practice Catchment Area Analysis in Urban Areas." In *Proceedings of the GIScience Research UK Conference*. Princeton, NJ: Citeseer. pp. 11–3.

Grayson, D. K. 1989. "The Chronology of North American Late Pleistocene Extinctions." *Journal of Archaeological Science* 16: 153–65.

Grooten, M., and R. E. A. Almond, eds. 2018. *Living Planet Report 2018: Aiming Higher*. Gland: WWF.

Guldemond, R. A. R., A. Purdon, and R. J. Van Aarde. 2017. "A Systematic Review of Elephant Impact across Africa." *PLoS One* 12: e0178935.

Guldemond, R., and R. Van Aarde. 2008. "A Meta-Analysis of the Impact of African Elephants on Savanna Vegetation." *The Journal of Wildlife Management* 72: 892–9.

Håkansson, N. T. 2004. "The Human Ecology of World Systems in East Africa: The Impact of the Ivory Trade." *Human Ecology* 32: 561–91.

Hoare, R. E., and J. T. Du Toit. 1999. "Coexistence between People and Elephants in African Savannas." *Conservation Biology* 13: 633–9.

Holt, R. D., H. M. Ricado, and F. J. Frank van Veen. 2010. "Theoretical Perspectives on Trophic Cascades: Current and Future Directions." In *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, edited by J. Terborgh and J. A. Estes, 301–18. Washington, DC: Island Press.

Johnson, M. 1935. *Over African Jungles: The Record of a Glorious Adventure over the Big Game Country of Africa 60,000 Miles by Airplane*. New York: Harcourt.

Jolly, G. M. 1969. "Sampling Methods for Aerial Censuses of Wildlife Populations." *East African Agricultural and Forestry Journal* 34: 46–9.

Jonasson, S. 1988. "Evaluation of the Point Intercept Method for the Estimation of Plant Biomass." *Oikos* 52: 101–6.

Kangwana, K. F. 1993. "Elephants and Maasai: Conflict and Conservation in Amboseli, Kenya." PhD diss., University of Cambridge.

Kariya, T., and H. Kurata. 2004. *Generalized Least Squares*. Hoboken, NJ: John Wiley & Sons.

Keiter, R. B. 2020. "The Greater Yellowstone Ecosystem Revisited: Law, Science, and the Pursuit of Ecosystem Management in an Iconic Landscape." HeinOnline. https://lawreview.colorado.edu/printed/the-greater-yellowstone-ecosystem-revisited-law-science-and-the-pursuit-of-ecosystem-management-in-an-iconic-landscape/.

Khalil, H. K. 2002. *Nonlinear Systems*, 3rd ed. London: Pearson.

Kimani, K., and J. Pickard. 1998. "Recent Trends and Implications of Group Ranch Sub-Division and Fragmentation in Kajiado District, Kenya." *Geographical Journal* 202–213 164: 202.

KWS. 2020. *Amboseli National Park Management Plan, 2020–2030*. Nairobi: KWS. https://kws.go.ke/content/amboseli-national-park-management-plan-2020-2030.

Lambert, J. D., and M. H. Carr. 1998. "The Paseo Pantera Project: A Case Study Using GIS to Improve Continental-Scale Conservation Planning." In *GIS Methodologies for Developing Conservation Strategies*, edited by B. Savitsky and T. Lacher, Jr., 138–48. New York: Columbia University Press.

Laws, R. M. 1970. "Elephants as Agents of Habitat and Landscape Change in East Africa." *Oikos* 21: 1–15.

Laws, R. M. 1981. "Large Mammal Feeding Strategies and Related Overabundance Problems." In *Problems in Management of Locally Abundant Wild Mammals*, edited by P. A. Jewell and S. Holt, 217–32. New York: Academic Press.

Leuthold, W. 1996. "Recovery of Woody Vegetation in Tsavo National Park, Kenya, 1970–94." *African Journal of Ecology* 34: 101–12.

Lindeman, R. L. 1942. "The Trophic-Dynamic Aspect of Ecology." *Ecology* 23: 399–417.

Lindsay, W. K. 1982. *Habitat Selection and Social Group Dynamics of African Elephants in Amboseli, Kenya*. Vancouver: University of British Columbia.

Lindsay, W. K. 1994. "Feeding Ecology and Population Demography of African Elephants in Amboseli, Kenya." PhD diss., University of Cambridge.

Mabunda, D., D. J. Pienaar, and J. Verhoef. 2003. "The Kruger National Park: A Century of Management and Research." In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, edited by J. T. du Toit, K. H. Rogers, and H. C. Biggs, 3–21. Washington, DC: Island Press.

Mose, V. N., and D. Western. 2015. "Spatial Cluster Analysis for Large Herbivore Distributions: Amboseli Ecosystem, Kenya." *Ecological Informatics* 30: 203–6.

Mose, V., and D. Western. 2022. "Elephant Cascades in the Savannas." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.21383715.v1.

Moss, C. J., H. Croze, and P. C. Lee. 2011. *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Chicago, IL: University of Chicago Press.

Nkurunziza, S., and S. Ejaz Ahmed. 2011. "Estimation Strategies for the Regression Coefficient Parameter Matrix in Multivariate Multiple Regression." *Statistica Neerlandica* 65: 387–406.

O'Connor, T. G., P. S. Goodman, and B. Clegg. 2007. "A Functional Hypothesis of the Threat of Local Extirpation of Woody Plant Species by Elephant in Africa." *Biological Conservation* 136: 329–45.

Odum, H. T. 1957. "Trophic Structure and Productivity of Silver Springs, Florida." *Ecological Monographs* 27: 55–112.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. "Exploitation Ecosystems in Gradients of Primary Productivity." *The American Naturalist* 118: 240–61.

Owen-Smith, R. N. 1988. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge University Press.

Paine, R. T. 1969. "A Note on Trophic Complexity and Community Stability." *The American Naturalist* 103: 91–3.

Pennycuick, C. J., and D. Western. 1972. "An Investigation of some Sources of Bias in Aerial Transect Sampling of Large Mammal Populations." *African Journal of Ecology* 10: 175–91.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-137. https://CRAN.R-project.org/package=nlme.

Potts, R., A. K. Behrensmeyer, J. T. Faith, C. A. Tryon, A. S. Brooks, J. E. Yellen, A. L. Deino, R. Kinyanjui, J. B. Clark, and C. M. Haradon. 2018. "Environmental Dynamics during the Onset of the Middle Stone Age in Eastern Africa." *Science* 360: 86–90.

Potts, R., R. Dommain, J. W. Moerman, A. K. Behrensmeyer, A. L. Deino, S. Riedl, E. J. Beverly, E. T. Brown, D. Deocampo, and R. Kinyanjui. 2020. "Increased Ecological Resource Variability during a Critical Transition in Hominin Evolution." *Science Advances* 6: eabc8975.

Poulsen, J. R., S. E. Koerner, S. Moore, V. P. Medjibe, S. Blake, C. J. Clark, M. E. Akou, M. Fay, A. Meier, and J. Okouyi. 2017. "Poaching Empties Critical Central African Wilderness of Forest Elephants." *Current Biology* 27: 134–5.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. "Challenges in the Quest for Keystones: Identifying Keystone Species Is Difficult—But Essential to Understanding How Loss of Species Will Affect Ecosystems." *BioScience* 46: 609–20.

Pratt, D. J., P. J. Greenway, and M. D. Gwynne. 1966. "A Classification of East African Rangeland, with an Appendix on Terminology." *Journal of Applied Ecology* 3: 369–82.

Reid, R. S. 2012. *Savannas of our Birth: People, Wildlife, and Change in East Africa*. Berkeley, CA: University of California Press.

Rosner, B., R. J. Glynn, and M. T. Lee. 2006. "The Wilcoxon Signed Rank Test for Paired Comparisons of Clustered Data." *Biometrics* 62: 185–92.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. "The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence." *Ecology* 85: 359–71.

Sarkar, S. 2006. *Long-and Short-Term Dynamics of the Wetlands in the Amboseli Savanna Ecosystem, Kenya*. Waterloo: University of Waterloo.

Schillings, C. G. 1906. *With Flashlight and Rifle: A Record of Hunting Adventures and of Studies in Wild Life in Equatorial East Africa*. London: Hutchinson.

Schoener, T. W., and D. A. Spiller. 1987. "Effect of Lizards on Spider Populations: Manipulative Reconstruction of a Natural Experiment." *Science* 236: 949–52.

Seip, D. R. 1992. "Factors Limiting Woodland Caribou Populations and their Interrelationships with Wolves and Moose in Southeastern British Columbia." *Canadian Journal of Zoology* 70: 1494–503.

Sinclair, A. R. E., and M. Norton-Griffiths, eds. 1979. "The Eruption of the Ruminants." In *Serengeti: Dynamics of an Ecosystem* 82–103. Chicago, IL: University of Chicago Press.

Skarpe, C., and S. Ringrose. 2014. "The Chobe Environment." In *Elephants and Savanna Woodland Ecosystems,* edited by C. Skarpe, J. T. du Toit, and S. R. Moe, 7–29. Chichester: Wiley.

Soulé, M. E., and J. Terborgh. 1999. "Conserving Nature at Regional and Continental Scales—A Scientific Program for North America." *BioScience* 49: 809–17.

Stoldt, M., T. Göttert, C. Mann, and U. Zeller. 2020. "Transfrontier Conservation Areas and Human-Wildlife Conflict: The Case of the Namibian Component of the Kavango-Zambezi (KAZA) TFCA." *Scientific Reports* 10: 1–16.

Thomson, J. 1887. *Through Masai Land: A Journey of Exploration among the Snowclad Volcanic Mountains and Strange Tribes of Eastern Equatorial Africa*. London: Low, Marston, Searle, & Rivington.

Toit, J. T., and S. R. Moe. 2015. "Elephants and Ecological Cascades." *Ecology* 96: 309–10.

Vesey-FitzGerald, D. F. 1960. "Grazing Succession among East African Game Animals." *Journal of Mammalogy* 41: 161–72.

von Höhnel, L. R. 1894. *Discovery of Lakes Rudolf and Stefanie: A Narrative of Count Samuel Teleki's Exploring & Hunting Expedition in Eastern Equatorial Africa in 1887 & 1888*. London: Longmans, Green.

Walker, B. H. 1981. "Stability Properties of Semiarid Savannas in Southern African Game Reserves." In *Problems in Management of Locally Abundant Wild Mammals*, edited by P. A. Jewell and S. Holt, 57–67. New York: Academic Press.

Wall, J., G. Wittemyer, B. Klinkenberg, V. LeMay, S. Blake, S. Strindberg, M. Henley, F. Vollrath, F. Maisels, and J. Ferwerda. 2021. "Human Footprint and Protected Areas Shape Elephant Range across Africa." *Current Biology* 31: 2437–45.

Western, D. 1973. *The Structure, Dynamics and Changes of the Amboseli Ecosystem*. Nairobi: University of Nairobi.

Western, D. 1975. "Water Availability and Its Influence on the Structure and Dynamics of a Savannah Large Mammal Community." *African Journal of Ecology* 13: 265–86.

Western, D. 1989. "The Ecological Role of Elephants in Africa." *Pachyderm* 12: 43–6.

Western, D. 2007. "A Half a Century of Habitat Change in Amboseli National Park, Kenya." *African Journal of Ecology* 45: 302–10.

Western, D. 2010. "People, Elephants, and Habitat: Detecting a Century of Change Using Repeat Photography." In *Repeat Photography: Methods and Applications in the Natural Sciences*, edited by R. H. Webb, D. E. Boyer, and R. M. Turner, 211–22. Washington, DC: Island Press.

Western, D., and A. K. Behrensmeyer. 2009. "Bone Assemblages Track Animal Community Structure over 40 Years in an African Savanna Ecosystem." *Science* 324: 1061–4.

Western, D., and W. K. Lindsay. 1984. "Seasonal Herd Dynamics of a Savanna Elephant Population." *African Journal of Ecology* 22: 229–44.

Western, D., and D. Maitumo. 2004. "Woodland Loss and Restoration in a Savanna Park: A 20-Year Experiment." *African Journal of Ecology* 42: 111–21.

Western, D., and V. N. Mose. 2021. "The Changing Role of Natural and Human Agencies Shaping the Ecology of an African Savanna Ecosystem." *Ecosphere* 12: e03536.

Western, D., V. N. Mose, D. Maitumo, and C. Mburu. 2021. "Long-Term Changes in the Plant Ecology of an African Savanna Landscape and the Implications for Ecosystem Theory and Conservation Management." *Ecological Processes* 10: 15.

Western, D., and C. Van Praet. 1973. "Cyclical Changes in the Habitat and Climate of an East African Ecosystem." *Nature* 241: 104–6.

Western, D., and M. Wright, eds. 1994. *Natural Connections: Perspectives in Community-Based Conservation*. Washington, DC: Island Press.

Whittaker, R. H., and G. E. Likens. 1975. "The Biosphere and Man." In *Primary Productivity of the Biosphere*. Ecological Studies., edited by H. Lieth and R. Whittaker, 305–28. Berlin: Springer Science & Business Media.

Woodroffe, R., S. Thirgood, and A. Rabinowitz. 2005. "The Future of Coexistence: Resolving Human-Wildlife Conflicts in a

Changing World." *Conservation Biology Series-Cambridge* 9: 388.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Appendix S1

Title: Cascading effects of elephant-human interactions and the role of space and mobility in sustaining biodiversity

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Fig S1: A high-wire electric fence set up in 2001 at Ilmarishari exclosure (A) to test the impact of elephant removal on woodland recovery. By 2008 the regenerating fever trees had shaded out the Suaeda-dominated shrublands which supplanted the woodlands destroyed by elephants in the 1970s. The aerial view of the exclosure in 2005 (B) showing extensive fever tree regeneration and regrowth in the swamps relative to the control open-water in the foreground. By 2018 the fever trees formed a dense canopy closing out *Suaeda* shrub (C).

Model details:

Model [2] results show that the ratio of grass to tree biomass density (y) reduced by 0.6 for every additional kilometer (x) away from the centre of the park, $(y = -0.6x + 9.3,\ R^2 = 0.54,\ P = 0.0061)$. For shrubs, the ratio (y_1) reduced by 0.28 with a unit increase in distance $(y_1 = -0.28x + 2.6,\ R^2 = 0.49,\ P = 0.0118)$. In the controlled experimental manipulation of elephant impact, the ratio of grass to tree biomass density (y_g) reduced by 7.42 over the years (x_e), $(y_e = -7.42x_e + 14881,\ R^2 = 0.38,\ P = 0.0158)$. That of shrubs (y_s) reduced by 0.9 $(y_s = -0.9x_e + 1795,\ R^2 = 0.41,\ P = 0.0341)$.