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Title: The Serengeti squeeze: cross-boundary human impacts compromise an iconic protected ecosystem

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Abstract: Protected areas provide major benefits for humans in the form of ecosystem services, but landscape degradation by human activity at their edges may compromise their ecological functioning. Using multiple lines of evidence from 40 years of research in the Serengeti-Mara ecosystem, we find that such edge degradation has effectively “squeezed” wildlife into the core protected area and has altered the ecosystem’s dynamics even within this 40,000 km² ecosystem. This spatial cascade reduced resilience in the core and was mediated by the movement of grazers which reduced grass fuel and fires, weakened capacity of soils to sequester nutrients and carbon, and decreased responsiveness of primary production to rainfall. Similar effects in other protected ecosystems worldwide may require rethinking of natural resource management outside protected areas.

One Sentence Summary: Anthropogenic impacts at the edges of an ecosystem change the ecological functionality at the core

Main Text: Biodiversity is critical for sustaining ecosystem services (*1–4*), yet the major challenge is how to conserve it. Protected areas (PAs), in which human activities such as hunting, grazing, logging or conversion to cropland are restricted represent the dominant conservation strategy worldwide (*5*), despite potential conflicts of interest with historic rights or well-being of indigenous people (*6*). However, the sustainability of the PA strategy to preserve biodiversity and ecosystem services is uncertain. One third of PAs are under intense human pressure globally (*7*), especially from anthropogenic activities along their borders and despite heavy protection (*8–11*). A major question is how these edge areas can be managed most effectively to best preserve both biodiversity and human livelihoods (*12*). Previous studies suggest that both the rate of landuse change and the growth of human populations can be fastest near protected area boundaries (*13–16*), which accelerate the rate of edge degradation through increased livestock production, crop cultivation, and extraction of natural resources such as charcoal and bushmeat. In regions with high human density, the sharp contrast in natural resources across PA boundaries leads to "hard edges" which exacerbates human-wildlife conflicts (*17*), leading to two opposing intervention strategies. Fencing PAs as a form of "land sparing" from intensively used surrounding areas can solve some human-wildlife conflicts but also prevents beneficial temporary use of areas outside the reserve by wildlife, and requires intensive management that can be too costly for large reserves in developing countries (*18–20*). An alternative strategy involves "land sharing", which promotes the coexistence of humans and wildlife, especially in buffer zones (*21*). The majority of the earth's PAs are not fenced, questioning if anthropogenic activities at the edges are increasingly compromising the ecological processes in the core. The objective of our research is to assess if edge effects are currently undermining the ecological integrity that PAs aim to protect.

The concept of spatial compression in Pas (Fig.1)

At low human population density, people can extract sufficient resources and receive additional benefits from Pas without compromising them and conversely PAs can profit from the presence of people. Under these conditions, livestock and wildlife can coexist outside core protected areas (CPAs; *22*, *23*). Unprotected areas (UPAs) can support ecotourism and harvesting of wildlife, while livestock keeping can create local nutrient hotspots that increase biodiversity (*24*, *25*). This can lead to mutually beneficial relationships between people and wildlife (*26*) over longs periods of time (*27*). However, steep increases in human populations (through population growth and/or migration towards CPAs) can result in unsustainable use and thus reduce wildlife populations both outside and along the edges of the CPAs (*28–30*). This may impose a form of habitat compression that increases wildlife densities within the CPAs by making their effective size smaller than their geographic size. Such habitat compression may result in apparently positive effects (e.g. increased wildlife densities) becoming negative in the long-term if they cause undesirable changes in the functioning and stability of the ecosystem.

Here, we show how spatial compression alters the key ecological functioning of the Serengeti-Mara ecosystem in Tanzania and Kenya, one of the largest, most iconic PAs in the world. This ecosystem is famous for its soft-edge land-sharing conservation strategies that buffer the CPAs formed by the Serengeti National Park (SNP), the Mara Reserve and several adjacent areas with similar and complementary management to the national parks (CPA: IUCN-cat. II, see (*31*), Table S1). The ecosystem is managed to protect the diversity of wildlife and ecological processes, foremost the migration of over 2 million large herbivores, primarily wildebeest

(*Connochaetes taurinus*), zebras (*Equus quagga*) and Thomson's gazelles (*Eudorcas thomsonii)* (*32*). The spatial layout of a set of protected areas with different management supports this migration (Fig. S1) by allowing animals free access to spatio-temporally variable forage within the CPA, adjacent PAs with Sustainable Resource Use (PASRU: IUCN-cat. V and VI) and UPAs. Using a combination of long-term field experiments, census data and remote sensing, we show that increasing human populations, and their accompanying livestock and land conversion practices, have "squeezed" the (migratory) grazing animals into an increasingly smaller part of the CPA. We provide evidence that compression of wildlife has resulted in increased grazing intensity in the CPA that decreases rangeland productivity, changes fire regimes, reduces soil carbon storage and alters seasonal water retention. Our study demonstrates how land use at the borders of a large PA modifies wildlife-vegetation interactions within and consequently changes multiple ecosystem processes and services in the CPA.

Increased human dominance outside the CPA

From 1999 to 2012, the human population in the areas surrounding Serengeti-Mara increased by 2.4% per year on average (Fig. S2-S6; (*31*)). The human population growth rate was higher in the UPA along the western boundaries, inhabited by Sukuma and Kuria agro-pastoralists, compared with the PASRU along the eastern boundaries of the CPA where Maasai pastoralists herd their livestock. Concomitantly, crop agriculture expanded from 37.0% of the region in 1984 to 54.0% in 2018 (Fig. S7; Table S2-S3; (*31*)). The growth of the cattle population (0.9% on average per year, 2002-2012) was especially high in the wetter Tanzanian Mara Region, towards Lake Victoria (4.2% per year), despite there being very little land outside the CPA left for grazing in this area. Sheep and goat populations increased steeply in all the regions bordering the CPA (3.8% per year; Fig. S8; (*31*)). Concurrently, grazing lands exhibited intensifying impacts as evidenced by decreasing herbaceous vegetation green up, most notably in the PASRU, (Fig. S9-S11; (*31*)) and virtually no fires outside the CPA since 2005 (Fig. 2, S12-S14; (*31*)).

Expanding edge effects induce spatial compression

We use unique and detailed data from the Narok subarea of the ecosystem to show how livestock densities increased not only close to the border but also within the CPA over the past four decades, likely displacing wild herbivores into the SNP and leading to declining densities in MMNR (Fig. 3, S15-S19, Tables S4-S6; (*31*)). Here, human settlement and population densities have increased enormously, especially close to the CPA boundary (note that increased people densities inside the MMNR in Fig. 3 represent park and lodge staff, not movement of local people living outside the reserve). The wildlife biomass inside the first 15km of the CPA reduced by 75% in the wet season and by 50% in the dry season from the 1970s to 2000s. The latter declines are largely due to changes in the abundance of the Loita sub-population of migratory wildebeest and zebra that traditionally use the MMNR as their dry season range. Although such detailed data are not available for the rest of the ecosystem, several indicators show that this spatial compression phenomenon happened throughout the ecosystem.

In recent years, Maasai pastoralists in the PASRU have moved their bomas towards the borders of the CPA (Fig. S20-S25; (*31*)) and even established bomas up to 10 km inside the CPA (Fig. 2). In addition, Maasi pastoralists with bomas outside the CPA might bring their herds on illegal multi-day grazing trips into the CPA, as opposed to short, nightly grazing trips by the agro-pastoralists on the west. The trend to push more livestock further into the CPA is probably in response to declines in palatable forage in the remaining communal village grazing lands (*30*, *33*).

The resulting cross-boundary human pressures also affect the extent of the migratory movements of large herbivores, a defining ecological process of the Serengeti-Mara ecosystem. Ecosystem-wide movement data obtained by GPS collaring of migratory wildebeest show avoidance of the CPA margins in the last two decades and use has especially decreased along the borders of PASRU and concentrated at the core (Fig. 4A-B, S26; (*31*)). Three lines of evidence suggest that these patterns are best explained by increased competition between migratory wildebeest and livestock.

First, the analysis of boundaries with UPAs where patrolling is medium (Fig. S1; (*31*)), such as the border of Maswa Game Reserve, indicates that agro-pastoralists enter the park with their livestock on a daily basis, producing an extensive network of livestock paths (Fig. 2, S22-S23, S27; (*31*)). This coincides with a strong reduction in maximum vegetation greenness (maxNDVI) within the first 7 km inside the CPA (>10%; Fig. 4G-H), as well as a significant decline in the area of the CPA burned in the past 16 years from 52% to 29% corresponding to 3184 km² in total (GLM: $F_{1,14}$=-5.9, $p < 0.05$; Fig. 4E-F). The most severe changes in maxNDVI and fire coincide with a high density of livestock paths and (temporary) livestock corrals (bomas), suggesting illegal livestock incursions into the protected area removes vegetation biomass (Fig. 2, S10, S13; (*31*)).

Second, these effects are ameliorated in areas with increased border control where illegal grazing is more effectively excluded. The boundaries of the UPAs with strong border control, such as the edges of the Grumeti Game Reserve, show less drastic changes in NDVI (Fig. 4, compare UPA Strong with UPA Medium), suggesting these areas are less intensively grazed by livestock. Along UPA Strong boundaries, wildebeest increased their use close to the border, whereas in the UPA Medium areas wildebeest use increased beginning at 7 km inside the border, corresponding to the distance of livestock incursions.

The third line of evidence suggesting livestock compete with wildlife comes from observing the response of wildebeest in the different PASRU boundaries (Fig. 4C-D, S26; (*31*)). In Narok where the intensity of use by wildebeest utilization was previously highest, wildebeest utilization has declined up to 15 km inside the CPA, while along the border with Loliondo Game Controlled Area (LGCA) the decreased use only stretches a few kilometers inside. Most notably, utilization in the Ngorongoro Conservation Area (NCA) increased in recent years. There are multiple explanations for these contrasting effects between the different PASRU. First, NCA has lower human and livestock population densities than in LGCA and Narok (Figs. S4-5, S8; (*31*)). Second, the most severe food competition between livestock and wildebeest should take place during the dry season when the wildebeest reside in the Mara (*34*). Third, wet season competition in NCA is further reduced due to the risk of transmission of malignant catarrhal fever by calving wildebeest and the resultant avoidance of wildebeest calving sites by Maasai pastoralists. Altogether, competition between wildebeest and livestock is highest in Narok and lowest in NCA (*35*), suggesting the NCA boundary still functions as a soft boundary in contrast to Narok. The observed squeeze thus occurs most strongly in the dry season, a pattern that is supported by detailed surveys from Narok (Fig. 2). Wildebeest collar data show a (1) displacement of wildlife away from the dry season range in Narok and towards Northern Serengeti and the Western Corridor (Fig. S26; (*31*)), and (2) increasing wildebeest utilization in the UPA Strong and UPA Medium (except for the first 7 km)(Fig. 4A-B).

Consequences for the ecological functioning of the CPA

In addition to the severe effects of human disturbance in the border regions of CPA, our data suggest that these compression effects (Figs. 2-4) spatially cascade to modify ecosystem processes over the entire CPA, not just the boundary. Grazing intensity (by wildlife) measured at eight long-term grazing exclosure (LTGE) sites, each with three pairs of ungrazed (exclosures) and control (unfenced) plots, across SNP (48 plots in total; Fig. S12; (*31*)) has increased by 16% between 2001-2016 (ca. 1.1% per year (Fig. 5A, S28A; (*31*)). A Generalized Linear Model with plot-pairs as subjects (blocks) and year and September-June rainfall as covariates, shows that this change is not explained by rainfall (Table S7; (*31*)). Concurrently, the total area burned in the CPA decreased from 55% to 34% without changes in fire management, while maxNDVI decreased by 8% on average from 0.78 to 0.71 (Fig. 5B-C). Wildebeest formerly spent the longest time on the Serengeti Plains, the Central Serengeti and parts of the Western Corridor before moving to the Mara Triangle and returning through the area bordering the LGCA. In recent years, the wildebeest distribution has extended farther south and west of the CPA into areas that receive greater rainfall and feature high wet season biomass of plants living on poorer quality soils (Fig. S26E, S28B). Increased use of such areas inside the CPA would be expected when herbivores are displaced from preferred grazing sites in Narok and LGCA as they are the only other areas with permanent water. These changes in wildebeest use, grazing intensities, area burned and maxNDVI in the core ecosystem cannot be explained by changes in wildebeest population numbers (Fig. S29; Table S8 (*31*)) or decreasing rainfall ((*36*); Fig. S30-S31; if anything, there was a trend of increasing rainfall). Changes occurred simultaneously with the increased human dominance outside the CPA and its boundary areas, and together provide strong evidence that ecological function is changing at the core of an ecosystem due to compression of wildlife.

It is unclear why this habitat compression has not resulted in an observable decline in wildebeest numbers, since the overall abundance of wildebeest is thought to be regulated by dry season food availability (*34*)**.** It is possible that the trend of increasing rainfall (Figs. S30-S31; (*31*)) has resulted in sufficient primary productivity to still support the current densities of wildebeest (Fig. 5A). Alternatively, the wildebeest population may not be near carrying capacity, or may not yet have reached a new equilibrium (*37*). While the long-term population trend is relatively stable and indicative of food limitation (Fig. S29), a large percentage of the population (up to 12% year^{-1}) is removed each year for bushmeat (*38*), and this offtake may dampen the role of food competition in wildebeest mortality, and potentially compensate other demographic components such as birth rates or juvenile survival. Overall, the future impacts of these changes in space use on animal numbers are uncertain and of potential concern.

The park-wide increased grazing intensities are associated with a number of ecosystem function changes. Data from the LTGE sites shows that plant biomass in grazed areas in the CPA depended much less on annual rainfall in the period 2009-2016 than over the same range of rainfall variation during the period 2001-2006 (GLM Year x Rainfall Interaction, X^2=5.31, P<0.03; Fig. 5A, Table S9) after accounting for the effect of grazing on biomass. Reduced vegetation responsiveness suggests that increased grazing intensities inside the park may reduce the resilience of plant productivity. Measurements of multi-year dynamics of soil organic carbon (SOC, 0-30 cm depth) in grazed plots reveal a significant unimodal response to grazing intensity (Fig. 5B), with negative changes at higher grazing intensities (GI>0.55). This response suggests that the increased grazing intensities due to a "squeeze" effect decreases soil carbon sequestration in Serengeti grasslands (*39*), which we see as a significant decline in the number of plots that sequestered more than 1 Mg C/ha between 2009-2017 (6 of 21 plots, 28.3%) than between 2001-2008 (14 of 24 plots, 58.6%)(X^2=4.01, P=0.04).

Other data from the LTGE experiment suggest three different ecosystem responses that might explain why compression and increased grazing intensity would yield lower resilience and carbon storage. First, higher grazing intensities were significantly associated with higher percent cover of largely unpalatable forbs and lower cover of known N-fixing species, including legumes, in grazed plots (Fig. 5C)(*40*). Second, as indicated by a significant quadratic regression model, higher grazing intensities shifted effects of grazers on root biomass significantly ($P < 0.01$) from positive to negative (Fig. 5D). Third, effects of grazers on production of hyphae by arbuscular mycorrhizal fungi, important plant symbionts for phosphorus uptake, shifted from positive to negative as grazing intensity increased ($P<0.01$; Fig. 5E)(*41*). These relationships suggest that the higher grazing intensities associated with habitat compression may weaken mutualistic relationships that assist nutrient acquisition (Fig. 5C,E) and increase belowground carbon inputs (Fig. 5D,E). Furthermore, increases in unpalatable forbs are associated with lower representation of dominant grass species, possibly further exacerbating the degradation of primary productivity that supports the diverse and dominant food webs of the Greater Serengeti-Mara Ecosystem (*42*). These changes may signal future degradation in CPA that has already happened in human-dominated community areas.

The way ahead

Today, wildlife competes with cattle for grass, generating a conflict in both UPAs where aspirations to increase cattle grazing are restricted by competition with wildlife and in PAs when cattle are moved into the park to compensate. While people were evicted from current CPAs in the 20th century, wildlife is still allowed to roam the village lands, creating potential conflict over this asymmetric historical relation. Our results illustrate that these conflicts at the periphery of large PAs can have strong impacts on the ecological functioning at the core. These results highlight the challenge in managing ecosystem edges for effective whole-ecosystem biodiversity conservation, given the current rate of human population expansion and land-use change in its surroundings.

As the GSME is among the largest PAs in Africa, the situation is likely to be considerably worse for smaller areas. The GSME is one of the few, and perhaps most iconic ecosystems whose PA boundaries were established based on ecological considerations of a larger landscape, intended to encompass migratory animals (*43*). However, most other PAs across Africa represent now only fragments of formerly much larger ecosystems (*44*). This landscape fragmentation has caused the strong decline or extinction of most large-scale migrations worldwide (*45*). This calls for novel strategies for improving the ecological integrity of fragmented ecosystems as well as for preserving the last remaining places where these large-scale migrations still persist.

This will require re-thinking how to maintain the integrity of ecosystem edges, especially under the rapidly increasing human densities and footprints in developing countries. For relatively intact and contiguous ecosystems such as the GSME, sustainable long-term solutions are likely to be found in ambitious land-use plans that actively manage resources beyond PA boundaries. Strategies where humans and wildlife share landscapes under conditions established and enforced by mutual agreement of local people and regional or national governments are likely the way forward. People with rural livelihoods can strongly profit from nature, and nature can profit from them. But only if neighboring communities are strongly involved in conservation

(*46*), preferably in long-term and locally-led programs with direct and long-term community benefits from conservation actions (*47*) and conservation management has long-term stability. This will require i) continued monitoring of both the ecological integrity and societal trends in the surroundings of PA's, ii) the building of more (justified) trust with local communities that they will keep sharing in the benefits of natural resource conservation, and iii) ensuring that livestock numbers, settlement and cropland expansion in the direct vicinity of core protected areas do not go beyond a point where they impair the key structure and functioning of the underlying socio-ecological system.

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Supplementary Materials:

Materials and Methods

Figures S1-S31

Tables S1-S9

References (48-81)

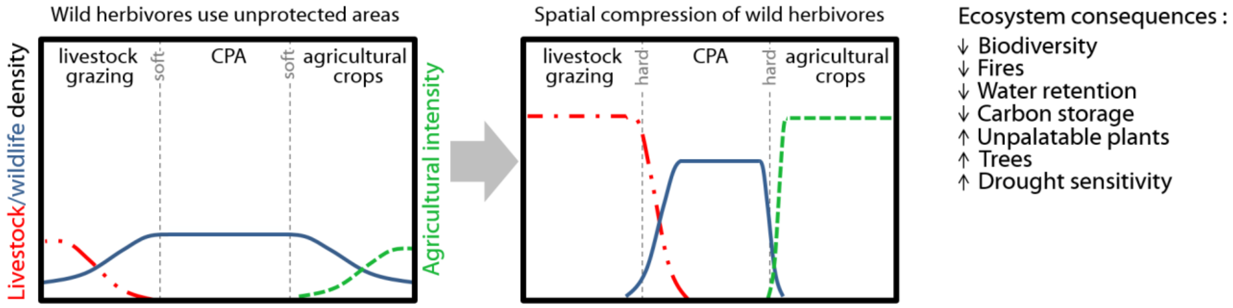

Fig. 1. The concept of spatial compression in protected areas. Unsustainable activities outside a soft-edge core protected area (CPA) resulting from human population growth spatially compress wildlife, leading to more intense use of protected land and multiple possible consequences for the magnitude and stability of ecosystem processes and services. Increased human population, livestock densities and/or agricultural intensities convert soft borders that effectively extend the CPA (left figure) into hard borders that effectively compress the CPA (right figure). Lines represent hypothesized wildlife (blue) and livestock (red) densities and agricultural intensity (green).

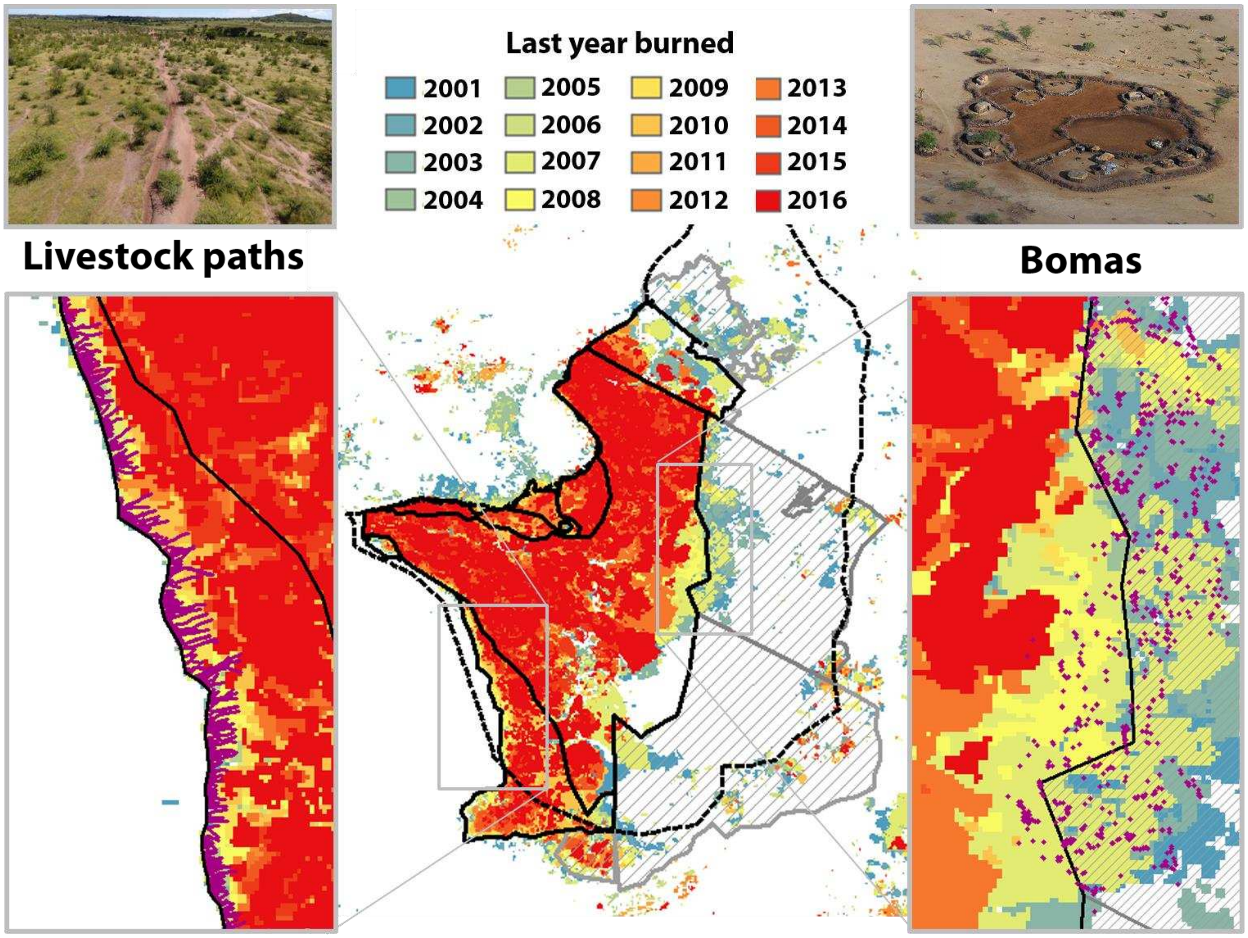

Fig. 2. Spatial compression of burned area in the Greater Serengeti-Mara Ecosystem. Different colors represent the last year each pixel burned between 2001 (blue) and 2016 (red) visualized using the MODIS burned area product. Magnifications show the same map overlaid with livestock paths (left) and bomas (right). Solid black lines represent borders of Core Protected Areas (CPAs). Grey hatched areas are Protected Areas of Sustainable Resource Use (PASRU) inhabited by people and grazed by livestock. The black dashed line is the boundary of the Greater Serengeti-Mara Ecosystem that represents the area formerly used by the migratory wildlife.

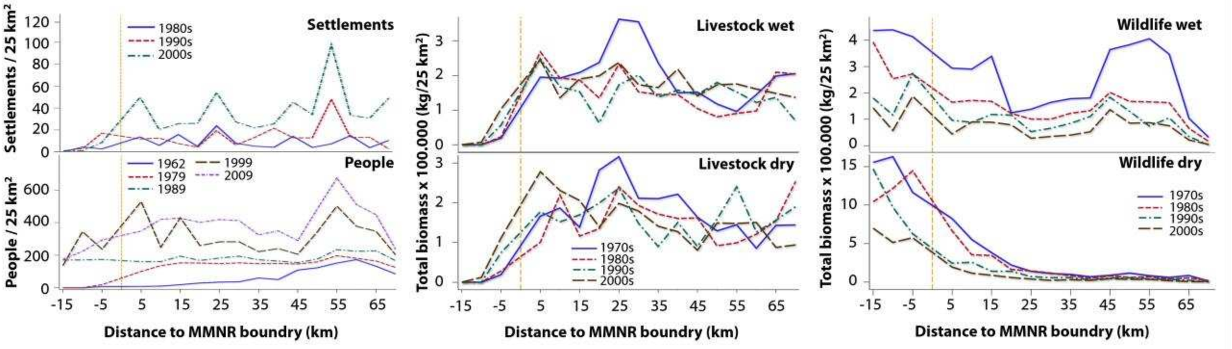

Fig. 3. **Spatial expansion of humans, livestock and the compression of wild herbivores over multiple decades**. Wildlife and livestock trends shown for both wet (top) and dry (bottom) season. Density estimates are plotted against distance to the border of Masai Mara National Reserve (MMNR) covering the first 15km inside the MMNR and 70km outside. Human settlement, people and livestock densities increase through time close to the border and even inside the MMNR. At the same time, wildlife densities decline, especially in the dry season, and these effects stretch increasingly farther into the MMNR.

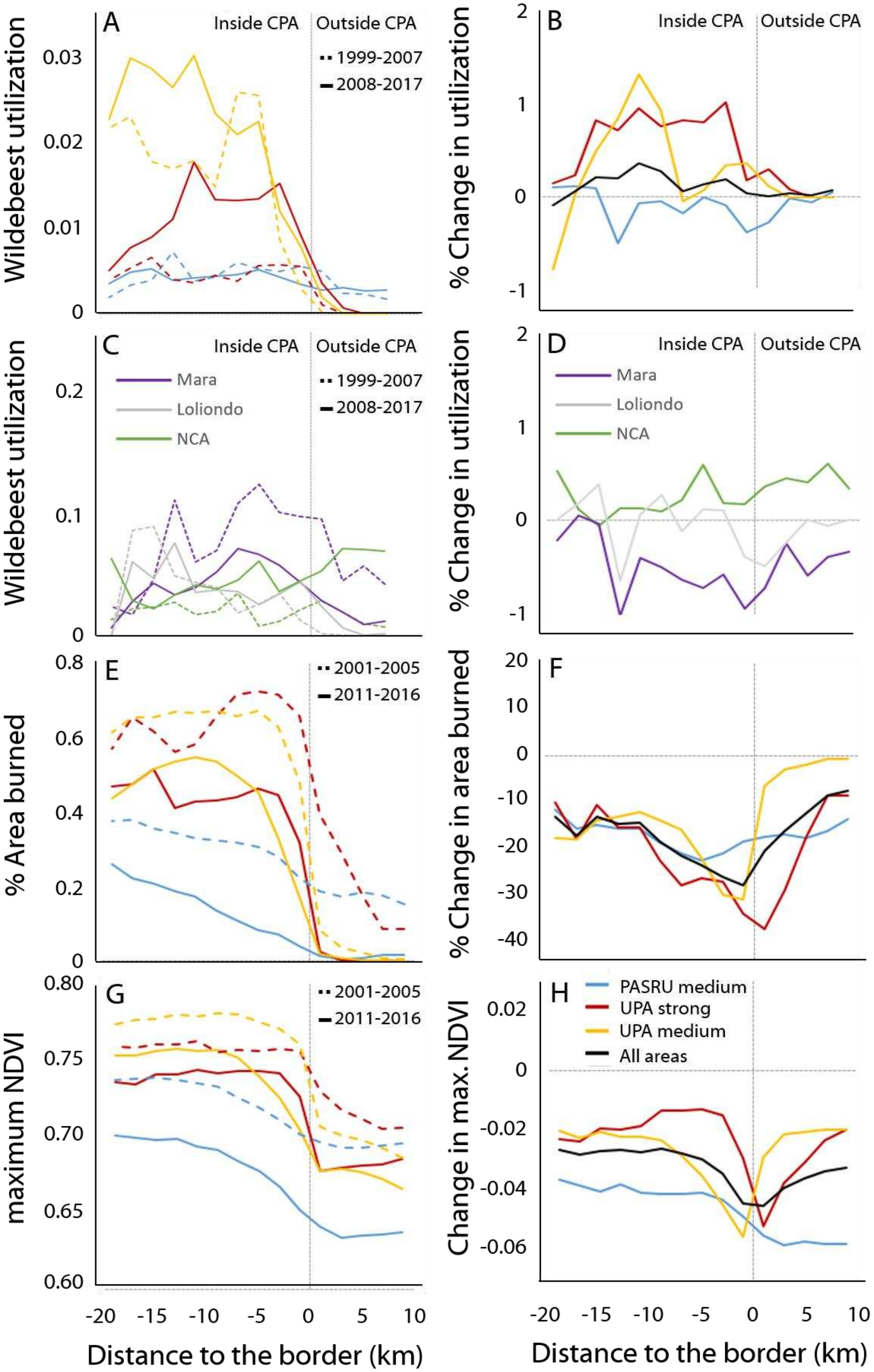
A
Inside CPA
Outside CPA
1999-2007
2008-2017
Wildebeest utilization
0.03
0.02
0.01
0
B
Inside CPA
Outside CPA
% Change in utilization
2
1
0
-1
C
Inside CPA
Outside CPA
Mara
Loliondo
NCA
1999-2007
2008-2017
Wildebeest utilization
0.2
0.1
0
D
Inside CPA
Outside CPA
Mara
Loliondo
NCA
% Change in utilization
2
1
0
-1
E
2001-2005
2011-2016
% Area burned
0.8
0.6
0.4
0.2
0
F
% Change in area burned
20
10
0
-10
-20
-30
-40
G
2001-2005
2011-2016
maximum NDVI
0.80
0.75
0.70
0.65
0.60
H
PASRU medium
UPA strong
UPA medium
All areas
Change in max. NDVI
0.02
0
-0.02
-0.04
-0.06
-20
-15
-10
-5
0
5
10
Distance to the border (km)
-20
-15
-10
-5
0
5
10
Distance to the border (km)

Fig. 4. **Changes in wildebeest occupancy, fire and vegetation greenness in the border regions of the Core Protected Areas (CPAs)**. Wildebeest utilization between 1999-2007 and 2008-2017 (A, C), mean area burned between 2001-2005 and 2011-2016 (E), mean maxNDVI between 2001-2005 and 2011-2016 (G) and the change between the two periods (B,D,F,H) as a function of distance to the border for three different border types between CPA and: 1) Protected Area with Sustainable Resource Use (PASRU) with medium border control against illegal activities (PASRU medium, blue line), 2) unprotected areas (UPA) with strong border control (UPA strong, red line), 3) UPA with medium border control (UPA medium, orange line). Panel C and D show the same information as the PASRU (blue lines) in panel A and B but now split up for the three different PASRU areas. Black line represents the overall weighted mean. Data covers both the Tanzanian and Kenyan side of the ecosystem.

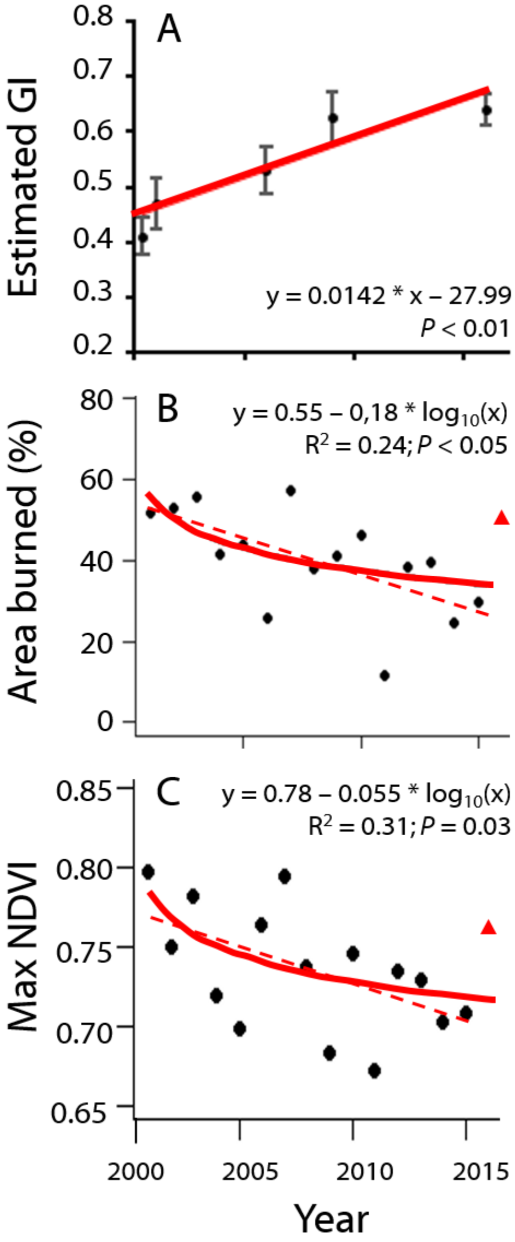

Fig. 5. Changes in grazing intensity, burned area and maxNDVI between 2001 and 2016 for the entire area designated as Core Protected Area. A) Grazing intensity (GI; mean ± SE), measured through herbivore exclosures, increases by 1.08% per year on average. B) Area burned decreased by 40% in 16 years time (solid red line). C) MaxNDVI decreased by 8% in 16 years time. The burned area and maxNDVI increased in 2016 (red triangle) due to management actions in eastern Serengeti National Park. Excluding this data point results in a stronger correlation and more explained variation (dashed red lines; Area burned=0.53-0.017*years, R^2=0.38, P=0.01; maxNDVI=0.77-0.047*years, R^2=0.33, P=0.03).

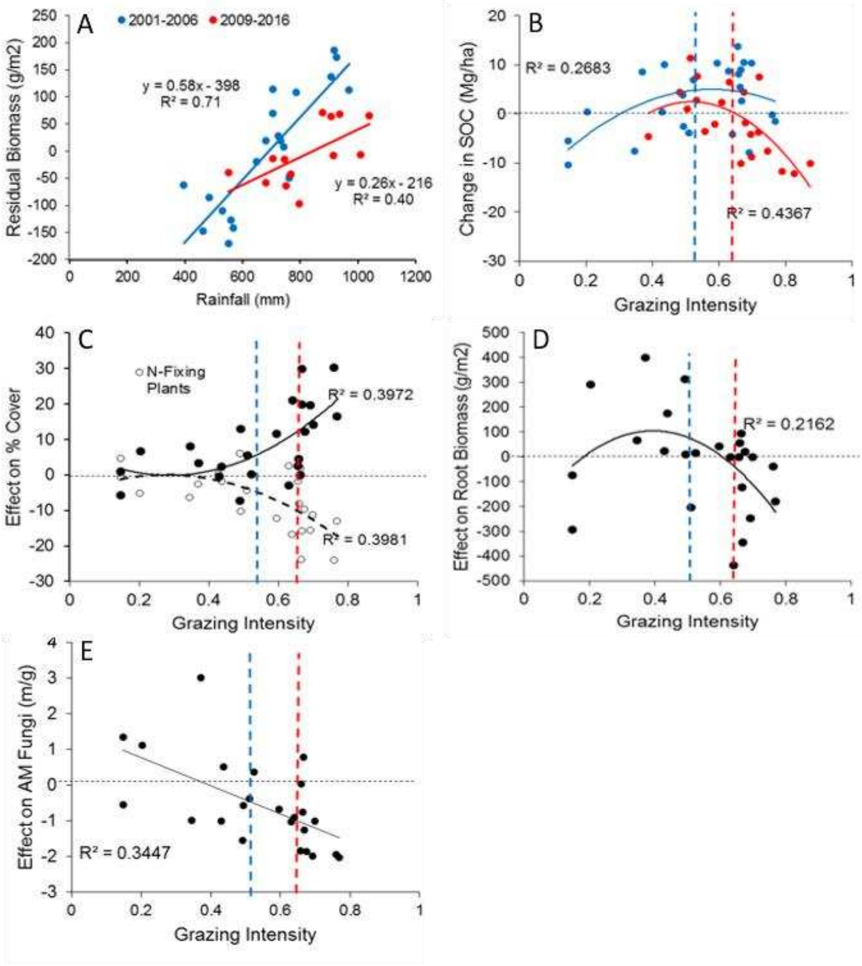

Fig. 6. Consequences of increased grazing for ecosystem processes. Data from 2001-2017 in the Serengeti Long-Term Grazing Exclosure experiment (LTGE; 8 sites with three exclosure-control plot pairs, *N* = 24). Linear models with quadratic functions contain significant coefficients ($P<0.01$), and fit significantly better than straight lines (R^2 improvements > 0.2). Vertical dashed lines represent mean grazing intensity across all sites in 2001-2008 (blue) and 2009-2016 (red). A) Residual aboveground biomass averaged across grazed plots at each site after accounting for the influence of grazing intensity in a GLM, exhibits significant ($P<0.01$) relationships with CHIRPS satellite-estimated rainfall across 8 sites in 2001, 2002, and 2006 (blue points, $N=21$), at 7 sites in 2009 and 6 sites in 2016 (red points, $N=13$). Slopes are significantly different ($P<0.04$). B) Changes in soil organic carbon (SOC) in each grazed plot from 2001 to 2008 (blue circles, $N=24$) and 2009 to 2017 (red circles, $N=21$). C-E) Effects of excluding herbivores in plot pairs (control–exclosure measure) at different mean grazing intensities (measured in 2006 and 2009) on C) percent cover of N-fixing plants, both grasses and legumes (open circles) and low palatability forb species (solid circles), D) root biomass and E) production of hyphae of arbuscular mycorrhizal (AM) fungi.

Supplementary Materials for

The Serengeti squeeze: cross-boundary human impacts compromise an iconic protected ecosystem

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Supplementary Text

1. Classification, characteristics, history and management of protected areas in the GSME

The Greater Serengeti-Mara Ecosystem (GSME) consists of a mosaic of different management areas and natural resource use strategies. We here define GSME as the limit to the (historical) migration of wildebeest and zebra between their dry and wet season ranges, plus the upper watersheds of rivers that provide the dry season ranges with water (Fig. S1)(*43*, *48*). Besides the world-famous Serengeti-Mara migration (or Southern migration) there is a smaller migration (Northern migration) from the Maasai Mara to the Loita Plains. The Mara-Loita wildebeest population numbered 50,000-100,000 animals prior to 1947 (*49*) but the population since suffered a very drastic decline (*50*). The current habitat use of the Serengeti-Mara migration lies largely within areas with some protected status (Fig. S1), while the wet season range of the Mara-Loita migration is situated outside protected areas.

There are 12 major protected areas within the boundaries of the GSME (Fig. S1) with different management strategies and resources (Table S1). We grouped these protected areas into 3 broad management types based on their IUCN-category and intensity of border controls. All areas classified as National Park or National Reserve (IUCN category II) or the adjacent areas that complement these core protected areas without any livestock grazing, agriculture or human settlement (IUCN category II-like) are here categorized as Core Protected Areas (CPA). Other protected landscapes or areas where livestock grazing is allowed and are inhabited by people (IUCN category V and VI) are classified as Protected Areas with Sustainable Resource Use (PASRU). We then subdivided the CPA category into areas with strong border control (CPA strong) and medium border control (CPA medium) to investigate whether border control intensity impacted the effects of habitat compression. Areas without any form of protection are classified as Unprotected Areas (UPA). Below, we present a short description of the current management, key characteristics and

Masai Mara National Reserve (MMNR)
The Masai Mara was originally established as a wildlife sanctuary in November 1948 and covered only 520 km^2, including the Mara Triangle. Stricter laws controlling the shooting of animals were introduced in 1957. The Mara National Reserve was expanded later to east of the Mara River and to cover a total area of 1831 km^2 and renamed the African District Council Game Reserve by the African District Council (Local Government) on 8 March 1961. District Council by-laws prohibited the Maasai and their livestock from entering an inner core area of 518 km^2. The Kenya Government provided the Maasai with an annual subsidy of 8000 British Pounds (*50*). The Narok County Council (NCC) assumed management of the Game Reserve in 1966, the year the Hardacre Local Government Commission recommended the abolition of the African District Councils and replacing them with County Councils. In 1974, 159 km^2 was hived off the reserve and returned to the local communities. The remaining 1672 km^2 was granted the status of a National Reserve under Legal Notice 271 (*51*). In 1976, the Kenya Government and NCC discussed reducing the area of the Reserve by a further 162 km^2 (*52*). The Masai Mara Game Reserve was re-designated the Masai Mara National Reserve under the Wildlife Conservation and Management Act of 1976. An area of 162 km^2 was hived off the reserve and given back to the local communities in 1984 through a formal notice, reducing the reserve size to

1510 km^2. In 1994 the Trans Mara County Council was formed and took control of the Mara Triangle (510 km^2) between the Mara river and the Isuria escarpment, whereas the Narok County Council retained control of the part of the reserve east of the Mara River. On 25 May 2001, the Mara Conservancy, a not-for-profit management company, was contracted to take over the management of the Mara Triangle under a private-public partnership arrangement. On 4 March 2013, the Narok County Government assumed the administration and management of the Masai Mara National Reserve because NCC was dissolved following the promulgation of the Kenya 2010 Constitution. The Serengeti National Park, excluding the Lamai Wedge, reached to the Masai Mara National Reserve border on 1 July 1959 (*49*). The Lamai Wedge was added to the Serengeti National Park in 1965.

There was apparently little or no forced eviction from the Mara to create the reserve. The Maasai could not use the Mara for cattle because of the high prevalence of tsetse fly. The reserve was intended to be owned by the Maasai and to conserve wildlife for the material improvement of the Maasai (*53*). To this day the Maasai, through the Maasai dominated Narok County Government, not the central government of Kenya, continue to control the Masai Mara National Reserve. For the longer history of the use by Maasai of the MNNR see the description of the subject under the Serengeti National Park below.

Masai Mara Conservancies (MMC)
The Greater Mara Ecosystem (ca. 7,500 km^2) includes Koɨyiaki, Lemek, Ol Chorro Oiroua, Olkinyei, Siana, Maji Moto, Naikara, Ol Derkesi, Kerinkani, Oloirien, and Kimintet Group Ranches. The Group Ranches were created after the Kenya government enacted the Land (Group Representative) Act in 1968 to enable private (group) ownership of formerly communally held areas. This policy lasted for three decades and was intended to promote investment and more productive use of the rangelands.

Growing concerns over poor management of the group ranches by group ranch committees, land tenure insecurity, increasing group ranch membership and influence of private land owners nearby catalyzed calls for group ranch subdivision into individual land parcels. Privatization of land tenure is already complete in most of the Mara group ranches. The private land owners have now converted large areas used by wildlife to wheat fields, irrigated farms (along the Mara River) and private ranches. Fencing of private land is also expanding rapidly, especially in recent years. Land privatization has also been associated with further land subdivision and sedentarization of formerly semi-nomadic Maasai pastoralists.

Five landowners established the first private wildlife conservancy in the Mara, Olchorro Oiroua, on 77.12 km^2 of land in 1992. In 2005, this was followed by the establishment of Olkinyei Conservancy through a partnership between a private investor in tourism and a group of neighboring local private land owners. Subsequently the number of wildlife conservancies in the Mara increased to 14 in 2017. The area covered by the conservancies also expanded from 32.4 km^2 in 2005 to 1420 km^2 in 2017. The number of local private landowners contributing land to the conservancies increased from 171 in 2005 to 13625 in 2017 (https://www.maraconservancies.org/). The conservancies employed 258 rangers in 2017. Land owners are paid for leasing their land to tourist operators and also benefit from employment in the conservancies.

Serengeti National Park (SNP)

The Serengeti National Park (14,750 km^2) in Tanzania is the largest protected area in the GSME. In 1981, it was designated as a UNESCO World Heritage Site and International Biosphere Reserve. It is visited by ca. 350,000 visitors each year. Maasai people from the north colonized the area in the early 1800's, replacing Mbulu and Datoga tribes. In the late 1800's, the region was the contact area between Maasai with a transhumance pastoralist lifestyle towards the east, and agropastoralists in Mara and Sukumaland in the west. In this period (as now), over 1 million wildebeest migrated from the Serengeti plains to the Mara region on a seasonal basis, and the area was renowned for high lion densities. A major catastrophe happened when rinderpest was introduced, likely from cattle brought from India to Ethiopia in 1889. By 1892, 95% of the cattle population in East Africa had died from rinderpest with major consequences for the local tribes in the region, especially the Maasai who declined to abject poverty and starvation. The agropastoralists groups in the west survived better due to their partial dependence on cultivation. This disaster for the people, livestock and wildlife followed a reduction of the human population by cholera in the 1880's. The rinderpest also decimated the wildlife as all ungulates are sensitive to the disease, and buffalo, wildebeest, zebra and giraffe almost disappeared from the center of the park, and were heavily-impacted throughout much of the region. Repeated rinderpest outbreaks in 1917-1918, 1923 and 1938-1941 kept the wildlife populations low, and it would take until 1970, after eradication campaigns in livestock, for the wildlife populations to recover. The sudden drop in grazing pressure in the early 1900's caused a massive tree and bush encroachment, followed by increased extent and intensity of fires, a series of events still visible in the current landscape through a cohort of now over 100 year old *Acacia tortilis* trees. In 1929 the British colonial government established a first hunting reserve of 2,286 km^2 in the southern and eastern part of the area, which became the basis for the later Serengeti National Park. In 1937, sports hunting was stopped in the protected area through the upgrading of its status to National Game Reserve, followed by establishment as a national park in 1951. SNP was brought to the international spotlight in the 1950's by the book and film *Serengeti Shall Not Die,* by Bernhard and Michael Grizmek. To preserve wildlife, the British colonial government evicted the Maasai population from the park in 1959, relocating them to the Ngorongoro Conservation Area (NCA), which was excised from the park to become the first multi-use area in Africa (see next section).

Ngorongoro Conservation Area (NCA)

The Ngorongoro Conservation Area of 8,094 km^2 encompasses the Ngorongoro highlands, the Ngorongoro Crater, the largest part of the short grass plains of the Serengeti-Mara ecosystem, the Salai plains and the Olduvai Gorge. While the crater was shortly farmed by Germans between 1890 and 1914, early conservation measures included the prohibition of hunting in the Ngorongoro Crater from 1928 onwards. The NCA was created in 1959 as a new home for about 10,000 Maasai that were evicted from the separated Serengeti National Park. The area is characterized by a multi-use strategy. At the time of inscription of the NCA, about 20,000 Maasai were living in the area with about 275,000 head of livestock, which was considered the carrying capacity of the area at the time. Since then, the human population has grown to over 50,000 (mostly Maasai) people. The primary management objectives of the area since its establishment are to conserve its natural resources (it hosts the wet season range of the wildebeest migration and the Ngorongoro Crater), protect the interests of the Maasai pastoralists, protect archeological sites (including Olduvai Gorge and the Laetoli footprints) and to promote tourism. The area is characterized by an active participation of resident communities in decision-making processes, including the development of benefit-sharing mechanisms for the ecotourism revenues. Hunting is not allowed in the area. Management decisions are taken by the Ngorongoro Conservation Area Authority (NCAA), an arm of the Tanzanian government in which the local Masaai communities are represented. The NCAA has put restrictions on agricultural farming and on livestock numbers in order to retain the natural beauty, ecotourism benefits and pastoral livelihoods of its inhabitants. Following similar measures in 1974, the 2009 Ngorongoro Wildlife Conservation Act prohibited human settlement and subsistence farming throughout the NCA. Recent developments see a gradual disappearance of the transhumance pastoralism by a sedentary life style of the Maasai people, increasing livestock numbers and a change in preference from cattle to more drought-tolerant small stock, to the point of concern of overgrazing the land and competition with wildlife.

Grumeti Game Reserve (GGR) and **Ikorongo Game Reserve** (IGR)
The Grumeti Game Reserve is situated on the important migration route of the wildebeest while migrating between the western corridor the Serengeti National Park (in Tanzania) and Masai Mara National Reserve (in Kenya). Initially gazetted as Game Controlled Areas, which allowed settlements and farming, both Grumeti (412 km^2) and Ikorongo (603 km^2) were upgraded to Game Reserves in 1994. In 2002, management of the reserves was taken over by foreign investors, after which trophy hunting was reduced and substantial efforts were put into reducing poaching. The management of both Grumeti and Ikorongo is supported by Singita Serengeti Ltd (formerly known as The Grumeti Reserves) in one ecological unit with Ikona Wildlife Management Area. The area is characterized by luxury, very exclusive tourism mostly aimed at non-hunting (photographic) safaris. Singita Serengeti channels a relatively large amount of revenue to neighboring communities to restrict illegal grazing and poaching and reduce human-wildlife conflict, aiming at co-management of natural resources and its benefits.

Ikona Wildlife Management Area (IWMA)
The Ikona Wildlife Management area of 242 km^2 was gazetted in 2006, and is situated between Grumeti Game Reserve, Ikorongo Game Reserve and Serengeti National Park. The Tanzanian Wildlife Act of 1998 sought to address the problem that local communities have often been marginalized from the decision-making process in natural resource management and receive an inequitable share of ecosystem benefits through the establishment of Wildlife Management Areas (WMAs). These WMA's should contribute to the livelihoods of participating communities, build community empowerment and, fundamentally, represent a buffer zone to ensure the long-term conservation and sustainable management of natural resources. IWMA is a key bottleneck in the annual migration of over 1 million wildebeest, that pass through this area twice per year. The village of Robanda and its directly surrounding grazing lands, situated in the southern part of the area, is excluded from the wildlife management area. The area is managed by 5 different villages inside and around it, receiving relatively strong support from Singita Serengeti. Due to the attractiveness of the passing migration, the area hosts a relatively large number of privately operated tourist camps and lodges that share benefits with the local communities. IWMA is currently separated into a relatively well-protected southern part with little livestock impact, and a northern part with relatively strong livestock impact from its adjacent villages. Today, IWMA leads all WMAs in Tanzania in income generation.

Maswa Game Reserve (MGR)
After being established as a protected area in 1962, Maswa Game Reserve (2,200 km^2) was gazetted in 1969. The game reserve status implies that occupation, livestock grazing and cropland are not allowed, and Tanzania Wildlife Authority (TAWA), formerly the Wildlife Division, is the formal management authority. The area has more nutrient poor and rocky soil than the Serengeti National Park as it is mostly outside the influence of the volcanic ash from the Ngorongoro Highlands that shaped the Serengeti plains. The area has very characteristic landforms (the very rugged kopjes landscape in the south) and unique birdlife. Also, it is an important migration route for the Serengeti wildebeest moving between the plains in NCA and the western corridor of SNP. And, the area is used periodically as a calving area by the migratory wildebeest population if the rains are late to arrive in the Serengeti plains. Currently, MGR is separated into different tourism leases that support the management of the game reserve, and is seeing a gradual transition from luxury trophy hunting to luxury photographic tourism.

Makao Wildlife Management Area (MWMA)
Makao Wildlife Management area (780 km^2) is situated south of Maswa GR and west of NCA and was gazetted in 2009 to promote responsible multi-use of the land and tourism benefit sharing. The WMA comprises 7 villages, and its establishment was facilitated by Frankfurt Zoological Society (FZS) through a project co-financed by the European Union. Due to its relative remote location, and close vicinity to Maswa GR, Serengeti NP and NCA it saw relatively late settlement by agropastoralists, leaving high abundance of wildlife. In 2011, the area saw a conflict where people from the region invaded the area based on land claims, who were then evicted from the WMA by the authorities. In addition to its resident wildlife, the area is used periodically as calving area by the migratory wildebeest population if the rains are late to arrive to the Serengeti plains. A private investor co-manages the area together with local communities, that get a 75% share of the ecotourism revenues of hotels and safaris. FZS is still facilitating the WMA with capacity building, advice on natural resource management and monitoring and good governance. As the other WMAs, Makao WMA falls under the responsibility of the Tanzania Wildlife Management Authority (TAWA).

Kijereshi Game Reserve (KGR)
Kijeresihi Game Reserve (66 km²) is situated south of the western corridor of Serengeti National Park close to lake Victoria, and was gazetted in 1994 as a wildlife management area. In 1998 the status was upgraded to Game Reserve. The most important tourist facilities are on the boundary with Serengeti National Park. Although livestock grazing is not allowed due to its status as a game reserve, the area is currently heavily used by livestock from neighboring villages and subject to incidental cropland farming.

Loliondo Game Controlled Area (LGCA)
In 1959, the British colonial administration set aside 4,000 km² of the Loliondo area as a game reserve for hunting of European royalty only. After independence, the status was changed to a game controlled area to allow for trophy hunting, which at that point was not allowed in game reserves. In 1992, then-president Mwinyi allocated the majority of the area for hunting use by the UAE royal family through the Ortello Business Cooperation (OBC), setting up decades of conflict between national-level hunting interests, and village land use rights. The western part of

Loliondo is dominated by the primarily pastoral Maasai, though agriculture is increasing in the area, while eastern Loliondo is dominated by the agro-pastoralist Sonjo people.

2. Human population dynamics

2.1 Data collection

A shapefile of the administrative boundaries (sub-location level) and the population density estimate resulting from the Kenyan population census in 1999 were downloaded from the International Livestock Research Institute (ILRI) GIS Web Service (*54*). Data from the Kenyan population census in 2009 was provided by the Kenya National Bureau of Statistics (*55*) and data were manually linked to the shapefile of 1999. Data from the 2002 population and housing census in Tanzania were provided by the Tanzania National Bureau of Statistics (TNBS) and put together into a ward-level spatial map by ILRI. A ward level shapefile for the 2012 population and housing census has been provided by the TNBS and was manually linked to the actual census data on population numbers also provided by the TNBS (*56*).

All data were aggregated to the ward level (Tanzania) and sub-location level (Kenya) as this was the highest administrative resolution available for all years in both countries. We selected only those wards/sub-locations that are located within 60 km from the parks boundaries and urban wards (> 1000 people per square kilometer) were excluded from the analyses. We divided the surroundings of the Core Protected Areas (CPA) into 6 regions based on spatial attributes (Fig. S2). The Kenyan side is separated into two regions based on the escarpment where Migori represents the generally agro-pastoralist region in the North-West and Narok the Maasai pastoralists in the North-East. The same division between agro-pastoralists (blue regions) in the West and Maasai pastoralists (green regions) is found in Tanzania where we further divided the Western side into the Mara region North of the Western Corridor and Simiyu region bordering the South-West of Serengeti National Park and Maswa Game Reserve. The Eastern side is further divided into Ngrorongoro which represents the Ngorongoro Conservation Area where human and livestock population are regulated; and Loliondo, which represents Loliondo Game Controlled area, a hunting area that is inhabited by Maasai pastoralists.

2.2 Spatial human population dynamics

Human population density is generally higher on the western side of the ecosystem and increases towards Lake Victoria (Fig. S3). Administrative units are also smaller and most of the area is used for agriculture in the West (see Supplementary Text 3), whereas in the East most of the area is communal grazing land shared by pastoralists, even across the international country borders. This makes the investigation of spatial dynamics on the Eastern side more difficult as the distributions of both livestock and people are much more dynamic, owing to the (formerly semi-nomadic) pastoralist lifestyle of the Maasai.

2.3 Spatio-temporal human population dynamics

The total human population within the first 60 km from the CPA border increased from about 4.6 million in 1999/2002 to almost 5.8 million people in 2009/2012. This is about 2.4% more people per year. However, there are large spatial differences in the rate of human population increase (Fig. S4), with the largest rate being that for the Mara region (8.1% per year) in Tanzania.

We then limited our analyses to only wards/locations proximate to the ecosystem (within 15 km) and found even higher rates of increase in population density, except for Loliondo and Ngorongoro (Fig. S5 and Fig. S6). The increase in human population density is generally much smaller along the eastern border of the CPA, especially in Loliondo and Ngorongoro, where restrictions on immigration keeps population density relatively low. People are most likely immigrating to the western boundary, however, to access remaining unconverted arable land, which is often located close to the CPA (*15*).

3. Agricultural expansion

3.1 Land cover classification

We mapped land cover in the Greater Serengeti-Mara ecosystem (GSME) in three different time periods: 1984, 2003 and 2018. We used support vector machine (SVM) classifiers implemented in the software ImageSVM (*57*) to classify multi-temporal stacks of 30-m resolution Landsat images for the four footprints covering the GSME (path/row: 169/061, 169/062, 170/061, 170/062). We used images from the Landsat 5 TM, 7 ETM+ (slc-on) and 8 satellites (www.glovis.usgs.gov) to create multi-temporal stacks of at least five images for each footprint and time period. To improve discrimination between the land cover classes, we also included an NDVI image calculated from the red and near infrared bands of one of the Landsat images, and the first-order variance (a measure of image texture) derived from the NDVI band, in the classification stack. We digitized training polygons using high resolution imagery in Google Earth (*58*) for the following vegetation classes: agriculture, savanna (including both grassland and woodland of varying density) and forest (here restricted only to evergreen riverine and highland forests). We also created training areas for clouds and water. Five hundred points were randomly sampled from the training polygons for each class and used to parameterize the SVM classifiers. Classifications were performed repeatedly with additional training data included where the products performed poorly. The combination of SVM classifiers implemented on multi-temporal image stacks representing different phenological states, with NDVI and texture bands, has been shown to be effective in discriminating between spectrally-similar agriculture and savanna classes (*15*). Each footprint was classified independently to control for differences in phenology and atmospheric conditions, and the resultant classifications were then mosaicked together. An image differencing approach implemented on the mosaics in ArcMap 10.5 (ESRI) (*59*) was used to assess areas in the ecosystem that converted from savanna and forest to agriculture between each time step. The resultant change maps for the periods between 1984 and 2003, 2003 and 2018, and 1984 and 2018 included the following vegetation classes: stable agriculture, agricultural conversion (natural habitat that had converted to agriculture between the two classification dates), stable forest and stable savanna. Images covered by clouds in any of the time periods were excluded from analysis in all periods.

3.2 Results

Figure S7 shows that the most rapid conversion from natural habitats to agriculture occurred in agro-pastoral western Serengeti between 1984 and 2003, and drives the overall increase of agriculture seen in this period of 9.2% of the total land area (Table S2 and Table S3 for a breakdown by region). These changes appear to have been driven by lack of arable land in the higher human population density areas near Lake Victoria, many of which were already converted to agriculture prior to 1984. The only areas left in which to establish new farms were located closer to the western boundary of the protected area where there were lower human population densities and less existing agriculture. For a more detailed analysis of the interaction of human demographic factors and agricultural expansion in the GSME, see (*15*). By 2003, what little natural habitat was left in western Serengeti was adjacent to the core protected area boundaries, and the change analysis between 2003 and 2018 shows further conversion of these remaining areas. This is particularly notable given the high cattle densities in the same area. Very few patches of unconverted land remain between GSME and Lake Victoria, which has no doubt driven the intense pressure to graze inside the protected area, which constitutes the last reservoir of standing grass biomass in that part of the ecosystem.

The most extensive conversion to new agriculture between 2003 and 2018 occurred in Narok, Kenya, near the wheat farms in the north-eastern group ranch areas, which accounts for much of the 10.2% increase in percent cover of agriculture in this period. An additional focus of conversion was seen south of Maswa GR and in the productive highland agricultural areas east of Ngorongoro, extending into the Lake Eyasi basin.

Land cover change in the pastoralist-dominated eastern parts of the ecosystem showed distinctly different patterns, influenced by livelihood, environmental and national differences. In Loliondo, east of Serengeti NP, agricultural conversion was far less extensive than in either western Serengeti or north of the Mara, was focused near settlements, and showed no clear relationships with the PA boundaries. This area constitutes a much softer edge between the core protected area and more human-dominated habitats. However, although conversion to agriculture in Loliondo has been less rapid, the area is undergoing other considerable changes, driven by degradation in the grazing areas, which manifests in the satellite imagery as increasing bare ground, and complicated the discrimination between agricultural and natural habitats in the classifications. These changes are likely driven by the interactions between increasing drought signatures, compression of livestock into smaller areas partially due to loss of grazing land through agricultural conversion, and changes in grazing management driven by disputes with competing land uses. Protection of remaining grazing areas from loss to outside agricultural interests, in concert with community participation in land use and grazing management plans could be critical in helping keep these areas open for both livestock keeping and wildlife conservation as viable livelihood strategies.

Taken together, analysis of land-cover change around the GSME from 1984 to 2018 shows considerable loss of natural areas, which could otherwise be used for livestock keeping and wildlife conservation and tourism. During this time, agriculture increased from 37.0% of the classified land area, to 54.0%, a corresponding loss of natural habitats around the GSME to agriculture of 17.0% (Table S2). These changes started out in the higher rainfall, more agriculturally-productive areas, but as those areas have become completely converted, have continued into sub-optimal farming areas traditionally used for livestock keeping. Nevertheless, livestock and human populations have increased across the ecosystem (see Supplementary Text 2 & 4), which, coupled with loss of land to agriculture, is driving the compression effects that are altering habitats even inside the core protected area. Even an ecosystem as large and iconic as

Serengeti-Mara is not immune from the processes that take place around its borders, and is in urgent need of conservation interventions to minimize human-induced ecological changes.

4. Livestock population dynamics

4.1 Data collection

Changes in livestock population abundance were investigated over a 9-year period for 5 of the 6 regions (see Supplementary Text 2, Fig. S2) that, to a large extent, represent administrative boundaries of districts and regions in Tanzania and Kenya that border the Core Protected Areas (CPA). The number of cattle and shoats (sum of sheep and goats) for Tanzania were extracted at the district level from regional reports for the 2002/2003 Agricultural Sample Survey (*60*) and the 2012 Population and Housing Census (*56*). Only districts bordering the CPA were included and density per region represents the weighed average for each districts. Livestock numbers for Narok, Kenya, were extracted from (*61*) for 2002 and 2011. We were not able to acquire accurate livestock data for the Migori region.

4.2 Livestock population dynamics

The number of cattle increased in all but one (Narok) region (Fig S8 top) and the highest cattle densities were found on the Western side of the CPA (Fig. S8 blue bars). The most significant increase was found in the Tanzanian Mara, bordering Lake Victoria, that receives the highest rainfall of the five regions. The driest regions (Narok and Ngorongoro) show only a small increase or decrease in cattle density.

Shoat density increased in all regions (Fig. S8 bottom) and faster than cattle did in all but one region (Tanzanian Mara). There was no evident difference in shoat density between the pastoralist (green bars) and the agro-pastoralist (blue bars) regions.

5. Grazing intensity

5.1 Data collection

To study the potential consequences of squeezing large herbivores into the Core Protected Areas (CPA), we used a combination of field experiments and remote-sensing techniques. We measured changes in grazing intensity through time using large herbivore exclosures installed in 1999 at 8 sites (3 exclosure per site) distributed across the Serengeti National Park (*62*). Specifically, grass biomass was measured inside and outside the exclosures at the end of the growing season (early June) each year since 2001. Grazing intensity is then calculated as GI = 1-(biomass outside)/(biomass inside). Normalized Difference Vegetation Index (NDVI) was then used as a measure of actual standing biomass, provided by Moderate-resolution Imaging Spectroradiometer (MODIS) with an approximate 250 x 250 m pixel resolution and 16-day interval between 2000 and 2016 (MOD13Q1)(*63*).

5.2 Data analyses

We used two complementary methods to determine changes in grazing intensity in GSME over time.

1. We analyzed temporal changes in the coefficient of variation and mean grazing intensity using large herbivore exclosures.
2. Heavily grazed areas do not accumulate biomass and therefore show a relatively low NDVI signal throughout the year. We therefore determined the maximum NDVI between September and May for years between 2000-2016 for the whole region using MODIS NDVI product to identify the heavily grazed areas. Subsequently, we calculated trends in maximum NDVI throughout the 17 years spanning 2000-2016 using linear regression models for each pixel to identify areas showing changes in maximum NDVI, areas that have become heavily grazed (by livestock) or have been released from high grazing pressure. To correct for areas that were burned during the growing season, we used MODIS MCD64A1 Burned Area Product that provides monthly indication of burned and non-burned pixels (ca. 500x500m)(*64*).

5.3 Results

5.3.1 Exclosure data

Grazing intensity measured at eight long-term grazing exclosure (LTGE) sites with ungrazed (fenced) and control (unfenced) plots across the Serengeti National Park has increased by 16% between 2001-2016 (ca. 1.1% per year (Fig. S28)), in a period without a clear trend in annual rainfall (*36*).

5.3.2 Maximum NDVI

Maximum NDVI was highest in the upland forest around the Ngorongoro Crater, in the Loliondo Game Controlled Area as well as in the Mara Wetlands (Fig. S9). Overall, maximum NDVI is higher inside the protected areas than outside. Within the protected areas, there is a general increase in max NDVI with rainfall, as expected, with the lowest maximum NDVI found on the Serengeti Plains and along the Mara river, probably reflecting extensive grazing by hippos (Hippopotamus amphibious)(*65*), other wildlife and livestock.

Changes in maximum NDVI were most pronounced outside the CPA on the eastern side, from Narok to Ngorongoro CA (Fig. S9, S10). On average, max NDVI decreased inside the CPA by 0.5% per year (2001-2016). This decrease was most evident on the border of the Maswa GR, the border between the Serengeti NP and the Ngorongoro CA and southern Loliondo GCA. These areas match those identified as having high densities of livestock paths and bomas (Fig. S10, see Supplementary Text 9)

Maximum NDVI decreased in each of the three areas (Fig. S11) and this decrease was stronger on the eastern (PASRU) than on the western side (UPA) of the CPA. On average, the maximum NDVI decreased by 0.1-0.2 on the village lands compared to the CPA and a clear border effect was evident on the eastern side up to about 10 km from the protected area boundary. In the West, this border effect was much weaker in areas with medium border controls (UPA medium), but increased in recent years. Areas with strong border controls in the West did not show a border effect, but a sharp decrease in maximum NDVI at the border instead (UPA strong).

6. Changes in area burned

6.1 Data collection

To investigate possible changes in the functioning of the ecosystems associated with human and livestock population growth we analyzed trends in the burned area over time. Livestock incursions into the protected areas should decrease grass cover, potentially reducing fire outbreaks. We used the MODIS MCD64A1 Burned Area Product Collection 6 that provides monthly indication of burned on non-burned pixel (ca. 500x500m)(*64*) to study changes over time.

6.2 Analyses

We aggregated monthly data to calendar years to produce an annual raster layer where pixels indicate either burned or not burned status. For each pixel we determined the distance to the closest protected area boundary using the proximity toolset in ArcGis Desktop 10.5 (negative distances used for areas inside the protected areas)(*59*). We partitioned our dataset into subsets representing three different management types (see Supplementary Text 1, Fig. S1):

1. PASRU medium represents the medium controlled border between the Core Protected Areas (CPA) and the Protected Areas with Sustainable Resource Use (PASRU). PASRU are Maasai inhabited and grazed village lands, including the Ngorongoro Conservation Area and Loliondo Game Controlled Area, Makao Wildlife Management Area (WMA) and Mara Wildlife Conservancies (Ngorongoro, Loliondo and Narok in Supplementary Text 2, Fig. S2).
2. UPA strong represents the border between CPA and unprotected areas (UPA) with strong control against illegal activities, including the Grumeti Game Reserve (GR), Ikona WMA and Ikorongo GR.
3. UPA medium represents borders between CPA with medium controls on illegal activities, including Serengeti National Park, Maswa GR and Masai Mara National Reserve. The western areas are inhabited predominantly by agro-pastoralists.

For each of the three borders we determined whether nearby pixels had burned during each of three time periods, 2001-2005, 2006-2010 and 2011-2016, and calculated the ratio of burned to non-burned pixels for each period and distance to the boundary of the CPA segmented into 2 km intervals. These analyses provide insight into the spatio-temporal patterns of burned areas.

6.3 Results

The total burned area decreased over time (Fig. S12). Areas in Narok, Loliondo, Ngorongoro and Kenyan Mara that burned during 2000-2005 (blue areas) did not burn in recent years. The gradient from green through yellow to red represents a contraction in the area burned and is found on all sides of the ecosystem. Only the core of the protected area, especially the wetter parts of the ecosystem, still burned in recent years. It is striking to notice the ca. 5 km orange strip on the border of Maswa Game Reserve that burned until 2008 and never since. The other area where clear effects are evident within the protected area boundaries is East Serengeti, bordering Loliondo, that burned until 2007. These areas show high overlap with the livestock paths and bomas (Supplementary Text 9, Fig. S13) that were found inside the protected areas. The contraction in the spatial spread of fire in the Masai Mara National Reserve is most probably also a result of illegal grazing activities (*30*, *33*).

There are differences in burned area dynamics between the three types of area. In the East (PASRU medium), areas outside the park used to burn at the beginning of the century, but this has reduced almost to zero. Inside the CPA, the burned area decreases steadily with increasing distance away from the border (Fig. S14). This could partly be explained by a slight increase in rainfall. The reduction in burned area is similar over a 20 km stretch from the border of the protected area, suggesting that the Maasai pastoralists are moving deeper into the park. This is confirmed by the presence of bomas up to 10 km inside the protected area in some regions (Fig. S13) and observations of livestock grazing deep inside the CPA (Supplementary Text 7). The Western side shows a different pattern, with the most pronounced effects found closer to the border. In areas with medium border control (UPA medium), fire suppression was found until about 4 km inside the protected areas between 2000 and 2005 but this had increased up to almost 10 km by 2010-2016. Beyond 10 km, the overall area burned decreased by about 20% but there was no longer any noticeable effect of distance to the border. This suggests that livestock have moved farther and farther into the protected areas in the last 15 years and corresponds well with the livestock paths (Fig. S13). Livestock create paths through their daily movements in and out of the protected areas, and the distance they can walk per day limits the extent of their border effects. This pattern starkly contrasts with those for the Eastern side (PASRU medium), where livestock are kept inside the CPA overnight. In areas with strong border controls (UPA strong), these border effects are much smaller and where present, occur only within the first 1 km from the border. Nevertheless, a reduction in overall mean area burned of about 10-20% during the last 10 years is also evident here.

7. Spatial compression of wildlife around the border of Maasai Mara National Reserve

7.1 Animal densities

A total of 62 aerial survey monitoring data for the Maasai Mara region of the Serengeti-Mara ecosystem were analyzed. The data covered the period 1977 to 2016. The surveys are conducted using systematic reconnaissance flights (see Fig. S15 for map of survey area) and the same sampling protocol has been used since counting began in 1977. The same fixed aerial transects and sampling units have also been used since counting started in 1977. The data consisted of the estimated number of animals of each species in each 5 x 5 km2 sampling unit. Only the 14 most common wildlife and three livestock species were considered. The number of animals per sampling unit were averaged over all surveys conducted in each of four decades comprising the 1970s, 1980s, 1990s and 2000s. For the migratory wildebeest and zebra, the decadal averages were computed separately for the wet and dry seasons. The distance from the center of each sampling unit to the Maasai Mara National Reserve boundary from outside (positive distance) and inside (negative distance) was computed and expressed in kilometers. Total biomass for wildlife and livestock were calculated for each decade using unit weights obtained from (*66*).

For each species, we modeled the count per sampling unit as a function of decade, distance, decade x distance and decade x distance x distance. Decade was treated as a fixed factor with four levels (1970s, 1980s, 1990s and 2000s) whereas distance as a continuous covariate. The model was fitted to the count data separately for each species. The counts were assumed to follow a negative binomial distribution. Because the count data often consisted of very many zeros we used the zero-inflated negative binomial regression model with a logistic link function (ZINB). Both the count (model) and zero-inflation (zeromodel) parts of the zero-inflated negative binomial regression model had the same relationship between the response and distance to the reserve boundary. The fixed effects required in the model for each species and decade were selected automatically using forward variable selection and the Akaike Information

Criterion (AIC) to decide whether a parameter should be retained in each of the two parts of the ZINB model. Parameters of the count and zero-inflation parts of the ZINB model were estimated and tested for significance using the t-test. For each species, the estimated sample counts and the corresponding predicted counts for each sampling unit as a function of distance from the Maasai Mara National Reserve boundary are summarized for each decade in Fig. S16. All the parameter estimates for the ZINB model for each species are reported in Table S4.

We also tested linear hypotheses for subsets of the selected parameters for the same species for different decades to further establish if the selected functional relationships were really different between the different decades. We illustrate this test using the example of buffalo counts for 1970s and 1980s as reported in Table S6.

7.2 Human settlements

The Directorate of Resource Surveys and Remote Sensing of Kenya (DRSRS) has been conducting aerial monitoring surveys of human settlements since 1977 as part of the environmental covariates affecting wildlife and livestock habitat conditions. Settlements are thus counted at the same time and in the same 5 x 5 km sampling units as wildlife and livestock during aerial surveys. The DRSRS conducted 62 aerial surveys in the Maasai Mara region of the Serengeti-Mara ecosystem from 1977 to 2016.

During the DRSRS aerial surveys, two rear seat observers per aircraft record the type and number of human settlements in each 5 x 5 km sampling unit and survey. Houses, sheds and storages are counted individually, but a cluster of buildings used for a specific purpose, such as a school are recorded as a single unit. A collection of buildings constitute a settlement. A total of nine different settlement types were considered for this analysis.

1. Permanent school, town, church, factory, cattle dip, etc.
2. Permanent mabati (iron roofed) house.
3. Permanent (Maasai) Manyatta.
4. Temporary (Maasai) Manyatta.
5. Permanent thatched house.
6. Permanent mabati shed
7. Temporary grass thatched shed.
8. Permanent grain storage.
9. Temporary boma.

We summed up all the nine types of settlements counted in each 5 x 5 km sampling unit in each survey and divided the total sample count by the sampling fraction for the survey (i.e. the percentage of the target area sampled in the survey) to convert the total sample counts to expected counts. The expected counts were then averaged across all 5 x 5 km sampling units falling within each 5 km distance band from the Maasai Mara National Reserve (MMNR) boundary for each of the four decades (1970s, 1980s, 1990s and 2000s).

7.3 Results

7.3.1 Example ZINB models for buffalo distribution for 1970s and 1980s.

This example shows that the functional forms and parameter estimates for the ZINB models for 1970s and 1980s for buffalo are different.

Part 1. Zero-inflated part of Zero-inflated negative binomial (ZINB) model for 1970s:
P0_1970s = Probability of zero count=**1** / (**1** + exp(-(-1.257221+0.081446 × Decade_1970s x Distance)));

Part 2. Count part of ZINB model for 1970s:
Expected_count_1970s= exp(4.751036+0.886901 × Decade_1970s-0.041058 × Decade_1970s x Distance);
Predicted buffalo count for 1970s=(**1**-P0_1970s) × Expected_count_1970s;

Part 1. Zero-inflated part of ZINB model for 1980s:
P0_1980s = Probability of zero count=**1** / (**1** + exp(-(-1.257221 - 1.770565 × Decade_1980s + 0.095526 × Decade_1980s x Distance)));

Part 2. Count part of ZINB model for 1980s:
Expected_count_1980s= exp(4.751036 - 0.092612 × Decade_1980s x Distance);

Predicted buffalo count for 1980s=(**1**-P0_1980s) × Expected_count_1980s;

Estimated parameter values for the same effect, e.g., Decade_1970s × Distance vs. Decade_1980s × Distance can be contrasted and shown to be significantly different using Wald, Lagrange multiplier, or likelihood ratio tests as shown for buffalo in Table S6 (Test0 and Test 1). Similarly, the same tests can be used to compare the entire ZINB regression models for two or all the four decades as illustrated for buffalo for the 1970s and the 1980s in Table S6 (Test2). In Table S6, parameter estimates for effects with the prefix Inf refer to effects in the zero-inflated part of the ZINB model whereas those without this prefix refer to effects in the count part of the ZINB model.
The shapes of the distribution of the predicted count for buffalo for the 1970s, 1980s, 1990s and 2000s is shown in Fig S19. This figure clearly demonstrates increasing compression of all the wildlife species into the MMNR from the 1970s to the 2000s.

7.3.2 Changes in wildlife and livestock densities in Narok

The densities of all the wildlife species decreased in contrast to the densities of cattle, sheep and goats (Fig. S16). Furthermore, the densities of most species decreased with distance to the border of the MMNR and this effect became stronger from the 1970s to the 2000s. The main exception is the Grant’s gazelle (*Gazella granti*) that apparently prefer village lands to the Core Protected Areas (CPA). Also, the densities of both wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga)* in the wet season were higher outside the MMNR. This results from the concentration of the wildebeest and zebra involved in the smaller northern migration in their wet season range in the Loita Plains (Supplementary Text 1) situated in the unprotected area to the north east of the MMNR. In contrast, the wildebeest and zebra involved in the larger southern migration only use the MMNR in the dry season (Supplementary Text 1). This is evident from the much higher wildebeest and zebra densities in the MMNR during the dry season. Note that the densities of the Grant’s gazelle, wildebeest and zebra decreased outside the MMNR in the wet season from the 1970s to the 2000s. However, the densities of livestock increased consistently and strikingly inside the MMNR over the last 40 years (Fig. S17).

8. Changes in wildebeest utilization

8.1 Methods

GPS collars (Followit, formerly 'Televilt,' GSM or Iridium transmitters with GPS location) were deployed on 59 migratory wildebeest between February 1999 and June 2017. Animals were immobilized by veterinarians from the Tanzania Wildlife Research Institute (TAWIRI) or the Tanzania National Parks (TANAPA) using an injectable dart containing 4-6 mg of etorphine and 80–100 mg of azaperone, fired from a veterinary rifle from a stationary vehicle near the animal. Veterinarians followed the handling and care protocols established by TAWIRI. All collared animals were adult females (>2 years old) in healthy condition occurring in herds. Collars were collected after ~2.0-2.5 years of deployment by triggering remotely-released drop-off mechanisms, or after the animal died.

The goal of the analysis was to identify changes in wildebeest utilization intensity over time and to determine whether these changes were related to the distance to the boundary of protected areas in Serengeti-Mara. We divided the GPS data into two equal time periods (1999-2007 and 2008-2017) and used Brownian bridge movement models (BBMM) to generate utilization distributions (UD's) for each individual (*67*, *68*). Briefly, BBMMs assume animal movement trajectories are connected by Brownian motion between sequential, time-specific GPS locations. Higher velocity movements result in more narrow distribution paths between points. Individual Brownian bridges were rasterized at a resolution of 1 km^2 (median daily displacement of female wildebeest was 4.5 km (*69*). Following estimation of individual UD's, we excluded cells containing the lower 5% of utilization values to remove areas with low probability of use (*68*). Because months were unevenly represented in the dataset and because the goal was to estimate changes in utilization across the entire migration footprint, we resampled the data so that each month was represented equally. We did this in two steps:
(1) dividing individual UD's into monthly Voronoi fractures, based on the individuals' GPS trajectory
(2) inversely weighting each fracture by the minimum monthly number of GPS locations for that time period, so that months with many GPS locations (across all individuals) had less weight than months with few GPS points. This procedure corrected for sample size differences across months.

Next, we combined (i.e. summed) all individual UD's within each of the two time periods to generate population-level UD's for each period and rescaled these surfaces so that total utilization summed to 1.0. Changes in utilization between time periods were calculated by taking the difference between the two rescaled UD surfaces. For this calculation, we only included cells in which wildebeest had occurred in both periods (i.e. utilization values > 0; n=63,730 cells). Nonetheless, some were used by a small number of individuals so the degree of certainty in the estimated change surface differed by area. We assessed certainty in the utilization change surface by running a boot-strap procedure that recalculated the surface 500 times. Each run used a randomly selected set of individuals from each time period, with replacement. Cells that had significantly increased or decreased across time periods were those where increases/decreases occurred in >95% of runs.

To understand how distances to the protected area boundaries related to the change in population-level utilization over the two time periods, we created buffers inside and outside the protected area boundary at 2km intervals for up to 8km outside and 20km inside. For each buffer interval, we calculated the total change in population-level utilization between the two periods, and summed all cells for which 50% of the cell area fell within the interval. We differentiated boundaries by three management categories (see S1): 1) Protected Area with Sustainable Resource Use (PASRU) that controlled against illegal activities such as illegal hunting or livestock grazing, 2) unprotected areas (UPA) with strong border control, and 3) UPA with medium border control (UPA medium). We differentiated the All analyses were performed in R using packages 'BBMM', 'adehabitatHR' and 'dismo'.

If livestock were displacing wildebeest from grazing areas, we expected this displacement to occur most intensively in areas with highest quality and/or quantity of forage. To test this hypothesis, we examined the relationship between changes in wildebeest utilization and two abiotic factors that largely determine forage quality and quantity: rainfall and soil nutrients (*69*). To characterize rainfall, we obtained data from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) rainfall product (*70*). To characterize soil nutrient quality, we relied on a soil nutrient product created by ISRIC at a 1km scale that represents the sum of exchangeable bases at 0-5cm of soil depth (*71*). However, rainfall was negatively correlated with soil nutrient content ($R^2_{adj} = 0.89$) so we focused our analysis on the relationship between rainfall and change in wildebeest utilization only. We regressed changes in wildebeest utilization against rainfall using a generalized additive model, and included spatial smoothing terms of geographic position to account for spatial dependence of residuals (*72*).

8.2. Results

Movements of GPS radio-collared animals suggest that wildebeest have shifted their spatial distribution markedly over the previous two decades (Fig. S26A-C). The intensity of use by wildebeest has generally increased in Western portions of the ecosystem and declined strongly in Northern portions of the ecosystem, particularly in the MMNR. Furthermore, there has been a pronounced decline in wildebeest utilization 0-10 km inside the boundary of the ecosystem, particularly in uncontrolled areas along the eastern and western boundaries (Fig. 4B). In controlled areas of the west (e.g. Grumeti, Maswa and Ikorongo Game Reserves), in contrast, wildebeest utilization has increased over time. Wildebeest utilization increased in wetter areas of the ecosystem (RAIN = $4.25e{-}08 \pm 9.05e{-}09$, $p<0.001$), though the deviance explained was only 2%. Given that changes in use were strongly clustered in space (Fig. S26C), we interpret these results as evidence that area-specific factors such as livestock management, fire control and human encroachment may be driving changes in wildebeest use over these time periods.

9. Bomas and livestock paths

9.1 Bomas and livestock paths through space and time

Reliable spatio-temporal data on livestock distribution across the entire Greater Serengeti-Mara Ecosystem were not available for our study period. We therefore mapped livestock paths (Fig. S27) and bomas (Fig. S20-S21) from satellite imagery to identify areas heavily used by livestock. Bomas are temporary structures of traditional Maasai homesteads and thorny scrub enclosures to coral livestock overnight and protect them from predators. As the 'scar' left by disused bomas can persist for decades to centuries (*73*), we included only active bomas in our dataset. We defined an active boma using two diagnostic features: 1) there must be a clear contrast between the colour of the substrate within the boma and the substrate outside the boma, and 2) the thorn fence surrounding the boma must be unbroken. Bomas often contain internal partitions to separate cattle, goats and sheep, to separate different family members' herds, or to separate livestock from people (Fig. S21). Where this occurred, we counted these as part of a single structure rather than as individual bomas. Livestock paths arise through the daily livestock movements into and out of the protected areas (Fig. S27). The livestock paths can be identified from satellite imagery, if livestock have used them for extended periods, so that vegetation cover disappears and compact bare soil emerges.

We analyzed boma and livestock distributions in two ways.
1. We mapped bomas and livestock paths using the most recent imagery to identify areas with the highest probability of illegal grazing event which we then linked to changes in fire frequency (see Supplementary Text 6) and grazing intensity (see Supplementary Text 5).
2. We investigated changes in boma density through time and analyzed this in relation to the boundaries of the Core Protected Areas (CPA, Supplementary Text 1).

9.2 Mapping livestock paths and bomas

9.2.1 Methods

We mapped livestock paths and bomas with Google Earth Pro (*74*) using the most recent imagery up till 28 August 2017. Bomas were identified inside the CPA and up to 10 km outside the CPA boundaries. Livestock paths were identified using the same imagery by scanning the entire outside border of the CPA, locating entry points and mapping the paths as far into the CPA as possible.

9.2.2 Results

Livestock paths were found mostly in the Simiyu region along the border of Maswa Game Reserve and South side of the Western Corridor of Serengeti National Park (Fig. S22, S23), confirming that people enter the protected areas here with their livestock likely on a daily basis (*75*). However, also in the North West of Serengeti National Park just North of Ikorongo Game Reserve high densities of livestock paths were found. Lastly, the Eastern side of Maasai Mara National Reserve also showed a high prevalence of livestock paths. Paths were visible up to 5 km inside the protected areas and livestock probably moved even further. Notably, hardly any livestock paths were found in Grumeti Game Reserve, Ikorongo Game Reserve and the Eastern side of the Serengeti National Park.

Bomas were found all around the Greater Serengeti-Mara Ecosystem, but the only area where they were found inside the protected areas repeatedly was along the Eastern boundary of Serengeti National Park along the border of Loliondo Game Controlled Area up to 10 km inside the protected area (Fig. S23).

9.3 Temporal changes in boma densities

9.3.1 Data collection

Using Google Earth Pro (*74*) we identified areas where two or more satellite images from different years overlapped. Within these areas of overlap we counted the number of bomas in each year, enabling us to calculate the change in boma density over time. Whilst it is illegal to graze livestock within national parks and game reserves in Kenya and Tanzania livestock encroachment into CPA is a frequent problem. Therefore, in addition to identifying areas of overlap within all the protected areas of the Serengeti-Mara, we included a 5 km buffer zone around the CPA. No buffer zone was included for Protected Areas with Sustainable Resource Use (PASRU) because livestock and bomas are permitted within these protected areas.

9.3.2 Data analysis

Using a generalized Poisson regression model (GLM) with a log link function we calculated the rate of change in boma density for each area of overlap and predicted the expected boma density for each area and year between 2001 and 2016. We then interpolated these values to create continuous rasters covering our entire study area. We assumed a priori that the rate of change in boma density would be affected by management and therefore used ordinary kriging, with management as an auxiliary variable, to interpolate within protected areas, and universal kriging to interpolate within the 5 km buffer zone (*76*). We combined the rasters of the buffer zone and the core protected area to create a single raster of the rate of change in boma density and 16 rasters of predicted boma density between 2001 and 2016. For some areas limited data led our model to predict unrealistically high boma densities, therefore we capped predicted boma densities at 56.4 bomas/km2, which was the maximum boma density actually observed.

9.3.3 Results

We identified a total of 55,940 bomas spread across 27,145 km2 (74.7% of our study area) between 2001 and 2017. Much of SNP, Maswa GR, Grumeti GR and the western Maasai Mara National Reserve contained no bomas at any point during our study period. Boma density was highest in Loliondo GCA, NCA, in the buffer zone, and in Makao WMA at the start of our study (Fig. S24). Boma densities increased outside the CPA, especially at the PASRU and UPA strong boundaries. There is an overall decrease in boma density inside CPA but this is likely driven by the establishment of Makao WMA and the disappearance of bomas from the Eastern Mara, as in Eastern SNP the boma densities inside the CPA have increased (Fig. S25).

10. Temporal trends in rainfall in the Greater Serengeti-Mara Ecosystem

10.1 Methods

To understand whether the changes in grazing intensity, maximum NDVI and burned area could results from rainfall dynamics, we analyzed spatiotemporal rainfall data from the Climate Hazard Group InfraRed Precipitation with Station data (CHIRPS)(*70*). Annual (July-June) rainfall estimates were regressed against time in years (2001-2016) on a pixel bases with a resolution of 5x5 km using linear models (LM).

10.2 Results

Changes in annual rainfall were only significant ($P < 0.05$) for a small area of central parts of the Serengeti National Park where rainfall increase between 10-20mm per year, equivalent to 150-300mm over the 15 year time span (Fig. S30). Although the trends for the rest of the ecosystem were not significant, most of the Greater Serengeti-Mara Ecosystem has experienced either no change in rainfall, or a slight increase (between 0-10 mm per year) (Fig. S30 and S31), with the exception of the NCA highlands where rainfall decreased (not significant). These trends can not explain our results as increasing rainfall would be expected to increase area burned, maximum NDVI, while decreasing grazing intensities.

11. Population trends in wildebeest numbers

11.1 Methods

The abundance of wildebeest in the Serengeti is estimated by calculating the density of animals in non-overlapping photos taken vertically from an aircraft flying parallel transects and extrapolated to the entire census area. The Serengeti wildebeest census has been using comparable techniques since 1957 with estimates occurring every 2 to 5 years.

The census is completed within two days and the timing coincides with the wet season distribution of migratory wildebeest on the short grass plains (post-calving, usually in April). Animals concentrate on the fertile high-quality grazing on these treeless short grass plains, giving unimpeded observations from the air. A series of reconnaissance flights establishes the extent of the herds and the inter-individual spacing. Conditions are ideal when animals are randomly spaced (i.e. not in lines or forming grazing fronts) and the herds have a clearly defined extent. The census is conducted when the population is as close as possible to ideal conditions.

Pre-determined east-west transects are flown at a 2.5km spacing and at a ground speed of approximately 150km/hour. The census area is determined by the start and end points for each transect and the most northern and southern transect that contain wildebeest resulting in a polygon. The beginning of a transect is marked as the first point where wildebeest are encountered and ends when the last wildebeest is seen, at which point the aircraft breaks the transect and aligns onto the next one. A GPS tracklog of the aircraft flight path with waypoints mark the beginning and end of each transect.

Non-overlapping vertical photos are taken on a 10-second timer from a porthole in the fuselage of the aircraft using a 50mm lens mounted on an SLR camera. The altitude of the aircraft is recorded every 30 seconds using a calibrated radar altimeter (altitude of the aircraft varies between 800 to 1100 feet above ground). The area on the ground for each picture is calculated using the lens angle (based on the optical dimensions and sensor size of the camera) and the aircraft's altitude above ground. The number of adult wildebeest are counted in each picture (traditionally by hand, but recently by image recognition algorithms with a subset of photos verified by expert counters) to give a density of animals (wildebeest/km^2) for each photo.

11.2 Analysis

The abundance of wildebeest is estimated using the Jolly 2 technique (*77*).Although new approaches have been developed that account for spatial and temporal autocorrelation, Jolly 2 is used to compare across all years to ensure variation is not attributed to a change in statistical approaches. The Jolly 2 technique uses the calculated mean density of wildebeest (wildebeest/km^2) for each transect separately (.i.e the average density of all photos in the transect). The mean density of wildebeest per transects are used to estimate the abundance and calculate the error for the entire census area (note, in the Jolly 2 method n = the number of transects, not the number of photos).

11.3 Results

Following the eradication of the rinderpest virus from the livestock population in the areas adjacent to the Serengeti in 1958, the wildebeest population recovered rapidly to a pre-rinderpest abundance (Fig. S29, Table S8). The population exceeded a million animals by 1977 having started from about 190,000 in 1957. Since the 1980's onward, the population has oscillated around 1.3 million wildebeest with the exception of a severe drought in 1993 that reduced the population by 300,000 animals in the following year. Analysis by Mduma (*34*) suggests that the overall abundance of wildebeest is regulated by the availability of food in the dry season. Furthermore, analysis of long-term data suggests the instantaneous recruitment rate is negative when the population exceeds 1.3 million (*78*). Despite large offtakes through illegal harvesting, encroachment of humans, and development of infrastructure in the last decade, there is no evidence that the population of wildebeest has declined.

12. Wildlife and livestock population trends in the Masai Mara National Reserve, wildlife conservancies and community areas in Narok County from 1977 to 2016

12.1 Methods

We partitioned Narok County into three land management types, comprising the Masai Mara National Reserve (CPA), Mara Conservancies (PASRU) and Narok Community Areas (UPA). We used Jolly's method 2 (*77*) for unequal transects to estimate the total population size and the associated standard errors for the four most common livestock and 13 most common large wildlife species in each of the three land management types in Narok County. The data consisted of 36 aerial surveys covering the conservancies and community areas and 62 aerial surveys covering the Masai Mara Ecosystem within the Narok County only. All the aerial surveys spanned 1977 to 2016.

For each land management type, we used a multivariate semi-parametric generalized linear mixed model (SGLMM) with a negative binomial error distribution and a log link function to model temporal trends for all the livestock species. The response variable was the population estimate for each species. The model consists of parametric and non-parametric components. The parametric, fixed effects part of the model consisted of species and species × time. Time is a continuous variable representing the year, month and day each aerial survey ended. The logarithm of the overall mean population estimate for each species in each land management type was used as an offset to adjust for interspecific differences in population size in the same land management type.

The non-parametric component of the trend model comprises two continuous random effects, each associated with a penalized spline variance-covariance structure. The first random spline effect fits a penalized cubic B-spline (P-spline) with a third-order difference penalty to random spline coefficients common to all the livestock species and hence models the time trend common to all the species. The second random spline effect similarly fits a penalized cubic B-spline with random spline coefficients specific to each species and therefore models the trend component specific to each species. Both the random spline effects had 20 equally spaced interior knots placed on the running date (27 January 1977,…, 27 November 2016 for Narok County) plus 3 evenly spaced exterior knots placed both at the start date and end date of the censuses. All the 12 resident wildlife species were also similarly and simultaneously modelled using a separate multivariate SGLMM. The migratory wildebeest and zebra were modelled together but by considering the wet and dry seasons separately.

We then calculated the percentage change in the expected population size for each species between 1977-1978 and 2016 for each livestock and resident wildlife species. For the migratory wildebeest and zebra we calculated the percentage changes in population size separately for the wet (1977-19778 versus 2016) and dry (1979 versus 2013-2014) seasons. For the community areas and wildlife conservancies we also computed the percentage change in population size between 2005 when wildlife conservancies were first created in Narok County and 2016.

12.2 Results

12.2.1 Wildlife and livestock population trends in the Mara Reserve from 1977 to 2016

The Masai Mara National Reserve (Mara Reserve) covers 1530 km^2, representing 8.5% of Narok County (17933.1 km^2). The number of cattle grazing illegally in the Mara Reserve increased almost 12-fold (1053%) from 1977-1978 to 2016. Similarly, the number of sheep and goats grazing illegally in the Mara Reserve increased nearly 13-fold (1174%) from 1977-1978 to 2016. As a result, cattle, sheep and goats are exerting strong and mounting pressures on the Mara Reserve (Fig S18, Table S5). In the same period (1977-1978 to 2016) the populations of all the 11 most common resident wildlife species decreased dramatically in the Mara Reserve by between 40.4% and 87.4% (Fig S18, Table S5). The number of resident wildebeest and zebra using the Mara Reserve in the wet season, likewise, drastically declined in the same period. (But large herds of about 50,000 animals of each species (wildebeest and zebra) stayed in the Reserve up to December 2016.) Far fewer (63.5% less) migratory wildebeest (174,269 animals) used the Mara Reserve in 2013-2014 compared to 477560 animals in 1977-1978 (Fig S18, Table S5).

12.2.2 Wildlife and livestock population trends in Mara Conservancies from 1977 to 2016

The first conservancy was created in Narok County in 2005. Since then the area covered by conservancies in the County continue to expand. Narok conservancies cover 1781.44 km^2 or 9.9% of Narok County (17933.1 km^2). From 1977-78 to 2016, the numbers of cattle (40%), sheep and goats (189.6%) increased dramatically but the number of donkeys decreased strikingly (Fig S18, Table S5). In sharp contrast, numbers of all the common large wildlife species but elephant decreased markedly by 54.3% to 93.3%. Elephant increased by 11.6% during 1977-2016 (Fig S18, Table S5). The numbers of wildebeest using the Narok wildlife conservancies in both the wet and dry seasons in 2016 were 75-85% smaller than the numbers using the same areas in 1977-1978. The number of zebra using the wildlife conservancies in the dry season of 2016 was similarly 75% fewer than in 1977-1978 (Fig S18, Table S5).

In the period since the establishment of conservancies spanning 2005-2016, the numbers of cattle, sheep and goats continued to increase whereas all wildlife species, except Burchell's zebra in the wet season, continued to decline. These trends demonstrate that conservation efforts undertaken by the wildlife conservancies have so far not succeeded in reversing the declining wildlife numbers in the conservancies in Narok County. The steep increase in numbers of cattle, sheep and goats inside the wildlife conservancies, unless checked, has the potential to further accelerate the wildlife population declines. It is noteworthy and worrisome that numbers of cattle, sheep and goats are increasing even faster in the period following the establishment of conservancies from 2005 to 2016.

12.2.3 Wildlife and livestock population trends in Narok Community Areas from 1977 to 2016

The community areas in Narok cover 14021.8 km^2 corresponding to 78.2% of the whole of Narok County (17933.1 km^2). Numbers of cattle decreased slightly whereas numbers of sheep and goats more than doubled from 1977-1978 to 2016 (Fig S18, Table S5). By contrast, numbers of all the 13 common large wildlife species except elephant decreased in the same period, with the majority of the species decreasing precipitously. Specifically, populations of 10 wildlife species declined by more than 80% in the 40 years from 1977 to 2016 (Fig S18, Table S5). Notably, elephant numbers more than doubled in the community areas between 1977-1978 and 2016 (Fig S18, Table S5). These declines are concurrent with major land use changes in Narok, including expansion of settlements (*79*) and a steep increase in the number of fences in the community areas, particularly in the Mara ecosystem, in recent years (*80*). A remote sensing analysis done in May 2017 found 4818 fences covering an area of 654 km^2 in the Mara Ecosystem in Narok County alone. These worrying developments portend an insecure future for wildlife and require urgent remedial action.

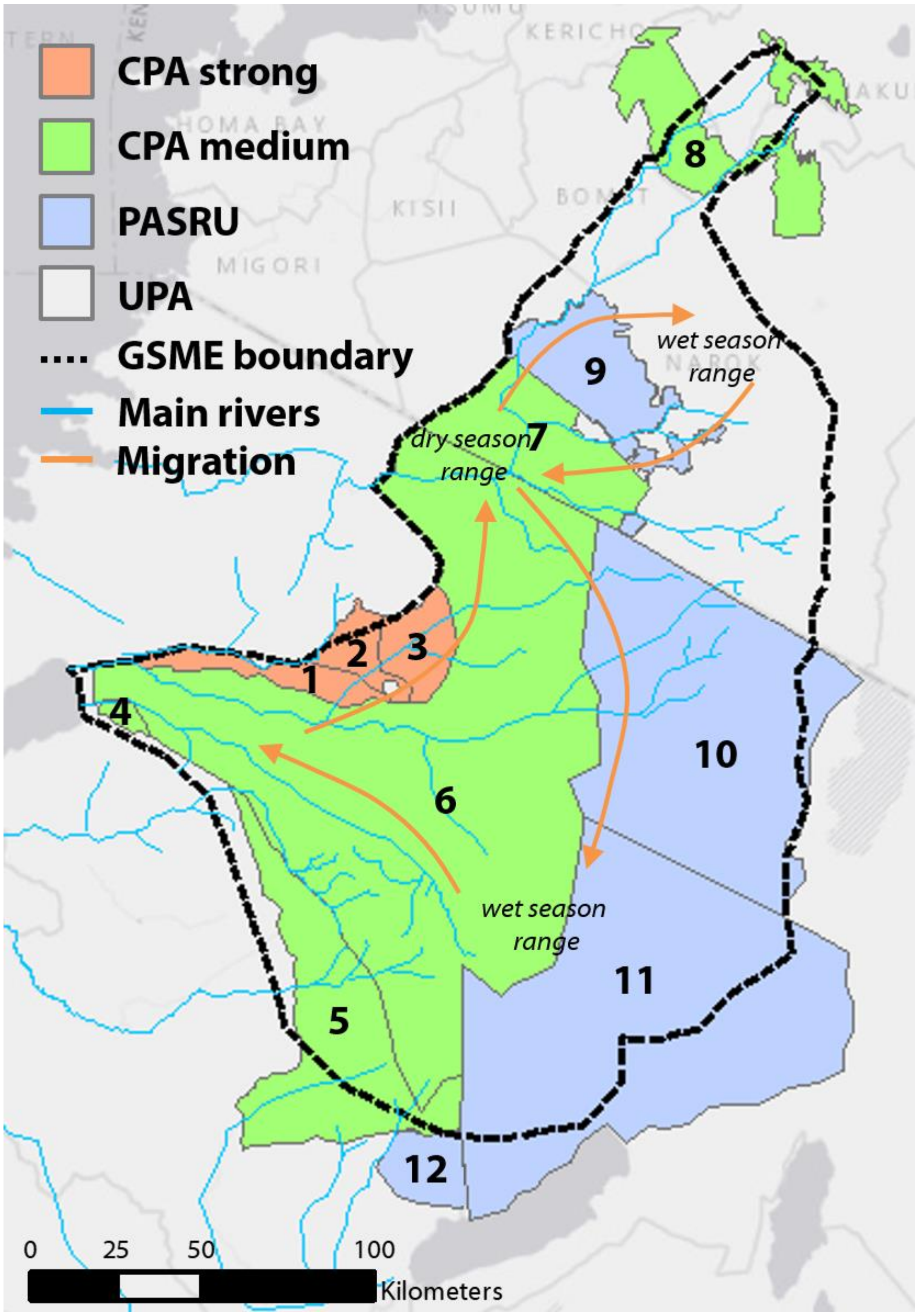

Fig. S1. Protected areas in The Greater Serengeti-Mara Ecosystem (GSME). Protected areas are classified into three categories based on the presence of livestock and the intensity of border controls. Strict Nature Reserves with strong border control include Grumeti GR (1; 513 km^2), Ikona WMA (2; 280 km^2) and Ikorongo GR (3; 545 km^2). Strict Nature Reserves with medium border control are Kijereshi GR (4; 94 km^2), Maswa GR (5; 2756 km^2) Serengeti NP (6; 13062 km^2), Maasai Mara NR (7; 1578 km^2) and Mau FR (8; 1649 km^2). Protected Areas with Sustainable Resource Use are Maasai Mara Conservancies (9; 1413 km^2), Loliondo GCA (10; 6185 km^2), Ngorongoro CA (11; 8222 km^2) and Makao WMA (12; 503 km^2). The boundary of the GSME (dashed line) is defined as the areas used by the wildebeest migration (orange arrows) plus the upstream watershed areas connected to this.

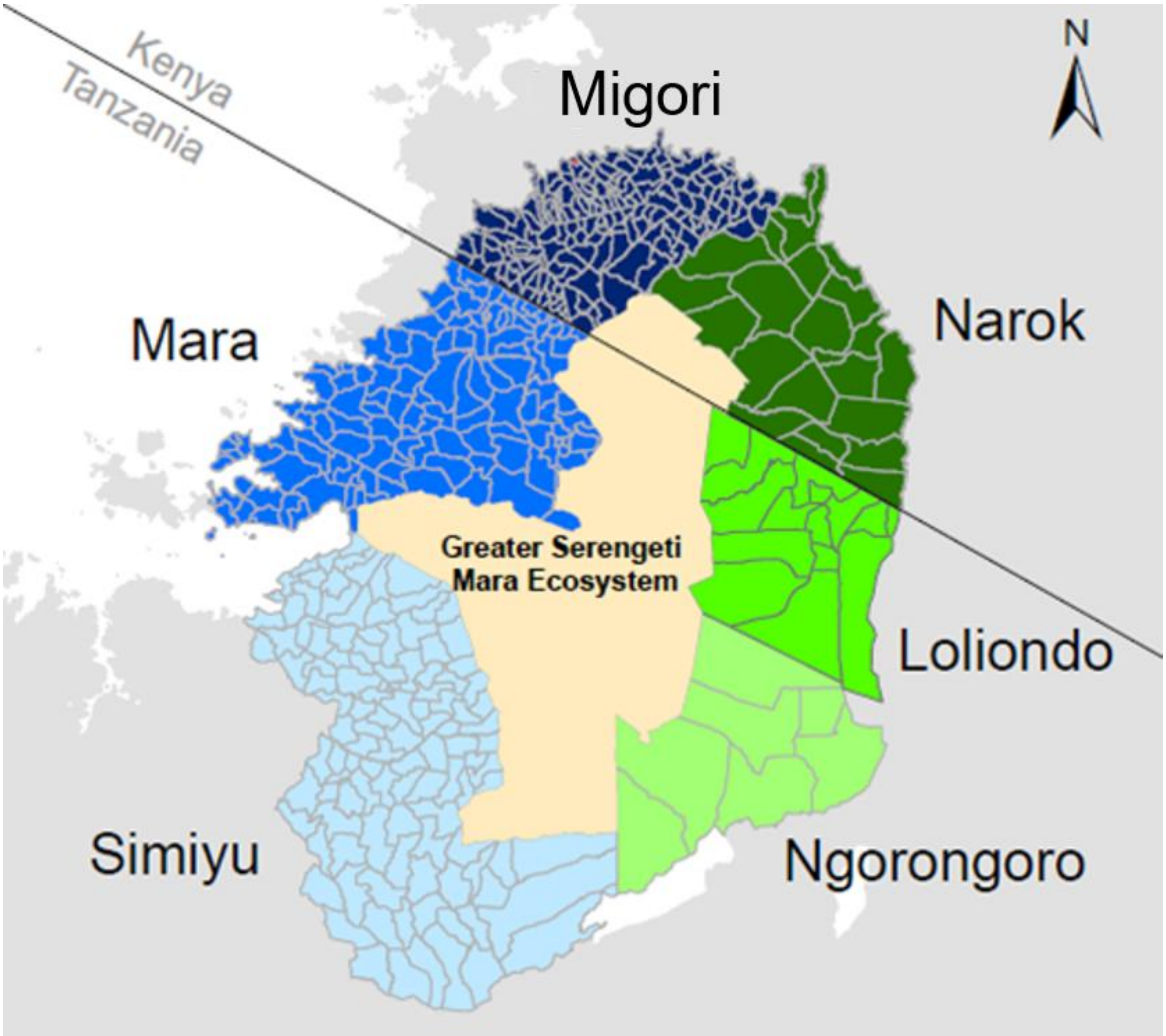

Fig. S2. The 6 distinct regions surrounding the Greater Serengeti-Mara Ecosystem based on country (Kenya, Tanzania), land-use (pastoralist, agro-pastoralist) and geographic location.

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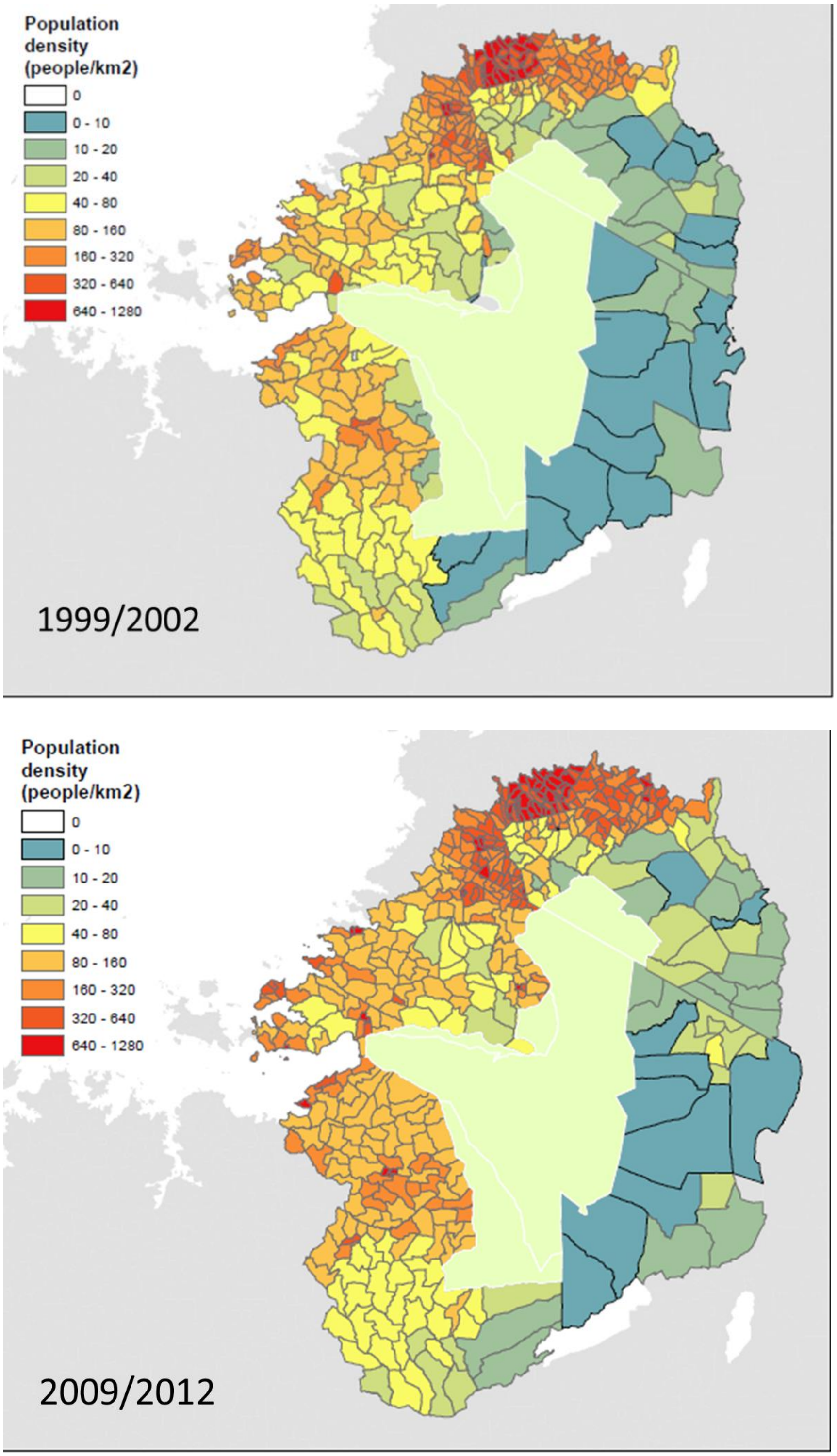

Fig. S3. Population densities for wards (Tanzania) and sub-locations (Kenya) within 60 km from the boundaries of the Core Protected Areas (CPA) 1999/2002 (top) and 2009/2012 (bottom).

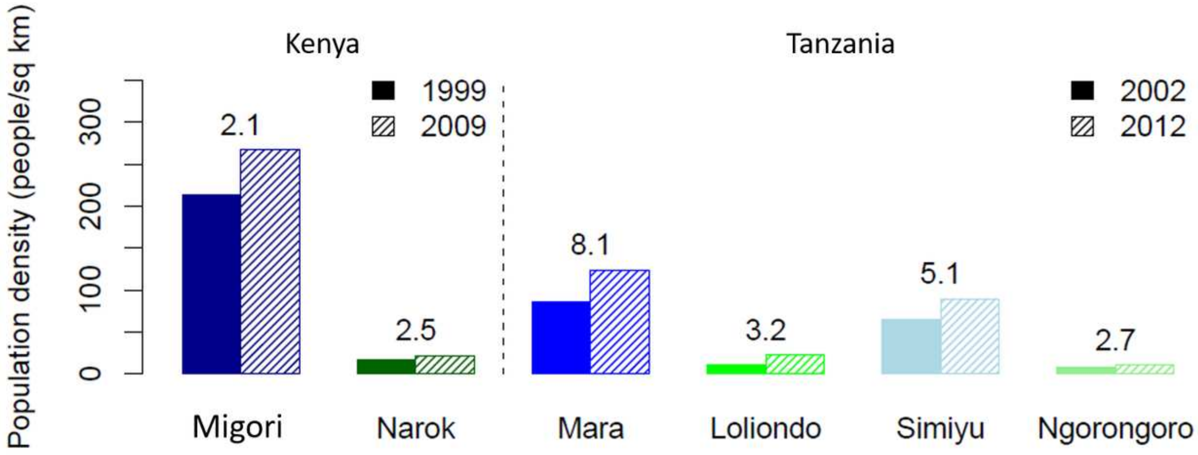

Fig. S4. Population densities within wards/sub-location situated within 60 km from the CPA border for the six regions surrounding CPA in 1999/2002 and 2009/2012. Numbers above the bars represent the annual percentage increase in human population. Blue bars represent agro-pastoralist regions on the western side of the CPA and green bars represent the Maasai pastoralist regions on the Eastern border.

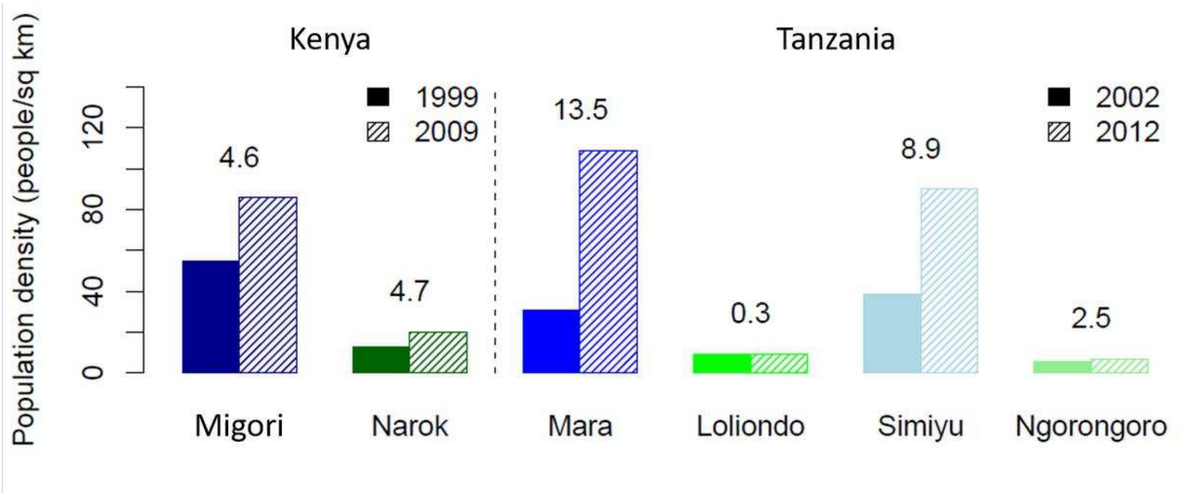

Fig. S5. **Population density within wards/sub-location located within 15 km from the CPA border for the six regions surrounding the CPA in 1999/2002 and 2009/2012.** Numbers above the bars represent the annual percentage increase in human population. Blue bars represent agro-pastoralist regions on the western side of the CPA and green bars represent Maasai pastoralist regions on the Eastern border.

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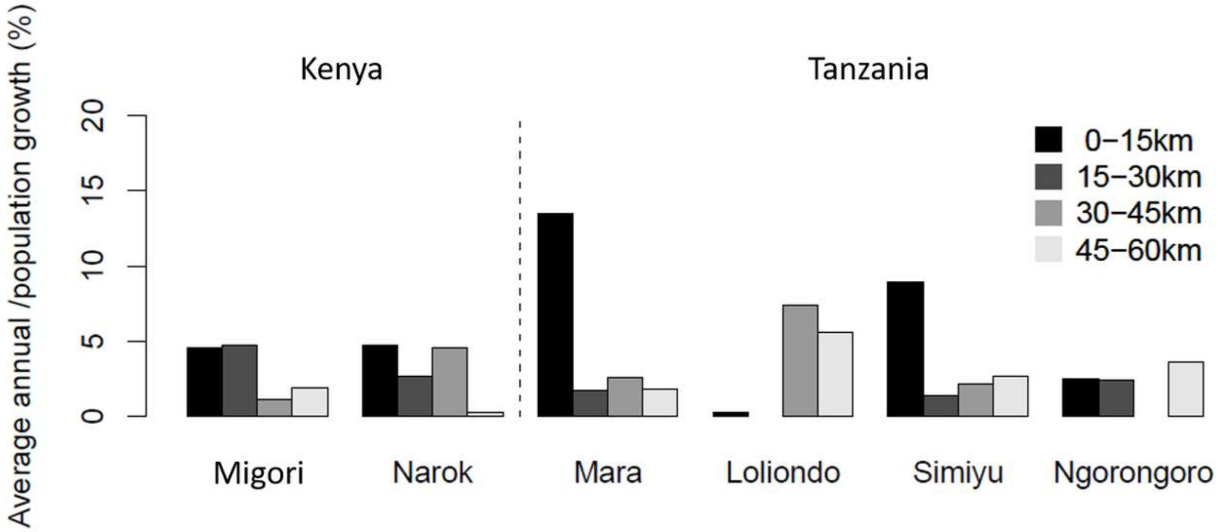

Fig. S6. **Annual population growth rate for the six regions, subdivided into wards/sub-location at increasing distances to the border of the CPA.**

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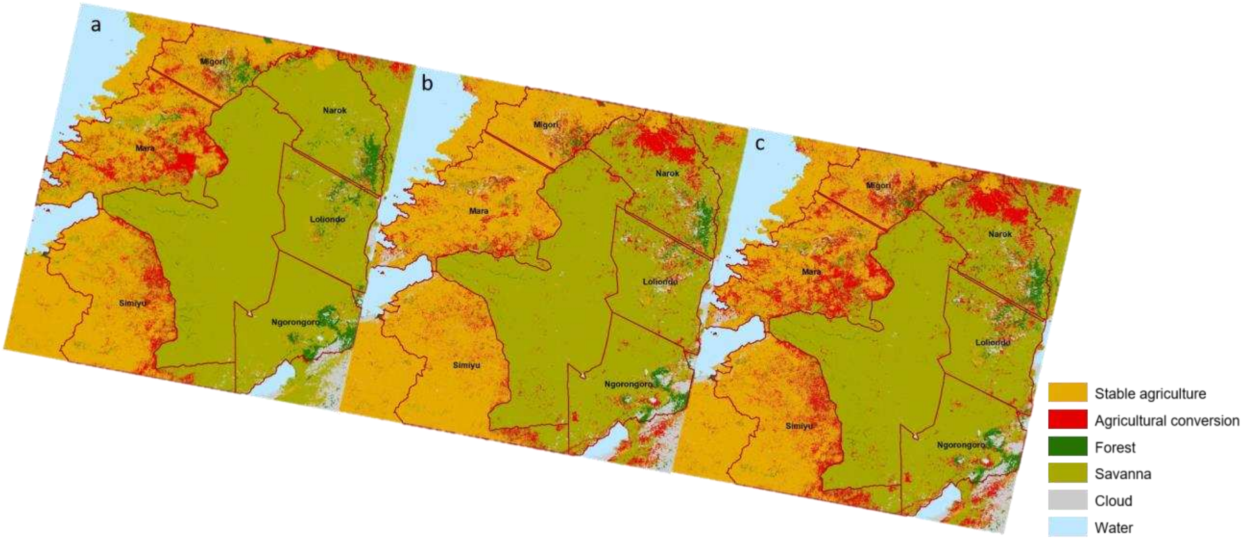

Fig S7. **Conversion from natural vegetation or rangeland to cropland ('agricultural conversion') around the Greater Serengeti-Mara Ecosystem between a) 1984-2003, b) 2003-2018 and c) 1984-2018.** Conversion was the most intense in the more densely-settled western agro-pastoral areas where the only remaining arable land was located close to the core protected area boundaries. Conversion of pastoral areas to the east of the park has increased in more recent years, though this area still constitutes a much softer boundary. "Stable agriculture' means that a pixel was cropland both at the first and the last year of the indicated period for each sub-figure.
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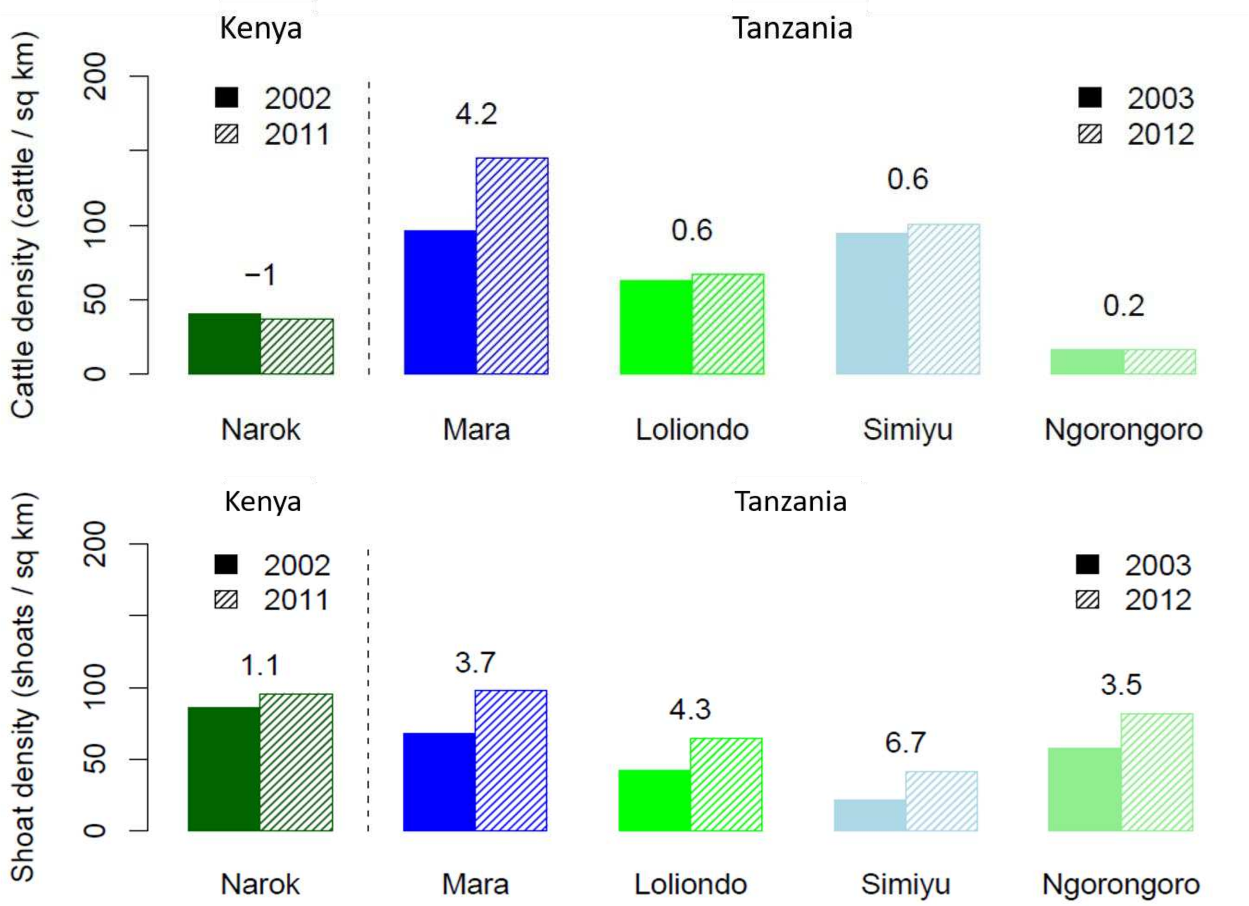
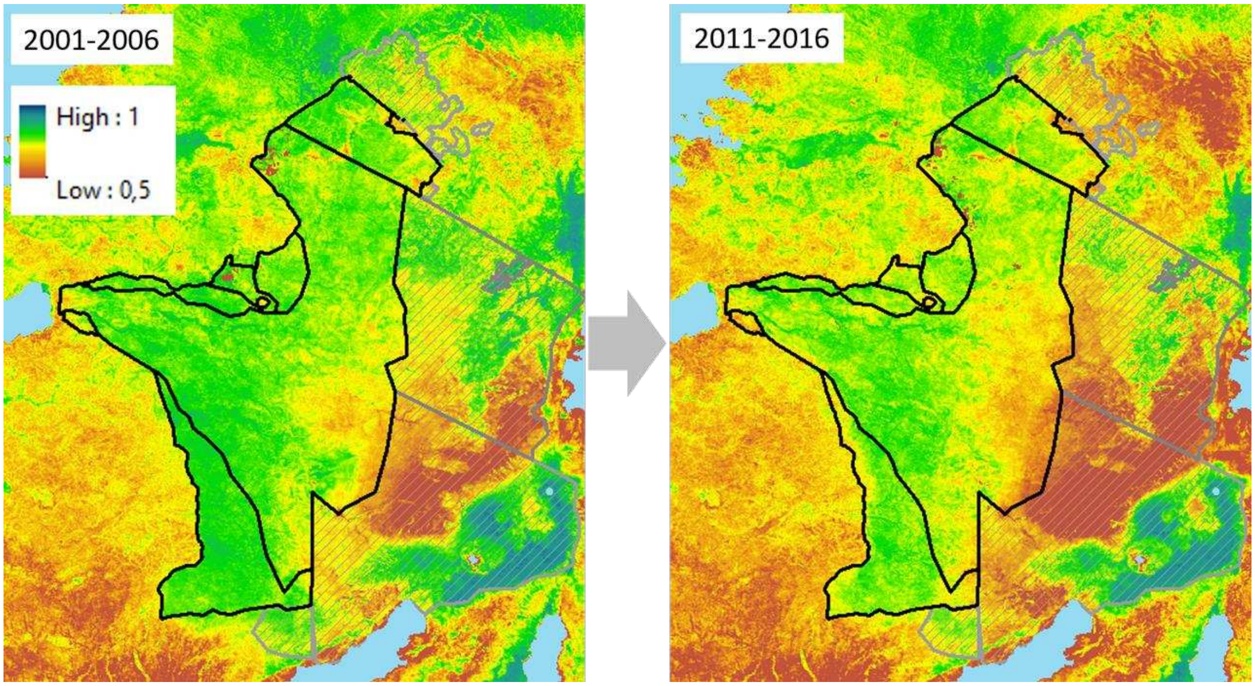


Fig. S8. Densities of cattle (top) and shoats (bottom) in 2002/2003 (filled bars) and 2011/2012 (shaded bars) for five regions bordering the CPA. The numbers above the bars indicate the average annual change in percentage over the 9-year period. Green bars represent the areas that border the CPA in the north and east, mostly inhabited by Maasai pastoralists, while blue bars represent the Sukuma and Kuria agro-pastoralist areas that border the CPA in the west.



5 **Fig. S9. Mean annual maximum NDVI for 2001-2006 (left) and 2011-2016 (right).**

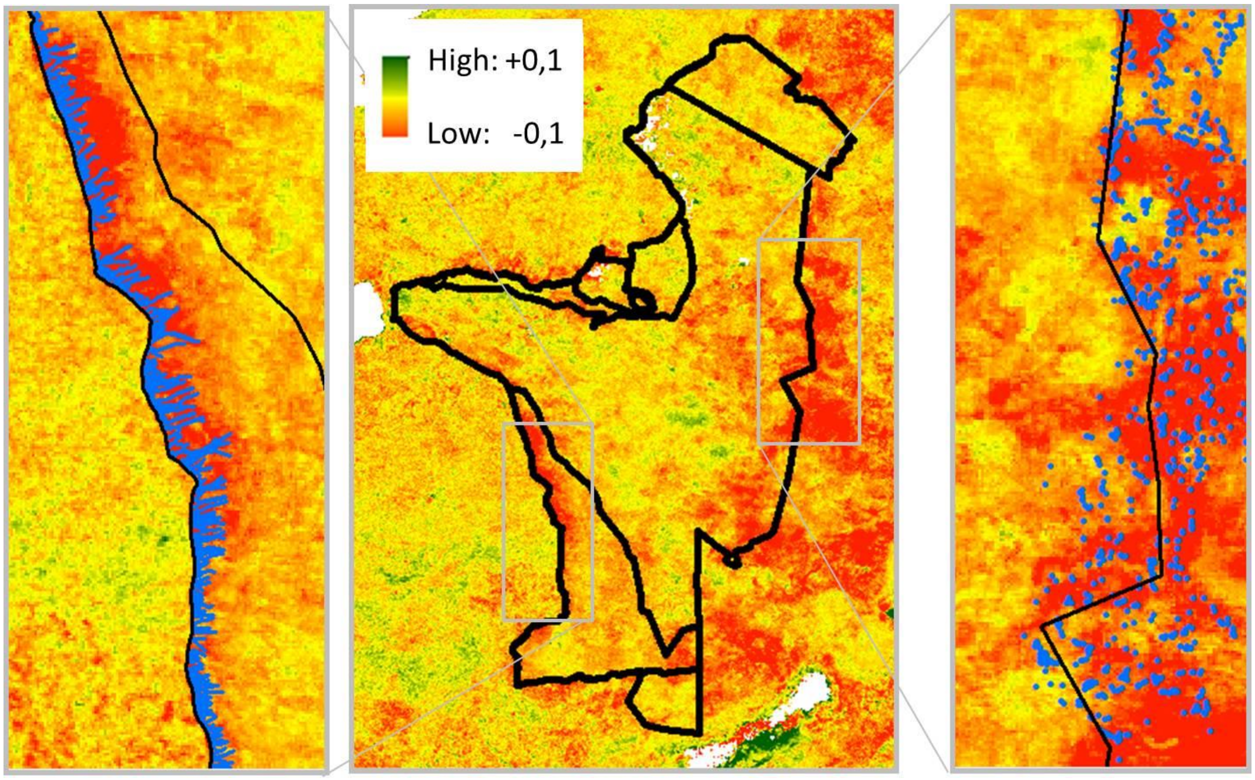


Fig. S10. Changes in mean maximum NDVI between 2001-2006 and 2011-2016.
Enlargements of the border of Maswa Game Reserve overlaid with the livestock paths (left) and 5 the Eastern border of the Serengeti National Park overlaid with mapped bomas (right).

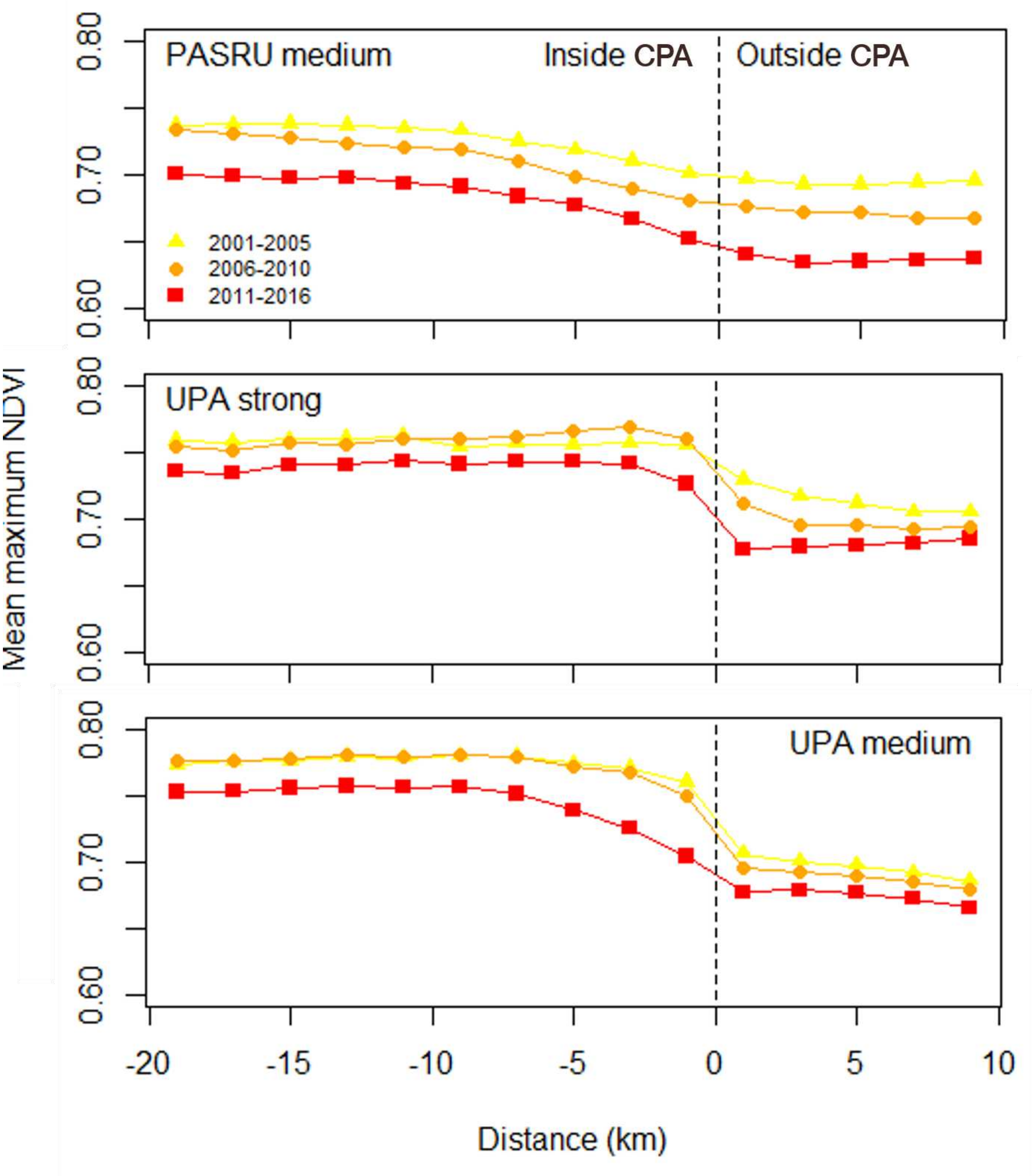


Fig. S11. Mean maximum NDVI as a function of distance to the border. Panels represent
5 borders between the Core Protected Areas (CPA) with the Protected Areas with Sustainable Resource Use (PASRU; top), the Unprotected Areas with medium border controls (UPA medium; bottom) and with strong border controls (UPA strong; middle). Different colors represent mean maximum NDVI between 2001-2005 (yellow), 2006-2010 (orange) and 2011-2016 (red). Positive distances are outside the CPA.

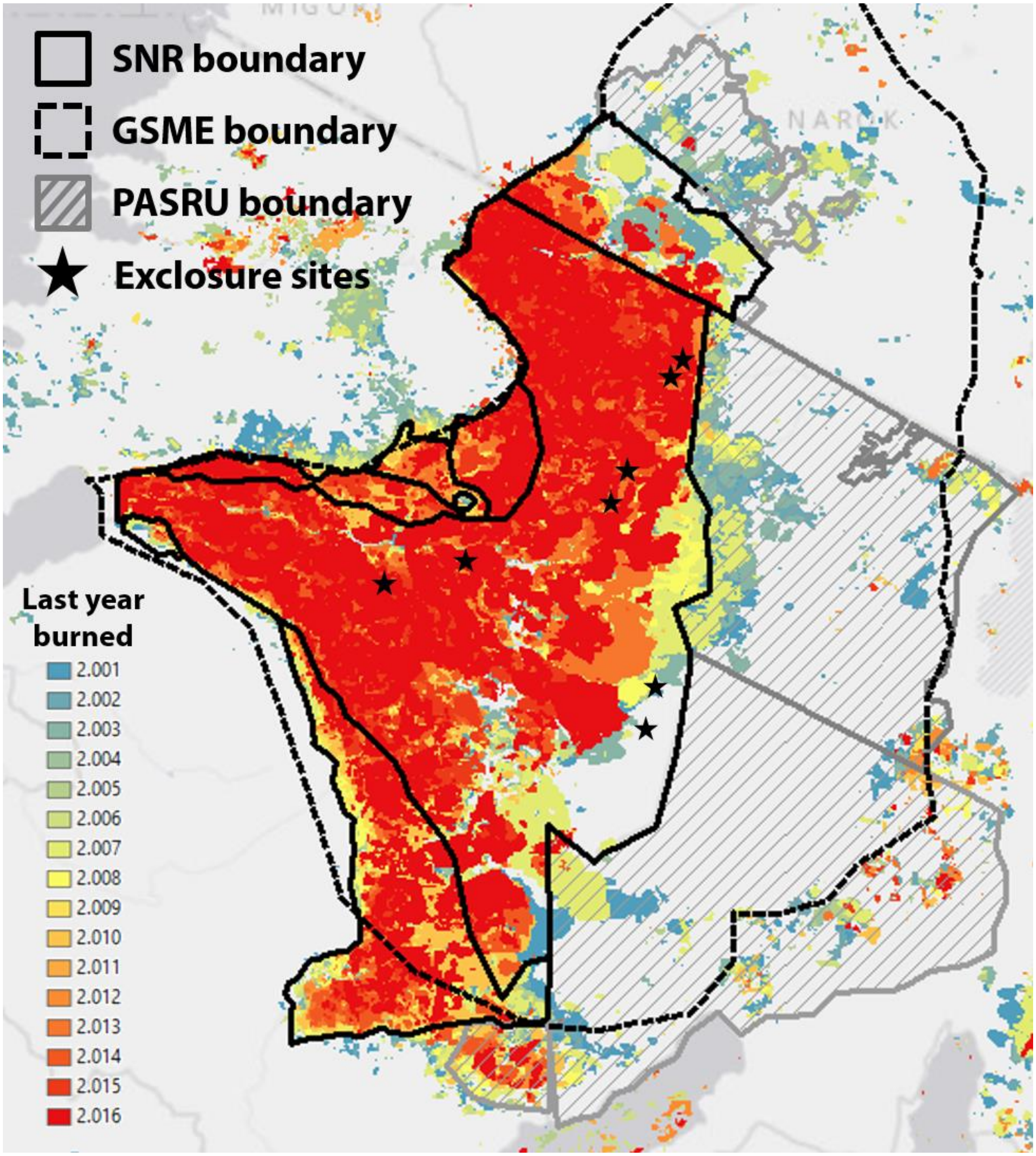


Fig. S12. Map of the last year each area burned. Lines delineate the Core Protected Areas (CPA; black solid lines), Protected Areas with Sustainable Resource Use (PASRU; grey solid lines) and the boundary of the Greater Serengeti-Mara Ecosystem (GSME; black dotted lines) that represents the original area used by the migratory wildlife. Colors indicate the year each area last burned. Areas with no color have not burned since 2001. The map was created using the MODIS MCD64 Burned Area Product (*64*). Black stars represent the sites with long-term herbivore exclosures.

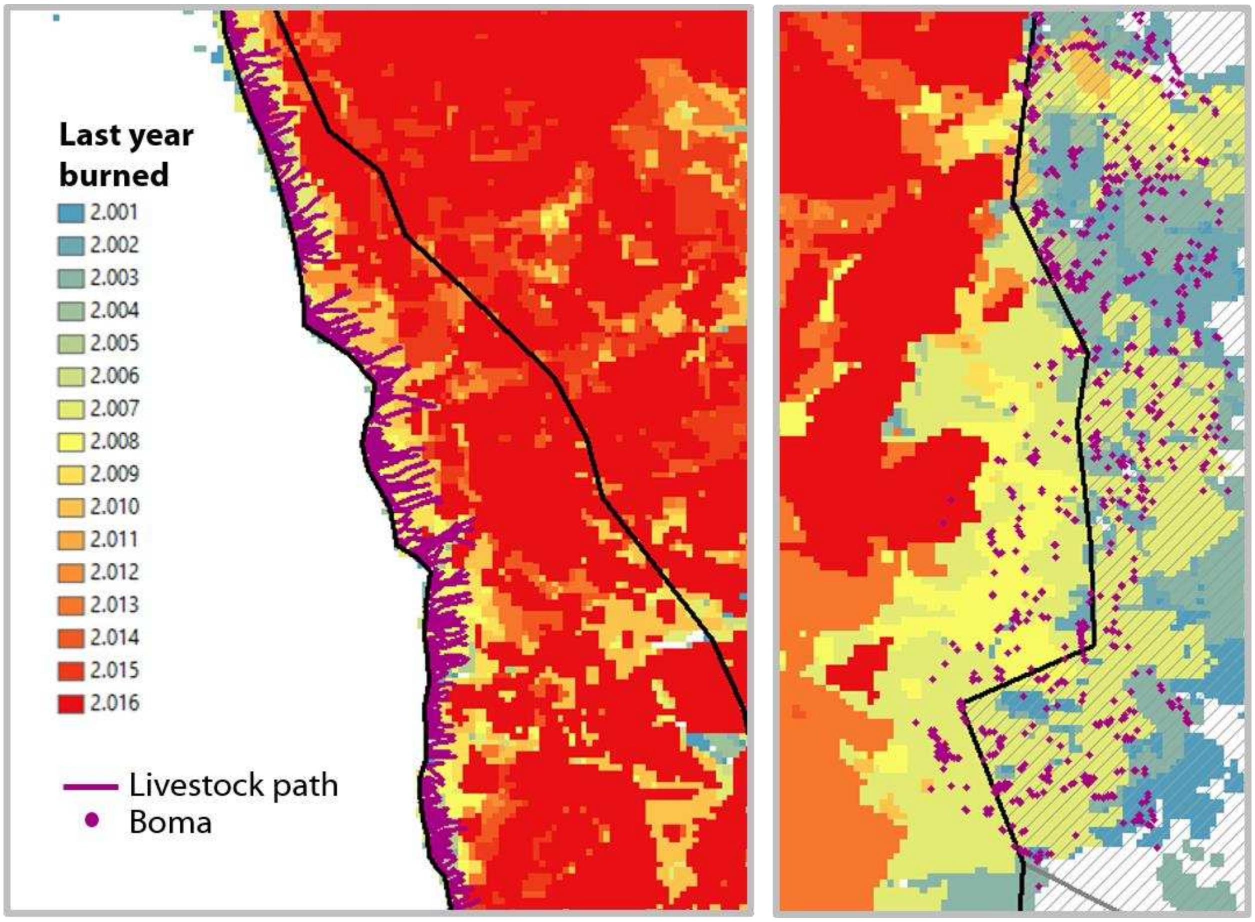


Fig. S13. **Map of the last year each area burned.** Same figure as in Fig. S12 but zoomed in on the border of Maswa Game Reserve (left) and Loliondo Game Controlled Area (right). Purple lines indicate livestock paths and purple dots represent bomas mapped using Google Earth (see Supplementary Text 9) and show a perfect match to the areas of reduced burning.

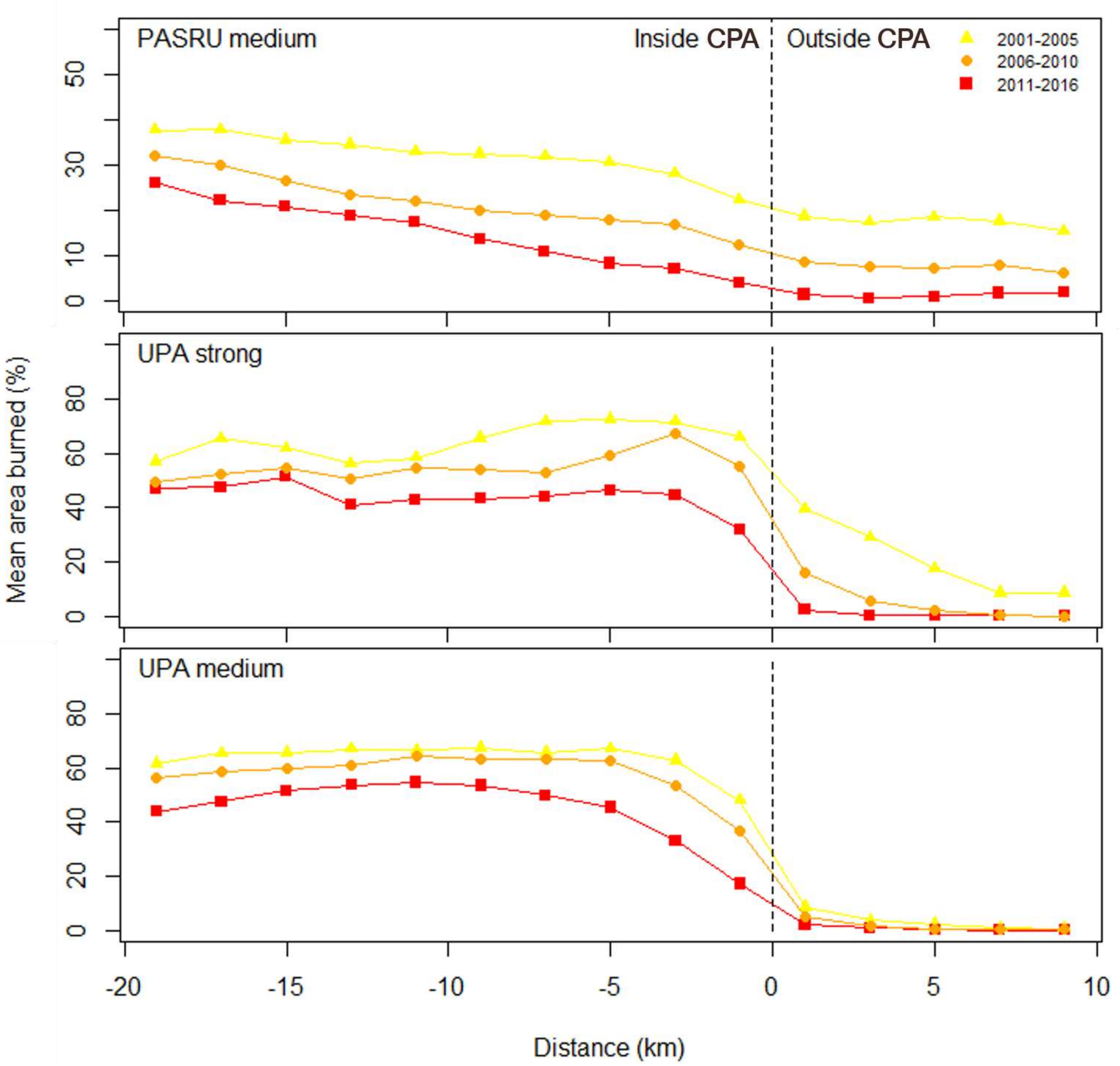


Fig. S14. Mean area burned as a function of distance to the border. Panels represent borders between the Core Protected Areas (CPA) and Protected Areas with Sustainable Resource Use (PASRU medium; top), the boundary with the unprotected area with medium border control (UPA medium; bottom) and with strong border control (UPA strong; middle). Different colors represent mean area burned during 2001-2005 (yellow), 2006-2010 (orange) and 2011-2016 (red). Negative distances refer to inside the CPA, whereas positive distances to the village lands (UPA and PASRU).

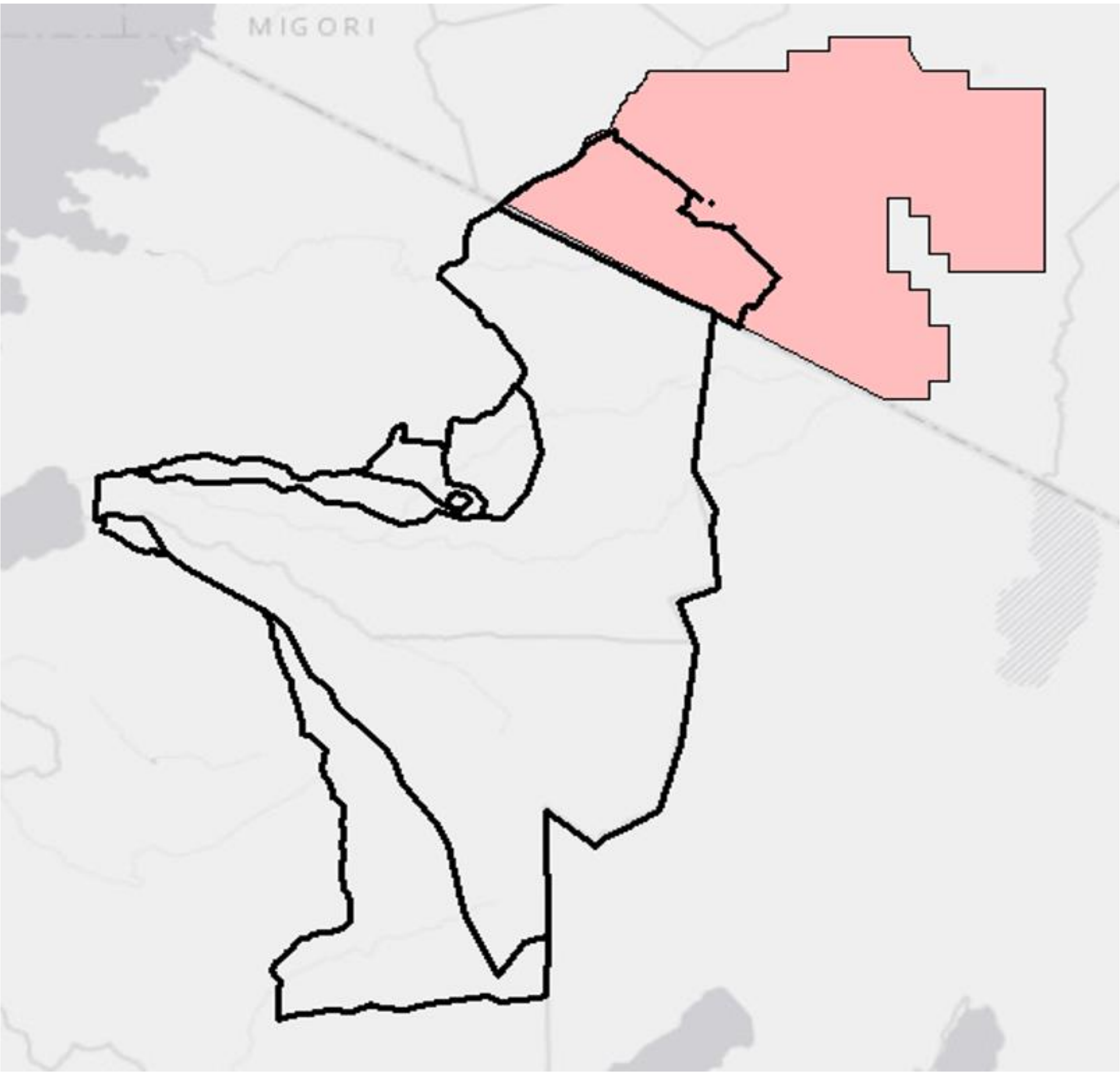
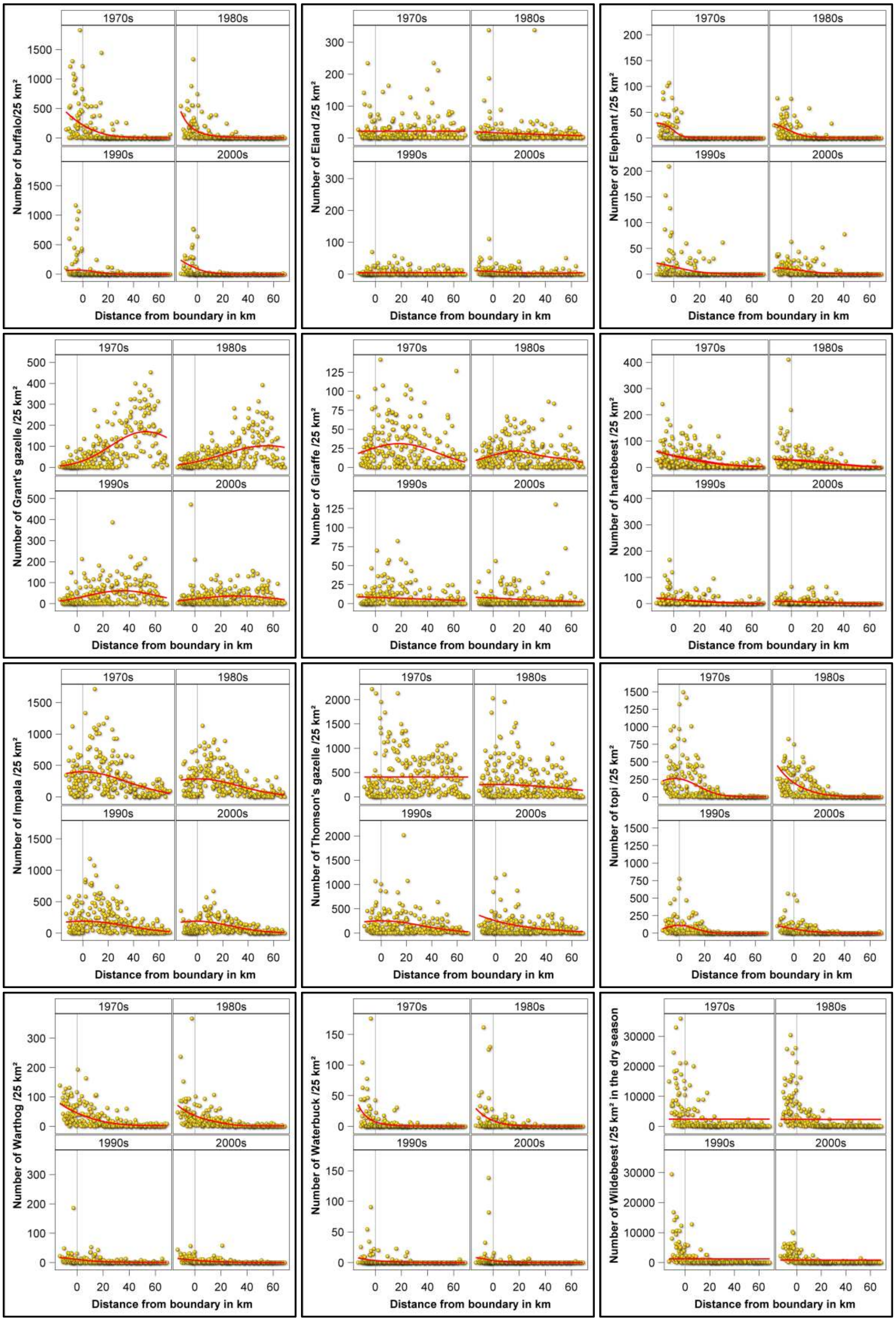


Fig. S15. Area surveyed during the 62 aerial surveys from 1977 to 2016. Black lines represent the boundaries of the Core Protected Area (CPA). Mara wildlife conservancies (PASRU) adjacent to the Maasai Mara National Reserve were only created from 2005 onward and were initially too small to have much of an impact on the analyses presented here.


1970s
1980s
1990s
2000s
Number of buffalo/25 km²
Number of Eland /25 km²
Number of Elephant /25 km²
Number of Grant's gazelle /25 km²
Number of Giraffe /25 km²
Number of hartebeest /25 km²
Number of Impala /25 km²
Number of Thomson's gazelle /25 km²
Number of topi /25 km²
Number of Warthog /25 km²
Number of Waterbuck /25 km²
Number of Wildebeest /25 km² in the dry season
Distance from boundary in km
0
20
40
60

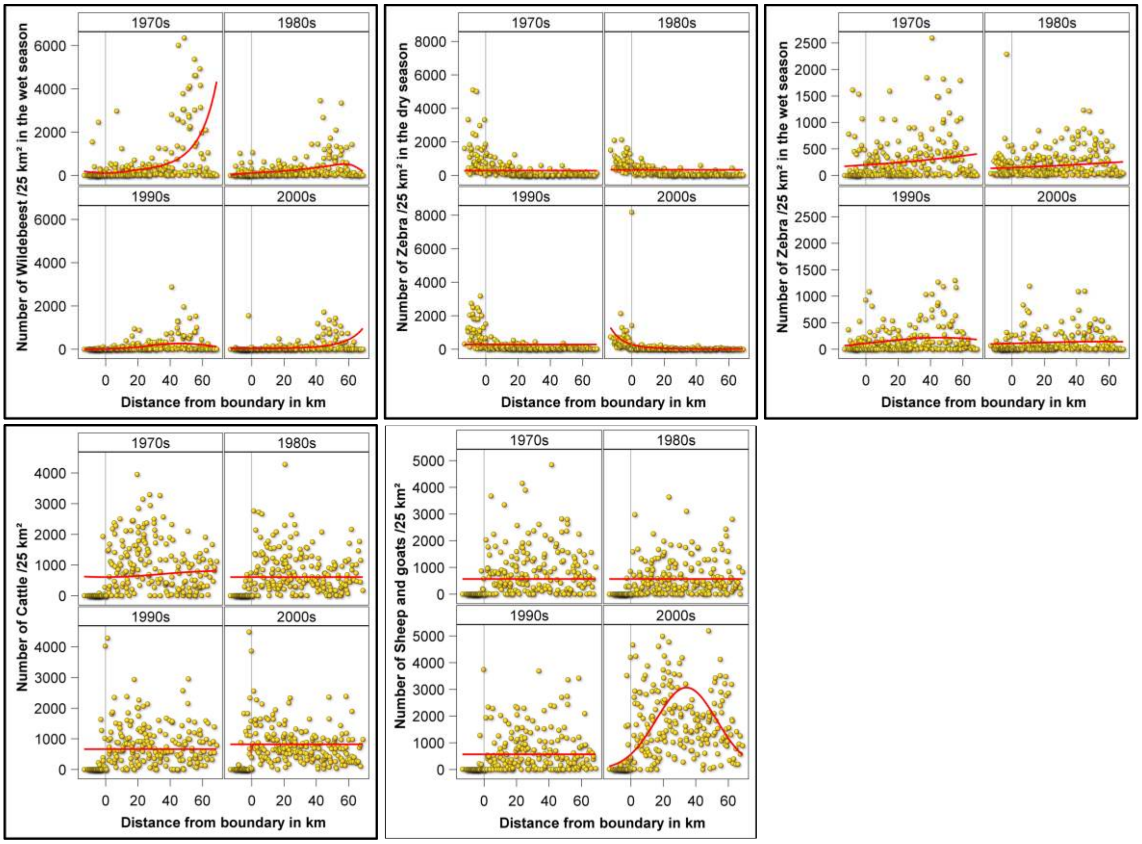


Fig. S16. Trends in herbivore densities as a function of distance to the border of the Masai Mara National Reserve (MMNR, Core Protected Area) for four decades (1977-2016). Negative distances refer to inside the MMNR. Points represent mean densities in 5 x 5 km sampling units from multiple aerial surveys per decade (n = 62 surveys). For the two migratory species (wildebeest and zebra) the dry (n=31 surveys) and wet (n=31 surveys) seasons have been modeled and plotted separately. The large southern migration only uses the Mara Region in the dry season. The smaller northern migration uses the Loita Plains situated to the north east of the MMNR as their wet season range, resulting in higher densities of wildebeest and zebra outside the MMNR in the wet season. See Table S4 for model outputs.

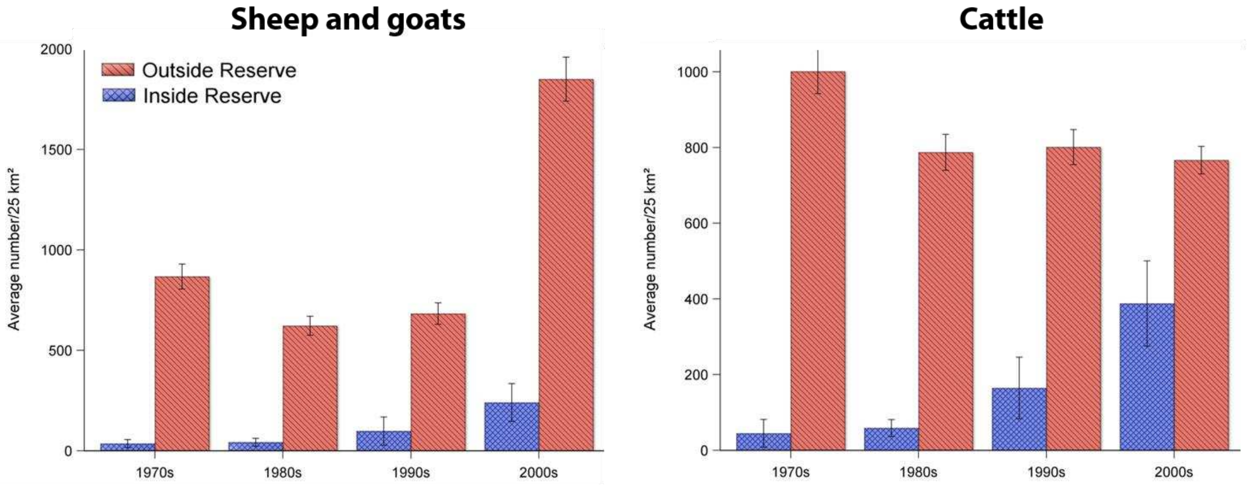
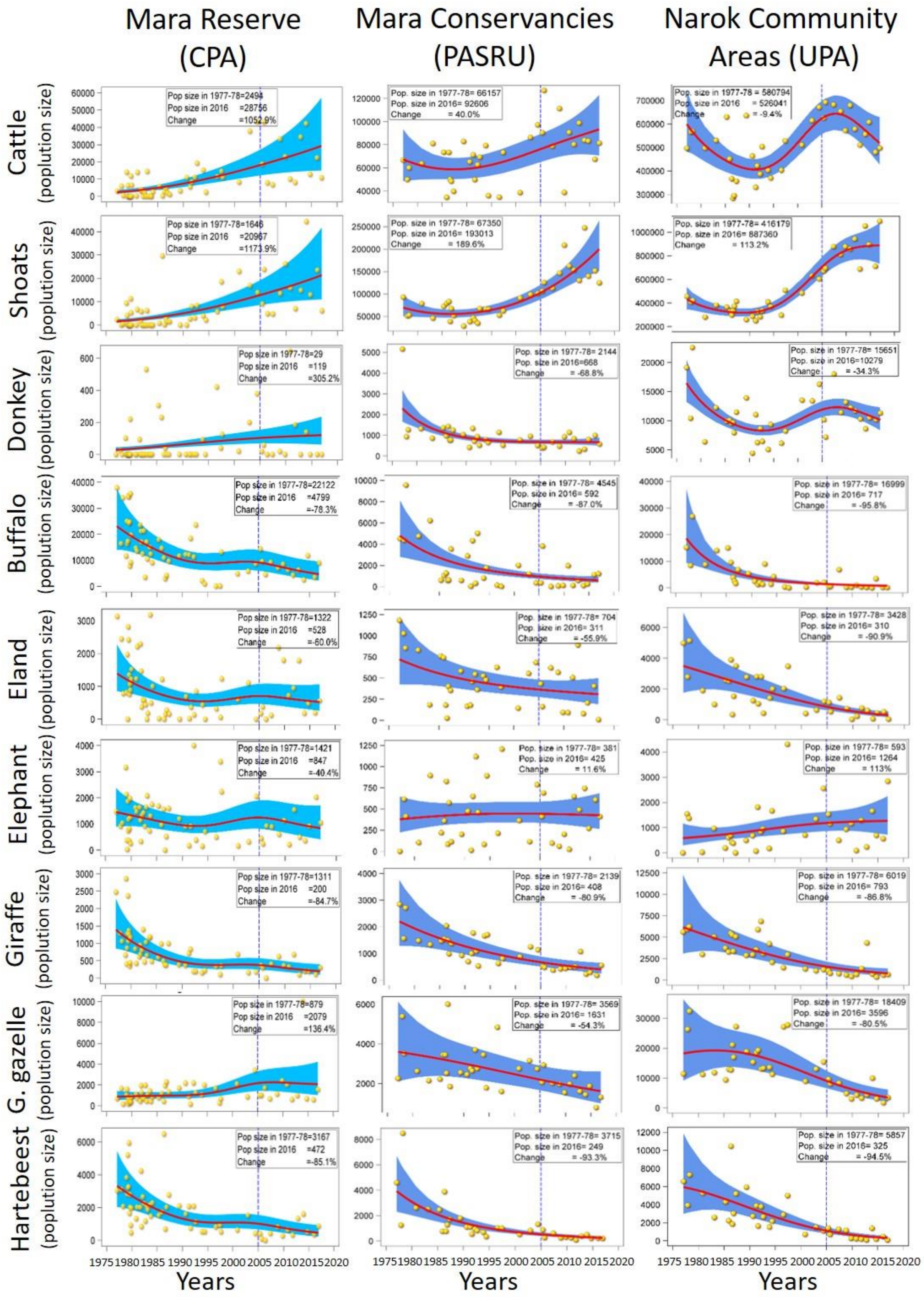


Fig. S17. **Temporal trends in densities of sheep and goats and cattle inside and outside the Maasai Mara National Reserve**. Bars represent mean ± SE. Statistical model outcomes of these trends are presented in TableS4.


Mara Reserve (CPA)
Mara Conservancies (PASRU)
Narok Community Areas (UPA)
Cattle (poplution size)
Pop size in 1977-78=2494
Pop size in 2016 =28756
Change =1052.9%
Pop. size in 1977-78= 66157
Pop. size in 2016= 92606
Change = 40.0%
Pop. size in 1977-78 = 580794
Pop. size in 2016 = 526041
Change = -9.4%
0 10000 20000 30000 40000 50000 60000
40000 60000 80000 100000 120000
300000 400000 500000 600000 700000
Shoats (poplution size)
Pop size in 1977-78=1646
Pop size in 2016 =20967
Change =1173.9%
Pop. size in 1977-78= 67350
Pop. size in 2016= 193013
Change = 189.6%
Pop. size in 1977-78= 416179
Pop. size in 2016= 887360
Change = 113.2%
0 10000 20000 30000 40000
50000 100000 150000 200000 250000
200000 400000 600000 800000 1000000
Donkey (poplution size)
Pop size in 1977-78=29
Pop size in 2016 =119
Change =305.2%
Pop. size in 1977-78= 2144
Pop. size in 2016=668
Change = -68.8%
Pop. size in 1977-78= 15651
Pop. size in 2016=10279
Change = -34.3%
0 200 400 600
0 1000 2000 3000 4000 5000
5000 10000 15000 20000
Buffalo (poplution size)
Pop size in 1977-78=22122
Pop size in 2016 =4799
Change =-78.3%
Pop. size in 1977-78= 4545
Pop. size in 2016= 592
Change = -87.0%
Pop. size in 1977-78= 16999
Pop. size in 2016= 717
Change = -95.8%
0 10000 20000 30000 40000
0 2000 4000 6000 8000 10000
0 10000 20000 30000 40000
Eland (poplution size)
Pop size in 1977-78=1322
Pop size in 2016 =528
Change =-60.0%
Pop. size in 1977-78= 704
Pop. size in 2016= 311
Change = -55.9%
Pop. size in 1977-78= 3428
Pop. size in 2016= 310
Change = -90.9%
0 1000 2000 3000
0 250 500 750 1000 1250
0 2000 4000 6000
Elephant (poplution size)
Pop size in 1977-78=1421
Pop size in 2016 =847
Change =-40.4%
Pop. size in 1977-78= 381
Pop. size in 2016= 425
Change = 11.6%
Pop. size in 1977-78= 593
Pop. size in 2016= 1264
Change = 113%
0 1000 2000 3000 4000
0 250 500 750 1000 1250
0 1000 2000 3000 4000
Giraffe (poplution size)
Pop size in 1977-78=1311
Pop size in 2016 =200
Change =-84.7%
Pop. size in 1977-78= 2139
Pop. size in 2016= 408
Change = -80.9%
Pop. size in 1977-78= 6019
Pop. size in 2016= 793
Change = -86.8%
0 500 1000 1500 2000 2500 3000
0 1000 2000 3000 4000
0 2500 5000 7500 10000 12500
G. gazelle (poplution size)
Pop size in 1977-78=879
Pop size in 2016 =2079
Change =136.4%
Pop. size in 1977-78= 3569
Pop. size in 2016= 1631
Change = -54.3%
Pop. size in 1977-78= 18409
Pop. size in 2016= 3596
Change = -80.5%
0 2000 4000 6000 8000 10000
2000 4000 6000
0 10000 20000 30000
Hartebeest (poplution size)
Pop size in 1977-78=3167
Pop size in 2016 =472
Change =-85.1%
Pop. size in 1977-78= 3715
Pop. size in 2016= 249
Change = -93.3%
Pop. size in 1977-78= 5857
Pop. size in 2016= 325
Change = -94.5%
0 2000 4000 6000
0 2000 4000 6000 8000
0 2000 4000 6000 8000 10000 12000
1975 1980 1985 1990 1995 2000 2005 2010 2015 2020
Years
1975 1980 1985 1990 1995 2000 2005 2010 2015 2020
Years
1975 1980 1985 1990 1995 2000 2005 2010 2015 2020
Years

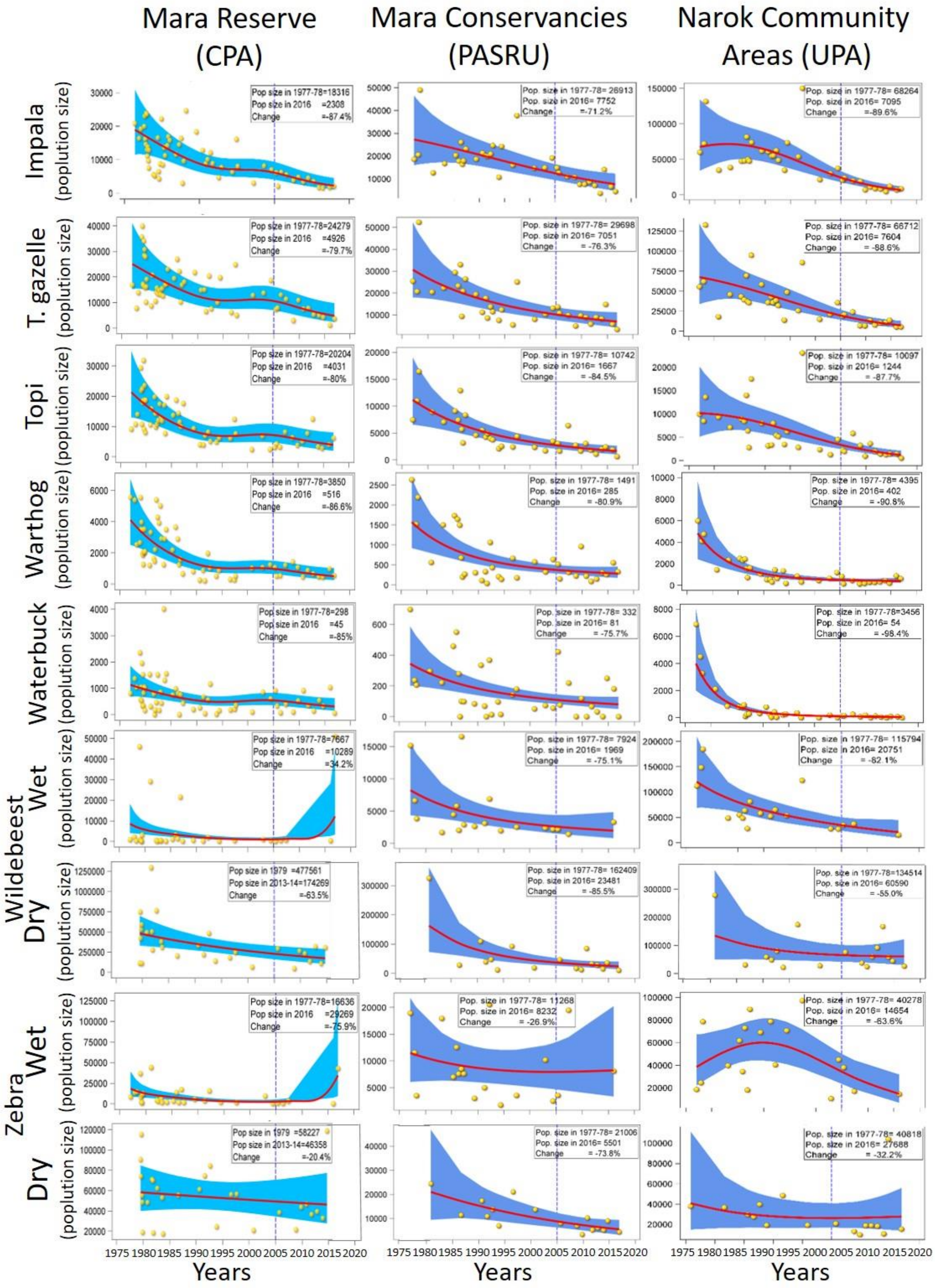


Fig. S18. Trends in wildlife and livestock densities for the Mara Reserve (CPA), Mara Conservancies (PASRU) and Narok Community Areas (UPA) between 1977 and 2016.

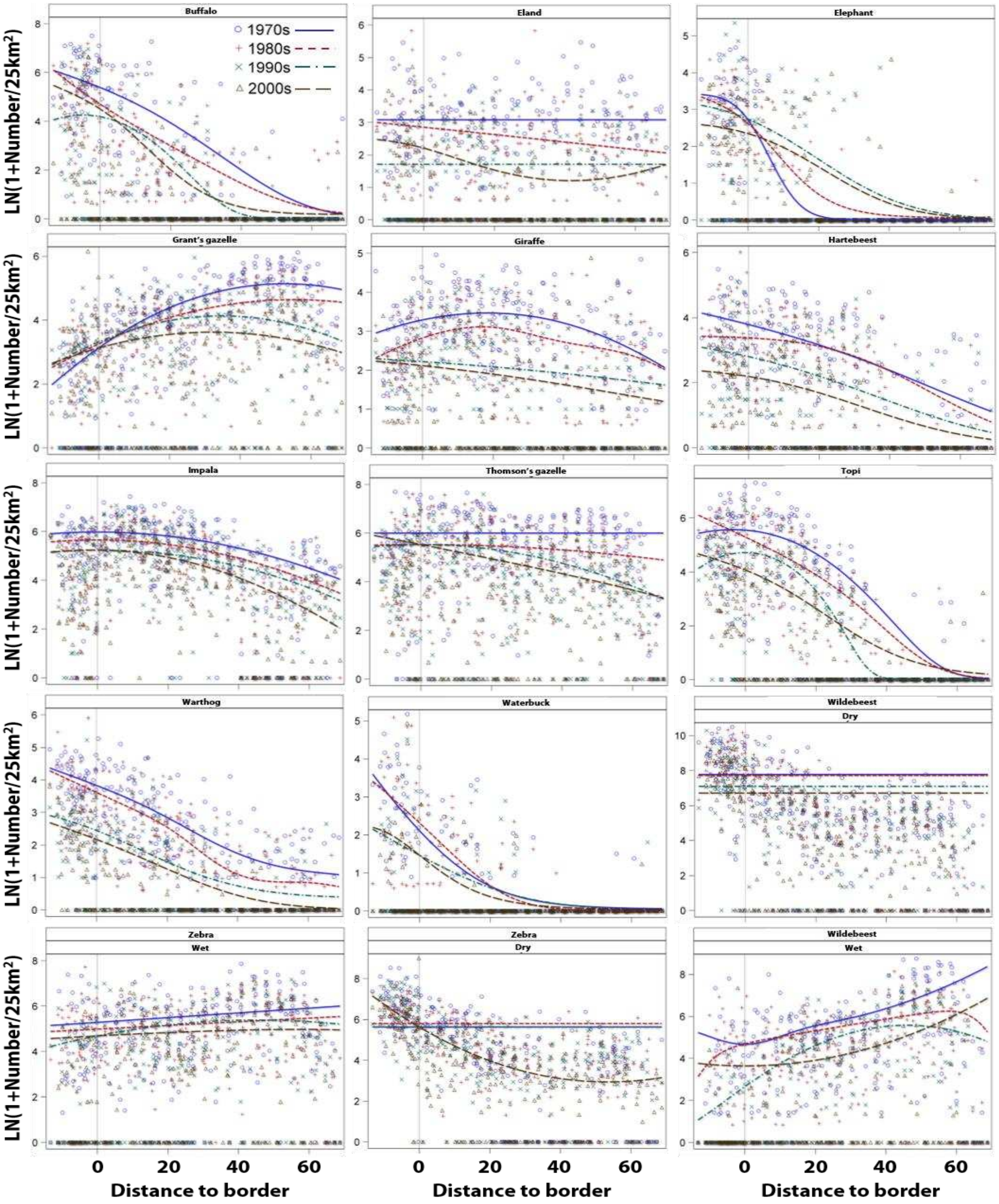


Fig. S19. Observed and predicted distributions of the count for all the wildlife and livestock species from the Masai Mara National Reserve boundary in the 1970s, 1980s, 1990s and 2000s.). Negative distances refer to inside the MMNR. Points represent mean densities in 5 x 5 km sampling units from multiple aerial surveys per decade (n = 62 surveys). For the two migratory species (wildebeest and zebra) the dry (n=31 surveys) and wet (n=31 surveys) seasons have been modeled and plotted separately.

Fig. S20. Image of a boma at the border of the Loliondo Game Controlled Area. Image taken by satellite (image Google Earth (*74*)).

Fig. S21. Satellite images of bomas from across the ecosystem. a) an active boma (top left) and disused bomas (below), b) two bomas containing livestock and a disused boma, c) here disused bomas are visible in between agricultural fields (images Google Earth (*74*)).

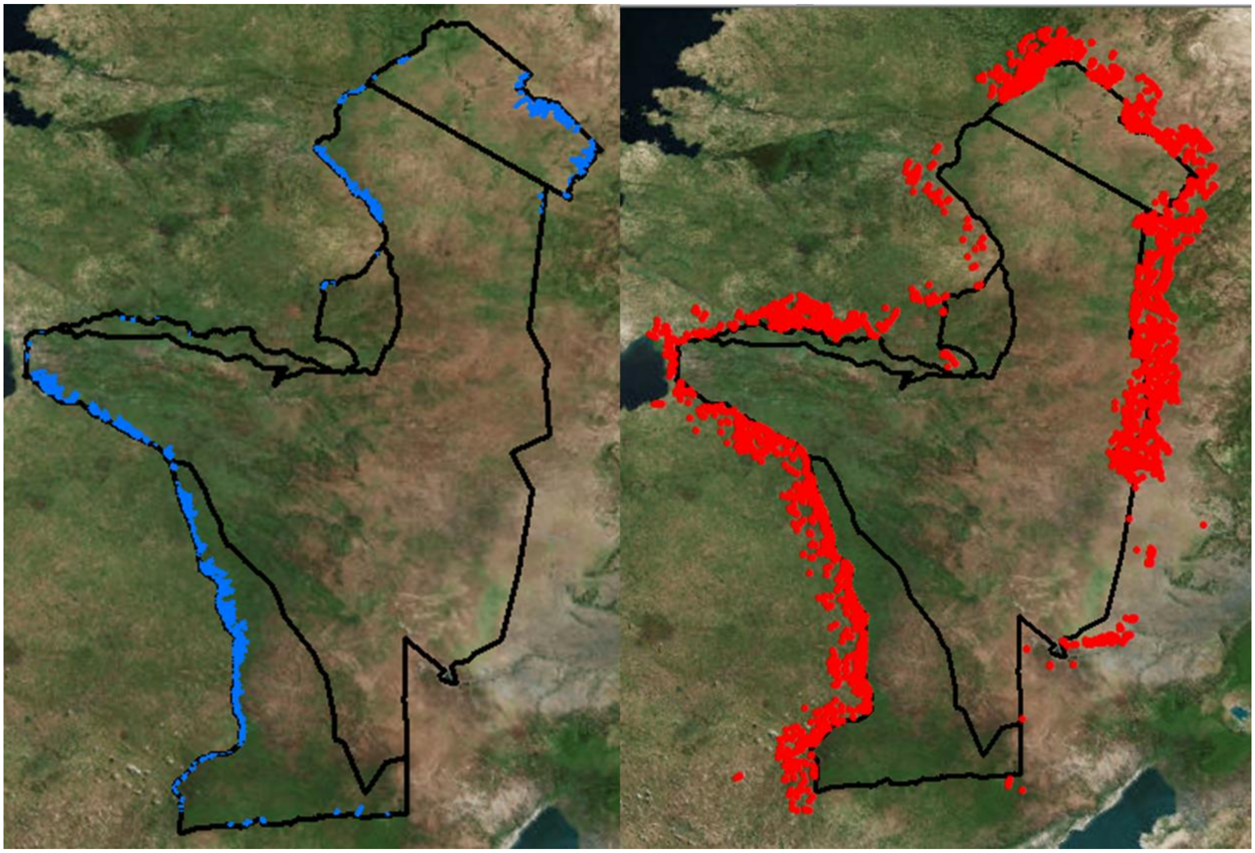


Fig. S22. Maps of livestock paths (left) and bomas (right). Livestock paths and bomas were
5 identified using Google Earths Pro’s (28 August 2017) (*74*).

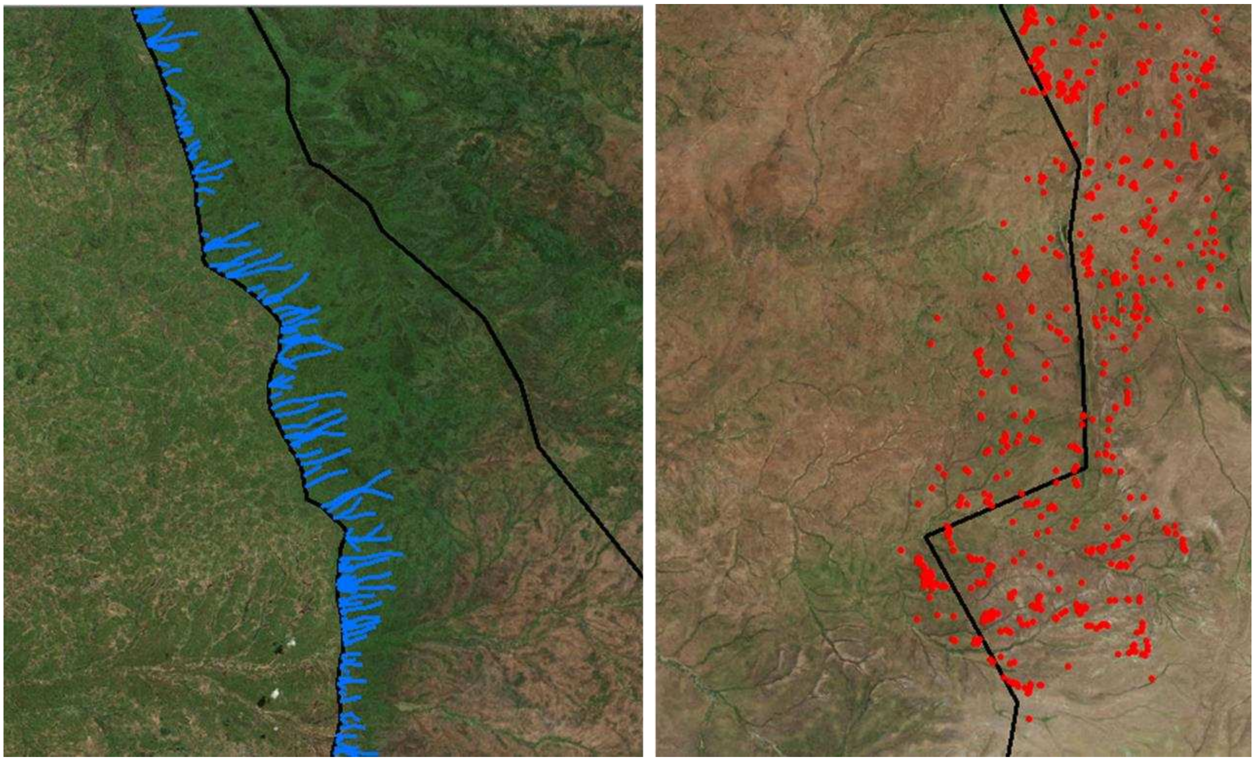


Fig. S23. Maps of livestock paths (left) and bomas (right). Same as in Fig. S22 but now zooming in on the border of Maswa Game Reserve (left) and the Eastern border of the Serengeti National Park.

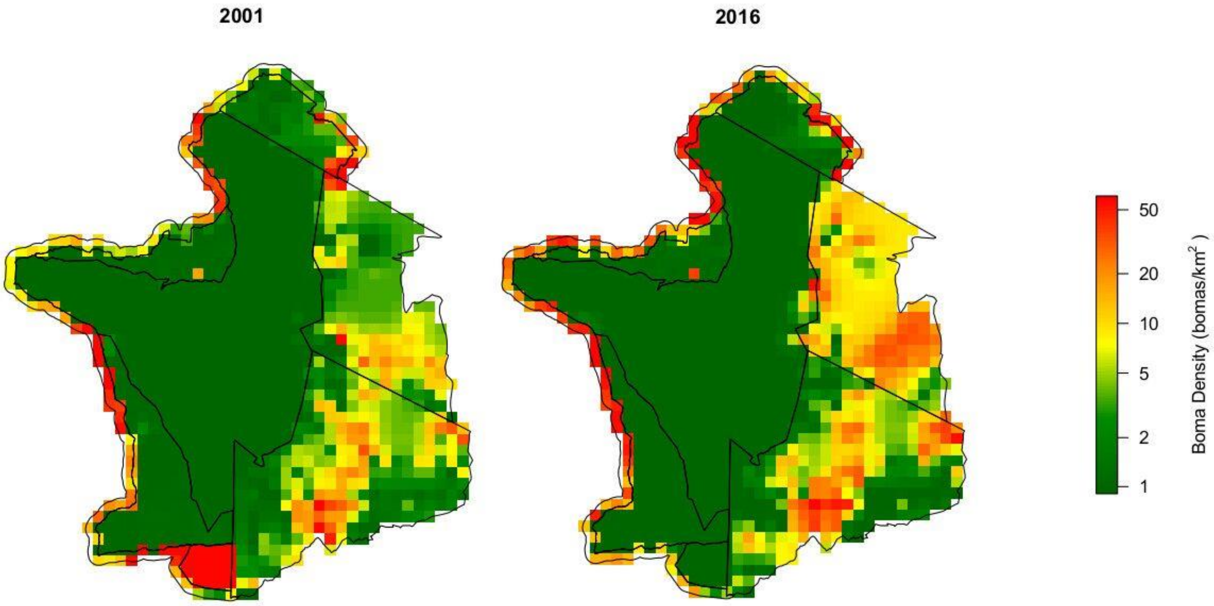


Fig. S24. The predicted boma density in 2001 and 2016. Note that the scale is logged. For display purposes we set all predicted boma densities less than one to zero to highlight variation at the upper end of the scale.

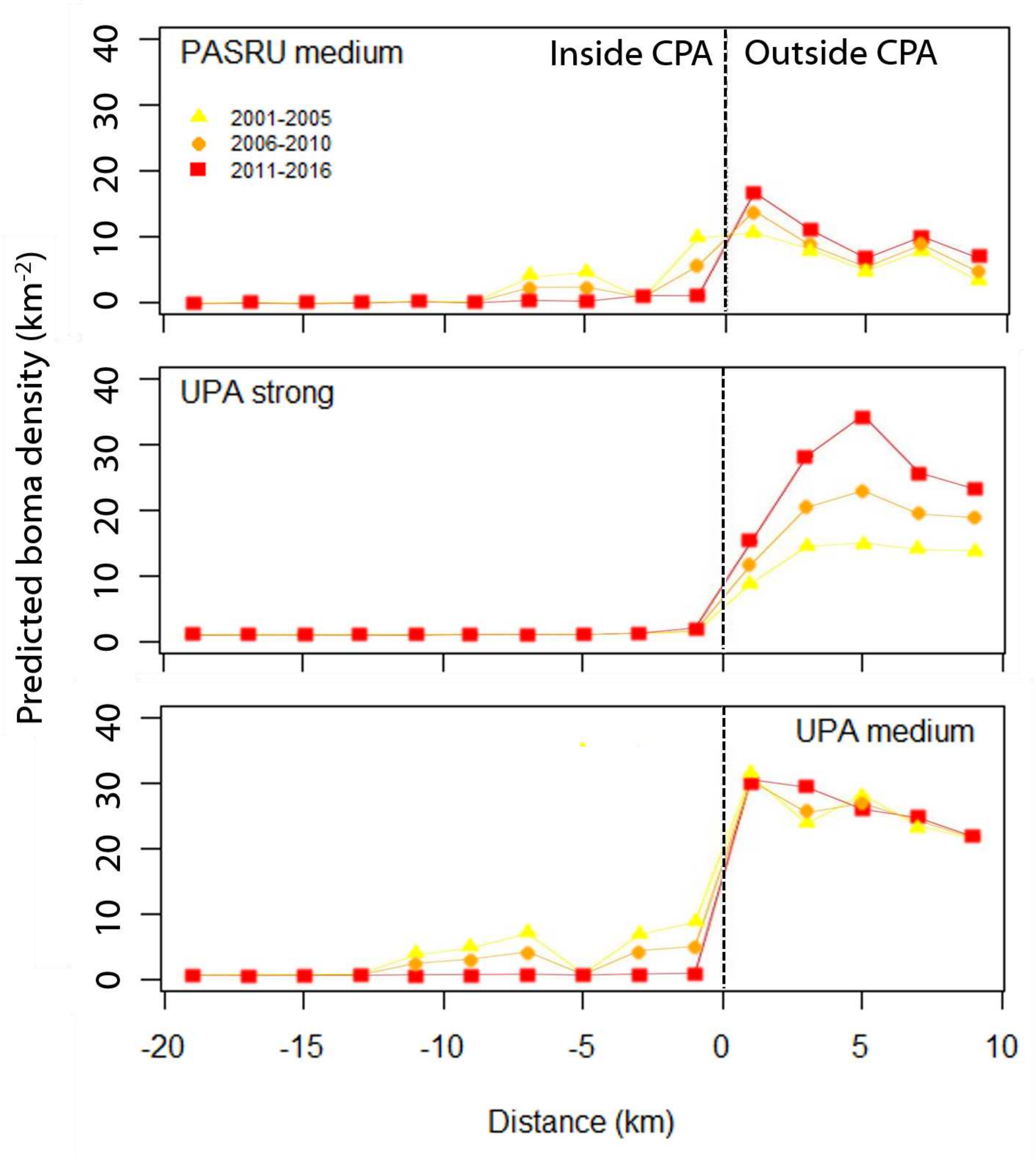


Fig. S25. The change in predicted boma density across the border of the CPA. Panels represent borders between the Core Protected Areas (CPA) and Protected Areas with Sustainable Resource Use (PASRU medium; top), the boundary with the unprotected area with medium border control (UPA medium; bottom) and with strong border control (UPA strong; middle). Different colors represent boma densities during 2001-2005 (yellow), 2006-2010 (orange) and 2011-2016 (red). Negative distances refer to inside the CPA, whereas positive distances to the village lands (UPA and PASRU).

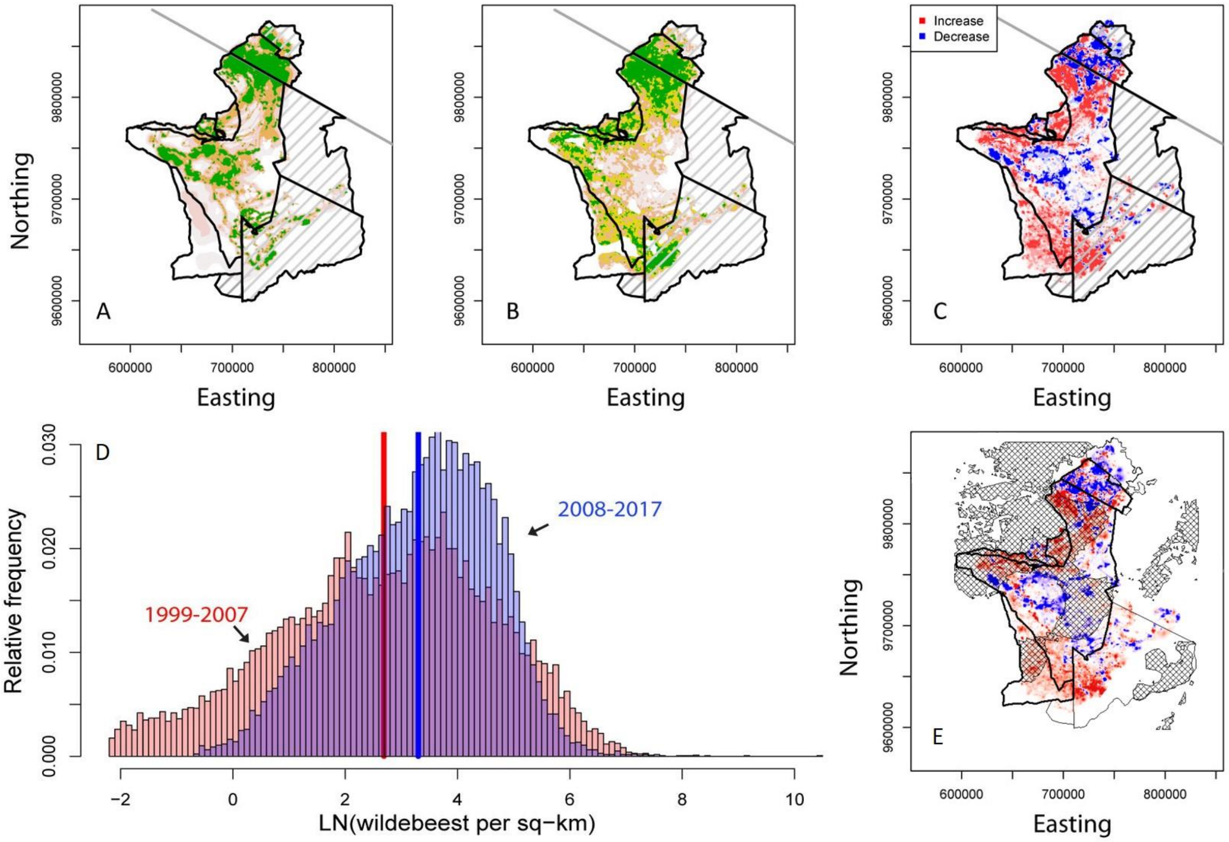


Fig. S26. Changes in wildebeest utilization through time and space. (A-B) Distribution patterns of wildebeest in the Serengeti-Mara Ecosystem during two time periods (1999-2007 and 2008-2017) (coordinate reference: UTM 36 south; Datum: Arc 1960; EPSG: 21036), as inferred from GPS collar data and Brownian Bridge Movement Models. Darker shading indicates greater intensity of use. (C) Absolute change in wildebeest utilization across the Serengeti over the last two decades (1999-2007 versus 2008-2017). Red indicates significantly increasing utilization, blue indicates significantly decreasing utilization, and color intensity corresponds to large (dark) versus small (light) changes. Grey hatched areas are Protected Areas of Sustainable Resource Use (PASRU) inhabited by people and grazed by livestock. (D) Shift in relative frequency distribution of radio-collared wildebeest occupancy (observations per 1 km2 grid cell) over the last two decades. In the last decade, the frequency of 1-km^2 grid cells visited by wildebeest has significantly changed relative to the previous decade (Kolmogorov-Smirnov 2-sided test: $D = 0.338$, $p<0.001$). Specifically, very highly visited grid cells (> 200 observations/km2) are observed less, but occurrence at low densities (less then 8 observations /km2) has declined. The vertical lines reflect the mean density of occupied grid cells in either period, reflecting an approximate doubling of the mean grid cell density (approximately 13 animals in 1999-2007 to more than 24 in 2008-2017 after anti-log conversion). (E) Wildebeest have shifted to use habitats of lower quality within the core protected areas, especially in the northern part of the ecosystem. Areas of low plant tissue nitrogen content (<0.9% N, hatched area) are overlaid on the change in habitat use of radio-collared wildebeest over the last two decades (C)). An exception is the increase in use of the southern shortgrass plains in eastern Ngorongoro Conservation Area. The landscape map for aboveground vegetation N concentration was derived through sampling 148 sites across the whole ecosystem, and interpolating the results using cokriging with a range of environmental predictors. See (*81*), Fig. 3a for further methods about how the plant N concentration map was derived.

Fig. S27. Images of livestock paths at the border of Maswa Game Reserve. Images were taken by drone (top, photo M.P. Veldhuis and E. Kihwele) and satellite (bottom, image Google Earth (*74*)).

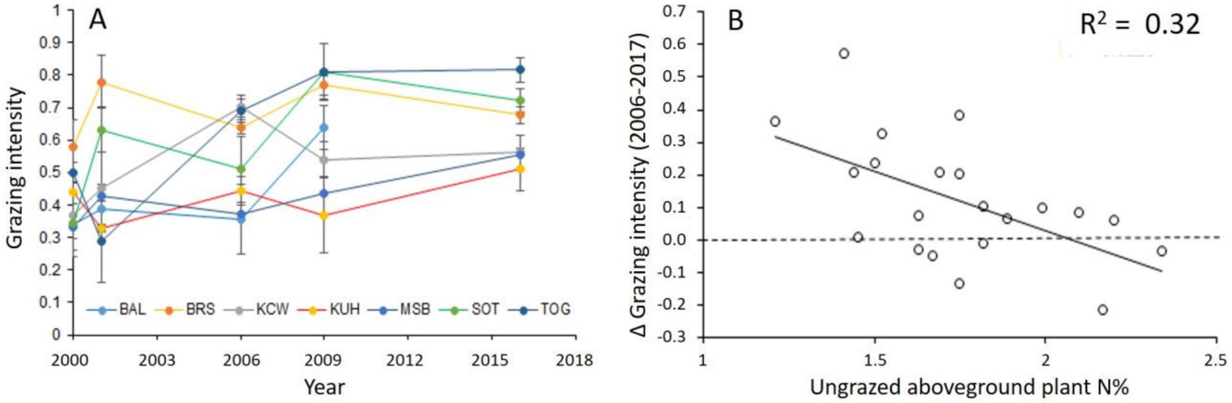


Fig. S28. Temporal trend in estimated grazing intensity for seven different sites (for locations see Fig. S12). (A) Grazing intensity (mean ± SE) is calculated from the exclosure biomass measurements at the end of the growing season: GI = 1-(biomass outside)/(biomass inside). Each mean is for 3 paired fenced and control plots at each site. Grazing intensity increased significantly across years ($P = 0.006$) , especially at high rainfall, high ungrazed biomass sites, as indicated by significant Site x Year and Rainfall x Year interactions (P <0.005) (Table S7). (B) Grazing intensities increased most in area of low plant quality. Difference in grazing intensity between 2006 and 2017 in the LTGE experiment associated with the mean %N of ungrazed aboveground plant tissue measured in 2017, an indicator of site-driven plant quality. N = 21, P < 0.01.

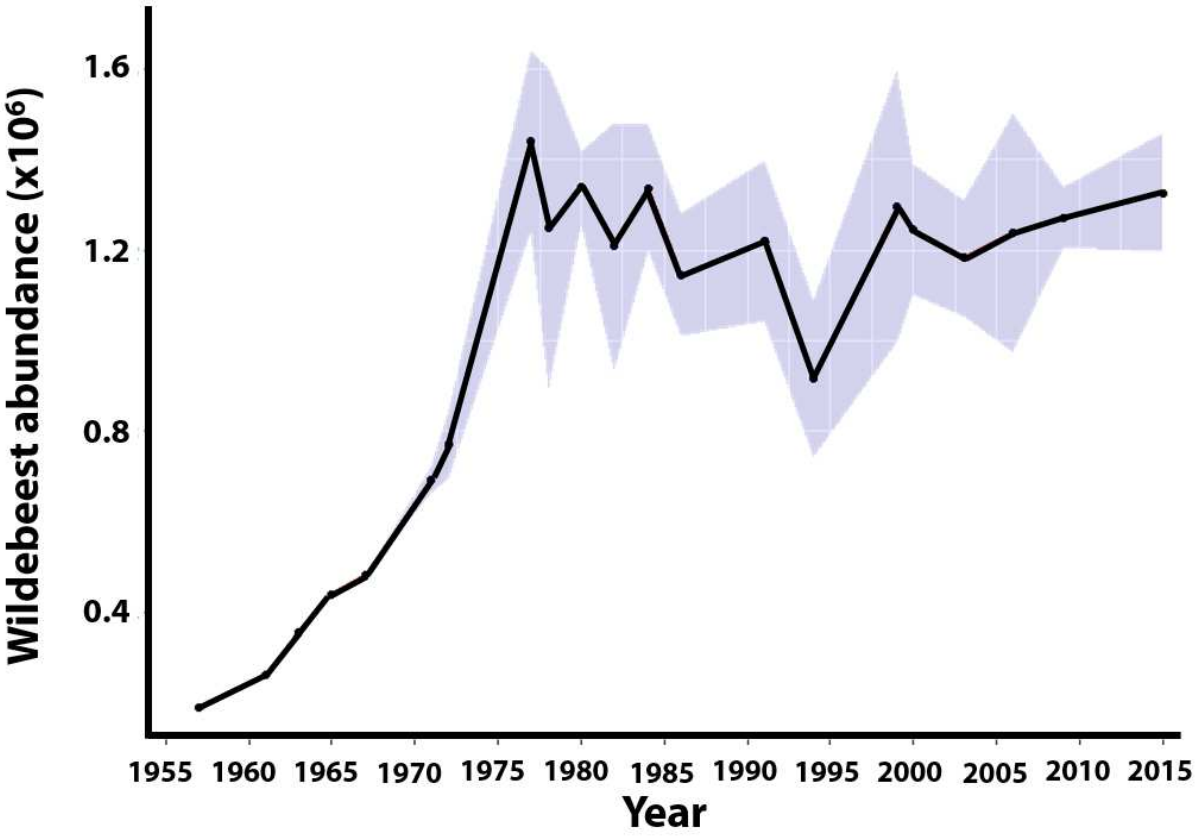


Fig. S29. The abundance of Serengeti wildebeest from 1957 to 2015 as estimated from aerial censuses. There is no evidence to suggest that the population of wildebeest has declined in 5 recent years despite human encroachment, extensive illegal offtakes, and infrastructure development. Shaded areas represent the standard error around each census point. Data from Conservation Information Monitoring Unit of the Tanzania Wildlife Research Institute.

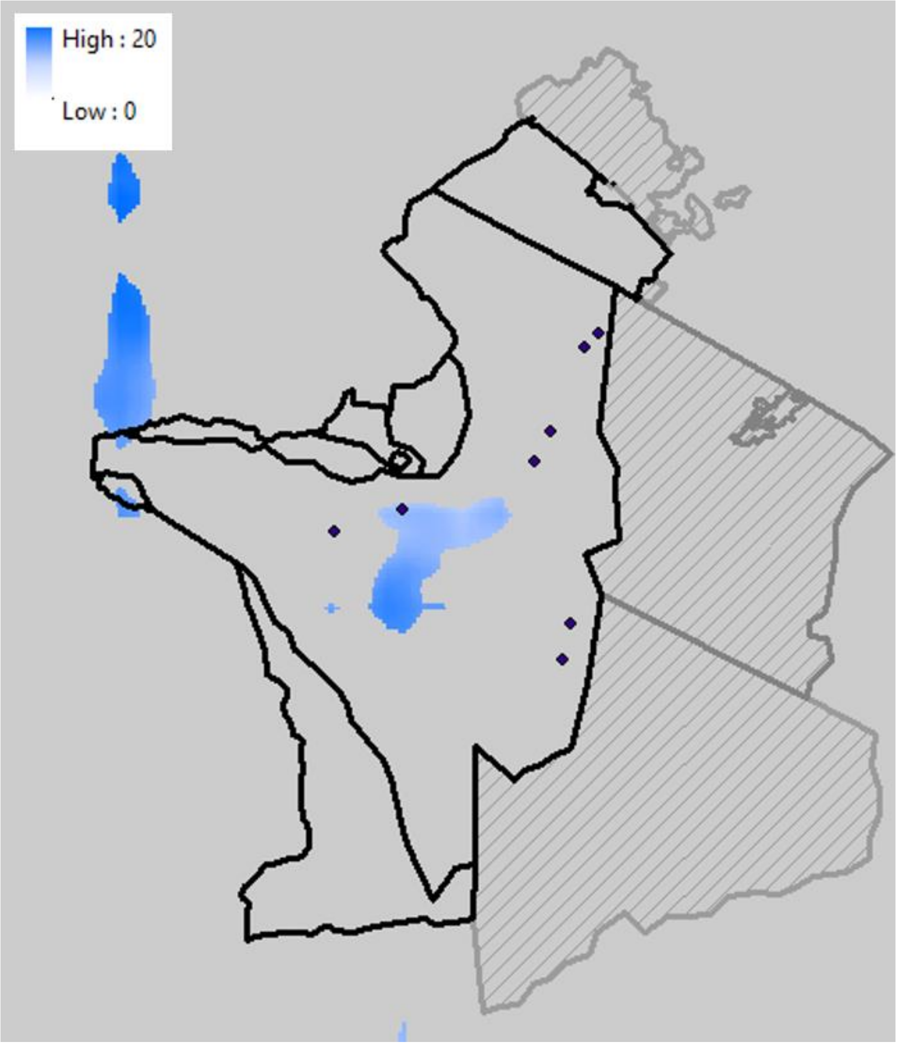


Fig. S30. Changes in mean annual rainfall across the Greater Serengeti-Mara Ecosystem between 2001 and 2016. Changes are shown as the slope of pixel-based linear regression between annual rainfall (mm/year, CHIRPS (*70*)) and years (2001 and 2016). Grey areas represent non-significant changes ($p > 0.05$).

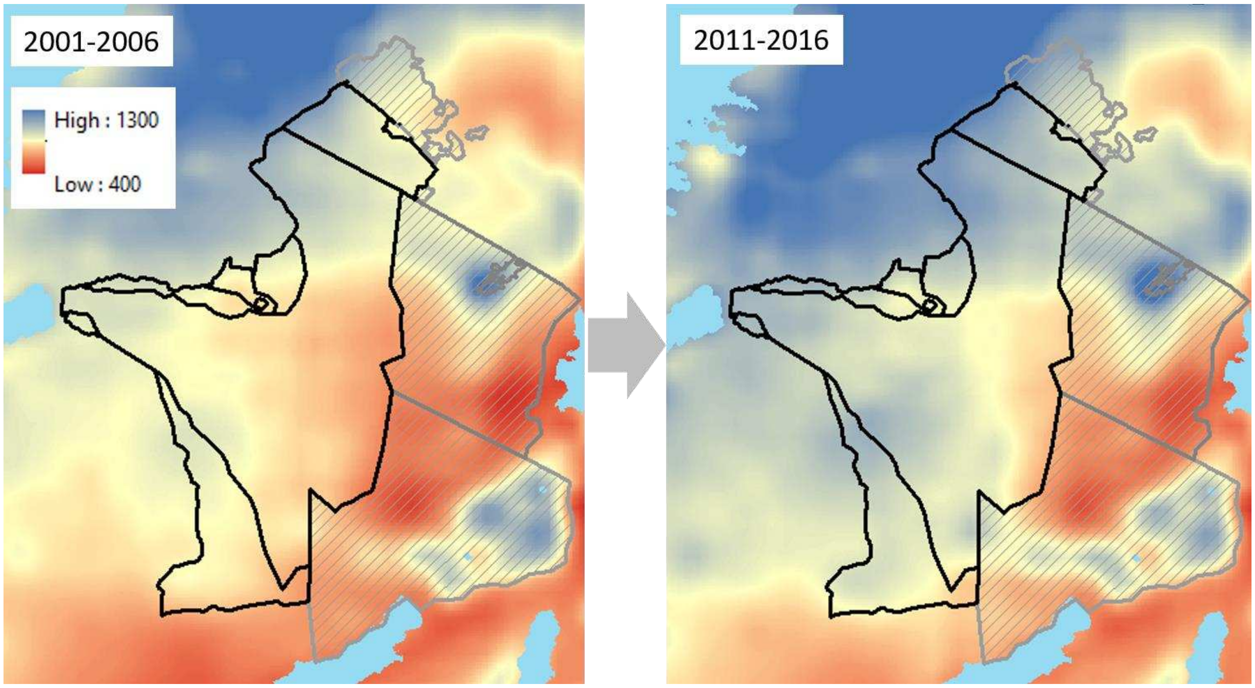


Fig. S31. Mean annual rainfall between 2001-2006 (left) and 2011-2016 (right). Annual rainfall (mm/year) estimates following the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS)(*70*).

Table S1. Conservation and management strategies and characteristics of protected areas in the Greater Serengeti-Mara Ecosystem.

Conservation management type	IUCN category	Human settlement allowed	Agriculture and/or forestry	Livestock grazing	Border control class	Protected areas in the GSME	Category
A	IUCN category II National park or national reserve	No	No	Prohibited	Medium	Serengeti NP, Maasai Mara NR	Core Protected Areas (CPA)
B	IUCN category II-like Area managed to complement the adjacent national park, with similar management	No	No	Prohibited	Strong	Grumeti GR, Ikorongo GR, Ikona WMA	CPA
C	IUCN category II-like Area managed to complement the adjacent national park, with similar management	No	No	Prohibited	Medium	Maswa GR, Kijereshi GR	CPA
D	IUCN category V – protected landscape with characteristic interaction of people and nature with traditional management practices incl. community conservancies	Regulated	No	Regulated	Medium	Ngorongoro CA, Maasai Mara Conservancies	Protected Area with Sustainable Resource Use (PASRU)
E	IUCN category VI – or VI Habitat/species management areas or Protected area with sustainable natural resource management	Yes	Regulated	Little regulation	Low	Loliondo GCA, Makao WMA	PASRU
F	Not a protected area	Unrestricted	Mostly unregulated, sometimes village land use management plans	Unregulated sometimes village land use management plans	NA	All other areas	UnProtected Area (UPA)

Table S2. The amount of stable agriculture and natural habitats newly-converted to agriculture around the Serengeti-Mara Ecosystem. Stable agriculture and agricultural conversion are presented as a percent of total land classified in each of the three change periods. Please note that there are slight discrepancies between the periods resulting from differences in cloud cover.

Cover type	1984-2003	2003-2018	1984-2018
Stable agriculture	37.0	46.2	37.0
Agricultural conversion	9.2	10.2	17.0

Table S3. The percent of agricultural conversion around the Serengeti-Mara Ecosystem. Agricultural conversion in each time period is presented as a percent of the total land area in each region considered in Fig. S2. Please note that there are slight discrepancies between the periods resulting from differences in cloud cover.

5

	1984-2003		2003-2018		1984-2018	
Region	Stable	Conversion	Stable	Conversion	Stable	Conversion
Simiyu	70.1	11.8	81.9	7.8	70.1	17.4
Mara	54.4	20.7	75.1	10.7	54.4	25.9
Loliondo	1.9	1.4	3.3	6.2	1.9	6.6
Ngorongoro	1.6	0.5	2.1	5.4	1.6	5.5
Narok	4.7	2.4	7.1	20.9	4.7	22.0
Migori	70.6	11.2	81.8	9.6	70.6	19.0
Total conversion	37.0	9.2	46.2	10.2	37.0	17.0

Table S4. Model outcomes of the trends in herbivore densities as a function of distance to the border of the Masai Mara National Reserve (MMNR, Core Protected Area) for four decades (1977-2016)(Fig. S16).

Species	Season	Parameter	Parameter Type	Decade	DF	Estimate	Standard Error	t Value	Approx Pr >	Model Type	Link
Buffalo	Both	Intercept	Model		1	4.751036	0.1113	42.69	<0.0001	ZINB	Logistic
Buffalo	Both	decade 1970s	Model	1970s	1	0.886901	0.200898	4.41	<0.0001	ZINB	Logistic
Buffalo	Both	Dist*decade 1970s	Model	1970s	1	-0.041058	0.00982	-4.18	<0.0001	ZINB	Logistic
Buffalo	Both	Dist*decade 1980s	Model	1980s	1	-0.092612	0.016076	-5.76	<0.0001	ZINB	Logistic
Buffalo	Both	Dist*decade 2000s	Model	2000s	1	-0.055916	0.010897	-5.13	<0.0001	ZINB	Logistic
Buffalo	Both	Dist*Dist*decade 1980s	Model	1980s	1	0.000829	0.000323	2.57	0.0102	ZINB	Logistic
Buffalo	Both	Dist*Dist*decade 1990s	Model	1990s	1	-0.002408	0.000476	-5.06	<0.0001	ZINB	Logistic
Buffalo	Both	Inf_Intercept	ZeroModel		1	-1.257221	0.247186	-5.09	<0.0001	ZINB	Logistic
Buffalo	Both	Inf_decade 1980s	ZeroModel	1980s	1	-1.770565	0.51758	-3.42	0.0006	ZINB	Logistic
Buffalo	Both	Inf_decade 1990s	ZeroModel	1990s	1	0.991264	0.324936	3.05	0.0023	ZINB	Logistic
Buffalo	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.081446	0.010834	7.52	<0.0001	ZINB	Logistic
Buffalo	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.095526	0.013745	6.95	<0.0001	ZINB	Logistic
Buffalo	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	0.063237	0.013919	4.54	<0.0001	ZINB	Logistic
Buffalo	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.177703	0.030788	5.77	<0.0001	ZINB	Logistic

Buffalo	Both	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	-0.001832	0.000595	-3.08	0.0021	ZINB	Logistic
Buffalo	Both	_Alpha	Internal		1	2.791442	0.253153	11.03	<0.0001	ZINB	Logistic
Elephant	Both	Intercept	Model		1	2.636135	0.118506	22.24	<0.0001	ZINB	Logistic
Elephant	Both	decade 1970s	Model	1970s	1	0.76893	0.195597	3.93	<0.0001	ZINB	Logistic
Elephant	Both	decade 1980s	Model	1980s	1	0.299322	0.174698	1.71	0.0866	ZINB	Logistic
Elephant	Both	decade 1990s	Model	1990s	1	0.670395	0.179439	3.74	0.0002	ZINB	Logistic
Elephant	Both	Dist*decade 1980s	Model	1980s	1	-0.030292	0.011579	-2.62	0.0089	ZINB	Logistic
Elephant	Both	Inf_Intercept	ZeroModel		1	-0.74674	0.194054	-3.85	0.0001	ZINB	Logistic
Elephant	Both	Inf_decade 1970s	ZeroModel	1970s	1	0.857609	0.340192	2.52	0.0117	ZINB	Logistic
Elephant	Both	Inf_decade 1990s	ZeroModel	1990s	1	0.621061	0.284172	2.19	0.0289	ZINB	Logistic
Elephant	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.2682	0.050211	5.34	<0.0001	ZINB	Logistic
Elephant	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.18371	0.030455	6.03	<0.0001	ZINB	Logistic
Elephant	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	0.091219	0.013967	6.53	<0.0001	ZINB	Logistic
Elephant	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.096984	0.012515	7.75	<0.0001	ZINB	Logistic
Elephant	Both	Inf_Dist*Dist*decade 1980s	ZeroModel	1980s	1	-0.001818	0.00065	-2.8	0.0051	ZINB	Logistic
Elephant	Both	_Alpha	Internal		1	1.070526	0.131436	8.14	<0.0001	ZINB	Logistic
Topi	Both	Intercept	Model		1	4.194621	0.115142	36.43	<0.0001	ZINB	Logistic
Topi	Both	decade 1970s	Model	1970s	1	1.492165	0.155849	9.57	<0.0001	ZINB	Logistic

Topi	Both	decade 1980s	Model	1980s	1	1.125714	0.16136	6.98	<0.0001	ZINB	Logistic
Topi	Both	decade 1990s	Model	1990s	1	0.653443	0.173728	3.76	0.0002	ZINB	Logistic
Topi	Both	Dist*decade 1980s	Model	1980s	1	-0.059484	0.006837	-8.7	<0.0001	ZINB	Logistic
Topi	Both	Dist*decade 2000s	Model	2000s	1	-0.036574	0.006911	-5.29	<0.0001	ZINB	Logistic
Topi	Both	Dist*Dist*decade 1970s	Model	1970s	1	-0.001186	0.000134	-8.87	<0.0001	ZINB	Logistic
Topi	Both	Dist*Dist*decade 1990s	Model	1990s	1	-0.002878	0.000403	-7.14	<0.0001	ZINB	Logistic
Topi	Both	Inf_Intercept	ZeroModel		1	-1.883921	0.173939	-10.83	<0.0001	ZINB	Logistic
Topi	Both	Inf_decade 1980s	ZeroModel	1980s	1	-1.564389	0.497614	-3.14	0.0017	ZINB	Logistic
Topi	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.077901	0.007919	9.84	<0.0001	ZINB	Logistic
Topi	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.110462	0.014362	7.69	<0.0001	ZINB	Logistic
Topi	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.128878	0.021678	5.95	<0.0001	ZINB	Logistic
Topi	Both	Inf_Dist*Dist*decade 1990s	ZeroModel	1990s	1	0.003153	0.000463	6.81	<0.0001	ZINB	Logistic
Topi	Both	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	-0.000813	0.000463	-1.76	0.0791	ZINB	Logistic
Topi	Both	_Alpha	Internal		1	1.279355	0.087622	14.6	<0.0001	ZINB	Logistic
Impala	Both	Intercept	Model		1	5.306805	0.057896	91.66	<0.0001	ZINB	Logistic
Impala	Both	decade 1970s	Model	1970s	1	0.743618	0.100602	7.39	<0.0001	ZINB	Logistic
Impala	Both	decade 1980s	Model	1980s	1	0.417561	0.09793	4.26	<0.0001	ZINB	Logistic

Impala	Both	Dist*Dist*decade 1970s	Model	1970s	1	-0.000414	0.00005053	-8.2	<0.0001	ZINB	Logistic
Impala	Both	Dist*Dist*decade 1980s	Model	1980s	1	-0.00047	0.000048696	-9.65	<0.0001	ZINB	Logistic
Impala	Both	Dist*Dist*decade 1990s	Model	1990s	1	-0.000392	0.000049402	-7.94	<0.0001	ZINB	Logistic
Impala	Both	Dist*Dist*decade 2000s	Model	2000s	1	-0.000647	0.000046781	-13.83	<0.0001	ZINB	Logistic
Impala	Both	Inf_Intercept	ZeroModel		1	-2.696466	0.151525	-17.8	<0.0001	ZINB	Logistic
Impala	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.026233	0.006037	4.35	<0.0001	ZINB	Logistic
Impala	Both	Inf_Dist*Dist*decade 1990s	ZeroModel	1990s	1	0.000367	0.000113	3.26	0.0011	ZINB	Logistic
Impala	Both	_Alpha	Internal		1	0.969617	0.045281	21.41	<0.0001	ZINB	Logistic
Hartebeest	Both	Intercept	Model		1	2.427562	0.119737	20.27	<0.0001	ZINB	Logistic
Hartebeest	Both	decade 1970s	Model	1970s	1	1.517363	0.170382	8.91	<0.0001	ZINB	Logistic
Hartebeest	Both	decade 1980s	Model	1980s	1	0.992601	0.152482	6.51	<0.0001	ZINB	Logistic
Hartebeest	Both	decade 1990s	Model	1990s	1	0.66816	0.179066	3.73	0.0002	ZINB	Logistic
Hartebeest	Both	Dist*decade 1970s	Model	1970s	1	-0.021131	0.005159	-4.1	<0.0001	ZINB	Logistic
Hartebeest	Both	Dist*decade 1990s	Model	1990s	1	-0.010319	0.006586	-1.57	0.1172	ZINB	Logistic
Hartebeest	Both	Inf_Intercept	ZeroModel		1	-0.868086	0.177464	-4.89	<0.0001	ZINB	Logistic
Hartebeest	Both	Inf_decade 1970s	ZeroModel	1970s	1	-0.787596	0.315288	-2.5	0.0125	ZINB	Logistic
Hartebeest	Both	Inf_decade 1980s	ZeroModel	1980s	1	-1.707212	0.448694	-3.8	0.0001	ZINB	Logistic

Hartebeest	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.047067	0.007707	6.11	<0.0001	ZINB	Logistic
Hartebeest	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.083745	0.012184	6.87	<0.0001	ZINB	Logistic
Hartebeest	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	0.053694	0.007348	7.31	<0.0001	ZINB	Logistic
Hartebeest	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.065468	0.008362	7.83	<0.0001	ZINB	Logistic
Hartebeest	Both	_Alpha	Internal		1	1.311834	0.11731	11.18	<0.0001	ZINB	Logistic
Warthog	Both	Intercept	Model		1	2.359403	0.110734	21.31	<0.0001	ZINB	Logistic
Warthog	Both	decade 1970s	Model	1970s	1	1.466369	0.143786	10.2	<0.0001	ZINB	Logistic
Warthog	Both	decade 1980s	Model	1980s	1	1.230725	0.142135	8.66	<0.0001	ZINB	Logistic
Warthog	Both	decade 1990s	Model	1990s	1	0.306494	0.156113	1.96	0.0496	ZINB	Logistic
Warthog	Both	Dist*decade 1970s	Model	1970s	1	-0.040005	0.003568	-11.21	<0.0001	ZINB	Logistic
Warthog	Both	Dist*decade 1980s	Model	1980s	1	-0.050977	0.003838	-13.28	<0.0001	ZINB	Logistic
Warthog	Both	Dist*decade 1990s	Model	1990s	1	-0.020033	0.005758	-3.48	0.0005	ZINB	Logistic
Warthog	Both	Dist*decade 2000s	Model	2000s	1	-0.030134	0.006713	-4.49	<0.0001	ZINB	Logistic
Warthog	Both	Inf_Intercept	ZeroModel		1	-1.008816	0.178705	-5.65	<0.0001	ZINB	Logistic
Warthog	Both	Inf_decade 1970s	ZeroModel	1970s	1	-3.027237	0.945235	-3.2	0.0014	ZINB	Logistic
Warthog	Both	Inf_decade 1980s	ZeroModel	1980s	1	-7.752746	2.964983	-2.61	0.0089	ZINB	Logistic
Warthog	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.172321	0.053941	3.19	0.0014	ZINB	Logistic
Warthog	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.429081	0.166094	2.58	0.0098	ZINB	Logistic

Warthog	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	0.097309	0.019565	4.97	<0.0001	ZINB	Logistic
Warthog	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.063228	0.008674	7.29	<0.0001	ZINB	Logistic
Warthog	Both	Inf_Dist*Dist*decade 1970s	ZeroModel	1970s	1	-0.001803	0.000705	-2.56	0.0106	ZINB	Logistic
Warthog	Both	Inf_Dist*Dist*decade 1980s	ZeroModel	1980s	1	-0.00506	0.00219	-2.31	0.0208	ZINB	Logistic
Warthog	Both	Inf_Dist*Dist*decade 1990s	ZeroModel	1990s	1	-0.000812	0.000376	-2.16	0.0307	ZINB	Logistic
Warthog	Both	_Alpha	Internal		1	0.908973	0.070518	12.89	<0.0001	ZINB	Logistic
Waterbuck	Both	Intercept	Model		1	2.553786	0.128703	19.84	<0.0001	ZINB	Logistic
Waterbuck	Both	Dist*decade 1970s	Model	1970s	1	-0.085099	0.020314	-4.19	<0.0001	ZINB	Logistic
Waterbuck	Both	Dist*decade 1980s	Model	1980s	1	-0.071282	0.014975	-4.76	<0.0001	ZINB	Logistic
Waterbuck	Both	Dist*decade 1990s	Model	1990s	1	-0.029301	0.014201	-2.06	0.0391	ZINB	Logistic
Waterbuck	Both	Dist*Dist*decade 1970s	Model	1970s	1	0.000993	0.0005	1.98	0.0473	ZINB	Logistic
Waterbuck	Both	Dist*Dist*decade 2000s	Model	2000s	1	-0.000871	0.000365	-2.38	0.0172	ZINB	Logistic
Waterbuck	Both	Inf_Intercept	ZeroModel		1	1.049468	0.203886	5.15	<0.0001	ZINB	Logistic
Waterbuck	Both	Inf_decade 1970s	ZeroModel	1970s	1	-1.30845	0.30976	-4.22	<0.0001	ZINB	Logistic
Waterbuck	Both	Inf_decade 1980s	ZeroModel	1980s	1	-1.949136	0.390403	-4.99	<0.0001	ZINB	Logistic
Waterbuck	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.063998	0.012957	4.94	<0.0001	ZINB	Logistic
Waterbuck	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.08561	0.019851	4.31	<0.0001	ZINB	Logistic

Waterbuck	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	0.048192	0.013343	3.61	0.0003	ZINB	Logistic
Waterbuck	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.129175	0.03132	4.12	<0.0001	ZINB	Logistic
Waterbuck	Both	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	-0.001749	0.000708	-2.47	0.0135	ZINB	Logistic
Waterbuck	Both	_Alpha	Internal		1	2.066091	0.433565	4.77	<0.0001	ZINB	Logistic
Wildebeest	Dry	Intercept	Model		1	6.854724	0.134758	50.87	<0.0001	ZINB	Logistic
Wildebeest	Dry	decade 1970s	Model	1970s	1	0.919394	0.183754	5	<0.0001	ZINB	Logistic
Wildebeest	Dry	decade 1980s	Model	1980s	1	1.013387	0.186204	5.44	<0.0001	ZINB	Logistic
Wildebeest	Dry	decade 1990s	Model	1990s	1	0.385266	0.187842	2.05	0.0403	ZINB	Logistic
Wildebeest	Dry	Inf_Intercept	ZeroModel		1	-1.873859	0.179524	-10.44	<0.0001	ZINB	Logistic
Wildebeest	Dry	Inf_Dist*Dist*decade 1970s	ZeroModel	1970s	1	-18.273774	41.120518	-0.44	0.6568	ZINB	Logistic
Wildebeest	Dry	_Alpha	Internal		1	3.832079	0.217171	17.65	<0.0001	ZINB	Logistic
Zebra	Dry	Intercept	Model		1	5.801697	0.050228	115.51	<0.0001	ZINB	Logistic
Zebra	Dry	Dist*decade 2000s	Model	2000s	1	-0.102586	0.012065	-8.5	<0.0001	ZINB	Logistic
Zebra	Dry	Dist*Dist*decade 2000s	Model	2000s	1	0.000958	0.000239	4.01	<0.0001	ZINB	Logistic
Zebra	Dry	Inf_Intercept	ZeroModel		1	-1.688153	0.124062	-13.61	<0.0001	ZINB	Logistic
Zebra	Dry	Inf_Dist*Dist*decade 1980s	ZeroModel	1980s	0	-1101.096615	.	.	.	ZINB	Logistic
Zebra	Dry	_Alpha	Internal		1	1.957421	0.102002	19.19	<0.0001	ZINB	Logistic
Giraffe	Both	Intercept	Model		1	2.487854	0.065751	37.84	<0.0001	ZINB	Logistic

Giraffe	Both	decade 1970s	Model	1970s	1	0.828591	0.118448	7	<0.0001	ZINB	Logistic
Giraffe	Both	decade 1980s	Model	1980s	1	0.27746	0.115269	2.41	0.0161	ZINB	Logistic
Giraffe	Both	Dist*decade 1970s	Model	1970s	1	0.022295	0.008625	2.58	0.0097	ZINB	Logistic
Giraffe	Both	Dist*decade 1980s	Model	1980s	1	0.033234	0.00849	3.91	<0.0001	ZINB	Logistic
Giraffe	Both	Dist*Dist*decade 1970s	Model	1970s	0	-0.000484	.	.	.	ZINB	Logistic
Giraffe	Both	Dist*Dist*decade 1980s	Model	1980s	0	-0.000668	.	.	.	ZINB	Logistic
Giraffe	Both	Inf_Intercept	ZeroModel		1	-0.430189	0.19843	-2.17	0.0302	ZINB	Logistic
Giraffe	Both	Inf_decade 1970s	ZeroModel	1970s	1	-2.273593	0.443171	-5.13	<0.0001	ZINB	Logistic
Giraffe	Both	Inf_decade 1980s	ZeroModel	1980s	1	-5.954579	2.135434	-2.79	0.0053	ZINB	Logistic
Giraffe	Both	Inf_decade 1990s	ZeroModel	1990s	1	-0.331365	0.291826	-1.14	0.2562	ZINB	Logistic
Giraffe	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.037653	0.009322	4.04	<0.0001	ZINB	Logistic
Giraffe	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.281642	0.117969	2.39	0.017	ZINB	Logistic
Giraffe	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	0.020958	0.006377	3.29	0.001	ZINB	Logistic
Giraffe	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.027279	0.006369	4.28	<0.0001	ZINB	Logistic
Giraffe	Both	Inf_Dist*Dist*decade 1980s	ZeroModel	1980s	1	-0.003551	0.001539	-2.31	0.021	ZINB	Logistic
Giraffe	Both	_Alpha	Internal		1	0.953526	0.06762	14.1	<0.0001	ZINB	Logistic
Eland	Both	Intercept	Model		1	2.475346	0.090989	27.2	<0.0001	ZINB	Logistic

Eland	Both	decade 1970s	Model	1970s	1	0.943876	0.127806	7.39	<0.0001	ZINB	Logistic
Eland	Both	decade 1980s	Model	1980s	1	0.701689	0.164194	4.27	<0.0001	ZINB	Logistic
Eland	Both	Dist*decade 1980s	Model	1980s	1	-0.015383	0.004167	-3.69	0.0002	ZINB	Logistic
Eland	Both	Inf_Intercept	ZeroModel		1	-0.759664	0.12415	-6.12	<0.0001	ZINB	Logistic
Eland	Both	Inf_decade 1990s	ZeroModel	1990s	1	1.246337	0.18352	6.79	<0.0001	ZINB	Logistic
Eland	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	-0.011267	0.006998	-1.61	0.1074	ZINB	Logistic
Eland	Both	Inf_Dist*decade 2000s	ZeroModel	2000s	1	0.103695	0.018086	5.73	<0.0001	ZINB	Logistic
Eland	Both	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	-0.001241	0.000338	-3.67	0.0002	ZINB	Logistic
Eland	Both	_Alpha	Internal		1	1.392657	0.131682	10.58	<0.0001	ZINB	Logistic
Thomson's gazelle	Both	Intercept	Model		1	5.621975	0.061829	90.93	<0.0001	ZINB	Logistic
Thomson's gazelle	Both	decade 1970s	Model	1970s	1	0.476865	0.09856	4.84	<0.0001	ZINB	Logistic
Thomson's gazelle	Both	Dist*decade 2000s	Model	2000s	1	-0.028727	0.002937	-9.78	<0.0001	ZINB	Logistic
Thomson's gazelle	Both	Dist*Dist*decade 1980s	Model	1980s	1	-0.000135	0.000058375	-2.32	0.0205	ZINB	Logistic
Thomson's gazelle	Both	Dist*Dist*decade 1990s	Model	1990s	1	-0.00048	0.000056221	-8.54	<0.0001	ZINB	Logistic
Thomson's gazelle	Both	Inf_Intercept	ZeroModel		1	-2.341682	0.130296	-17.97	<0.0001	ZINB	Logistic
Thomson's gazelle	Both	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	0.000308	0.00011	2.8	0.0052	ZINB	Logistic

Thomson's gazelle	Both	_Alpha	Internal		1	1.368437	0.067181	20.37	<0.0001	ZINB	Logistic
Ostrich	Both	Intercept	Model		1	1.108509	0.134076	8.27	<0.0001	ZINB	Logistic
Ostrich	Both	decade 1970s	Model	1970s	1	0.688791	0.176229	3.91	<0.0001	ZINB	Logistic
Ostrich	Both	decade 1980s	Model	1980s	1	0.453023	0.19957	2.27	0.0232	ZINB	Logistic
Ostrich	Both	decade 1990s	Model	1990s	1	0.698057	0.267998	2.6	0.0092	ZINB	Logistic
Ostrich	Both	Dist*decade 1980s	Model	1980s	1	0.023169	0.01603	1.45	0.1483	ZINB	Logistic
Ostrich	Both	Dist*decade 1990s	Model	1990s	1	0.001864	0.006179	0.3	0.7629	ZINB	Logistic
Ostrich	Both	Dist*Dist*decade 1980s	Model	1980s	1	-0.000564	0.000309	-1.82	0.068	ZINB	Logistic
Ostrich	Both	Inf_Intercept	ZeroModel		1	-0.416051	0.209554	-1.99	0.0471	ZINB	Logistic
Ostrich	Both	Inf_decade 1990s	ZeroModel	1990s	1	1.430573	0.282323	5.07	<0.0001	ZINB	Logistic
Ostrich	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	0.1075	0.022235	4.83	<0.0001	ZINB	Logistic
Ostrich	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	0.176043	0.039628	4.44	<0.0001	ZINB	Logistic
Ostrich	Both	Inf_Dist*Dist*decade 1970s	ZeroModel	1970s	1	-0.001761	0.000435	-4.05	<0.0001	ZINB	Logistic
Ostrich	Both	Inf_Dist*Dist*decade 1980s	ZeroModel	1980s	1	-0.004082	0.001122	-3.64	0.0003	ZINB	Logistic
Ostrich	Both	Inf_Dist*Dist*decade 1990s	ZeroModel	1990s	1	-0.00051	0.000158	-3.22	0.0013	ZINB	Logistic
Ostrich	Both	_Alpha	Internal		1	1.490277	0.261748	5.69	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Intercept	Model		1	3.395445	0.057347	59.21	<0.0001	ZINB	Logistic

Grant's gazelle	Both	decade 1990s	Model	1990s	1	0.194774	0.119266	1.63	0.1024	ZINB	Logistic
Grant's gazelle	Both	Dist*decade 1970s	Model	1970s	1	0.068281	0.007904	8.64	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Dist*decade 1980s	Model	1980s	1	0.046933	0.007707	6.09	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Dist*decade 1990s	Model	1990s	1	0.046213	0.008997	5.14	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Dist*decade 2000s	Model	2000s	1	0.032025	0.008418	3.8	0.0001	ZINB	Logistic
Grant's gazelle	Both	Dist*Dist*decade 1970s	Model	1970s	1	-0.000662	0.000152	-4.36	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Dist*Dist*decade 1980s	Model	1980s	1	-0.000434	0.000152	-2.86	0.0043	ZINB	Logistic
Grant's gazelle	Both	Dist*Dist*decade 1990s	Model	1990s	1	-0.00069	0.000168	-4.11	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Dist*Dist*decade 2000s	Model	2000s	1	-0.000497	0.000167	-2.98	0.0029	ZINB	Logistic
Grant's gazelle	Both	Inf_Intercept	ZeroModel		1	-1.00464	0.105526	-9.52	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Inf_decade 1980s	ZeroModel	1980s	1	-0.615728	0.287124	-2.14	0.032	ZINB	Logistic
Grant's gazelle	Both	Inf_Dist*decade 1970s	ZeroModel	1970s	1	-0.052055	0.011404	-4.56	<0.0001	ZINB	Logistic
Grant's gazelle	Both	Inf_Dist*decade 1980s	ZeroModel	1980s	1	-0.03281	0.012572	-2.61	0.0091	ZINB	Logistic
Grant's gazelle	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	1	-0.008069	0.005502	-1.47	0.1425	ZINB	Logistic

Grant's gazelle	Both	_Alpha	Internal		1	0.838819	0.044679	18.77	<0.0001	ZINB	Logistic
Zebra	Wet	Intercept	Model		1	4.912284	0.099883	49.18	<0.0001	ZINB	Logistic
Zebra	Wet	decade 1970s	Model	1970s	1	0.600568	0.157558	3.81	0.0001	ZINB	Logistic
Zebra	Wet	decade 1980s	Model	1980s	1	0.302486	0.145818	2.07	0.038	ZINB	Logistic
Zebra	Wet	Dist*decade 1970s	Model	1970s	1	0.010463	0.003639	2.88	0.004	ZINB	Logistic
Zebra	Wet	Dist*decade 1980s	Model	1980s	1	0.008093	0.003323	2.44	0.0149	ZINB	Logistic
Zebra	Wet	Dist*decade 1990s	Model	1990s	1	0.031055	0.011869	2.62	0.0089	ZINB	Logistic
Zebra	Wet	Dist*decade 2000s	Model	2000s	1	0.008356	0.003593	2.33	0.02	ZINB	Logistic
Zebra	Wet	Dist*Dist*decade 1990s	Model	1990s	1	-0.000342	0.000233	-1.46	0.1433	ZINB	Logistic
Zebra	Wet	Inf_Intercept	ZeroModel		1	-1.34729	0.085836	-15.7	<0.0001	ZINB	Logistic
Zebra	Wet	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	0.000213	0.000086371	2.47	0.0137	ZINB	Logistic
Zebra	Wet	_Alpha	Internal		1	1.290415	0.067228	19.19	<0.0001	ZINB	Logistic
Wildebeest	Wet	Intercept	Model		1	4.301608	0.209421	20.54	<0.0001	ZINB	Logistic
Wildebeest	Wet	decade 1970s	Model	1970s	1	1.04574	0.257198	4.07	<0.0001	ZINB	Logistic
Wildebeest	Wet	decade 1980s	Model	1980s	1	0.457709	0.253984	1.8	0.0715	ZINB	Logistic
Wildebeest	Wet	decade 1990s	Model	1990s	1	-1.034718	0.324142	-3.19	0.0014	ZINB	Logistic
Wildebeest	Wet	Dist*decade 1980s	Model	1980s	1	0.028046	0.004394	6.38	<0.0001	ZINB	Logistic
Wildebeest	Wet	Dist*decade 1990s	Model	1990s	1	0.127982	0.020737	6.17	<0.0001	ZINB	Logistic

Wildebeest	Wet	Dist*Dist*decade 1970s	Model	1970s	1	0.00064	0.00008739	7.32	<0.0001	ZINB	Logistic
Wildebeest	Wet	Dist*Dist*decade 1990s	Model	1990s	1	-0.001493	0.000366	-4.07	<0.0001	ZINB	Logistic
Wildebeest	Wet	Dist*Dist*decade 2000s	Model	2000s	1	0.000687	0.000132	5.21	<0.0001	ZINB	Logistic
Wildebeest	Wet	Inf_Intercept	ZeroModel		1	-0.023269	0.107618	-0.22	0.8288	ZINB	Logistic
Wildebeest	Wet	Inf_decade 1980s	ZeroModel	1980s	1	-2.597772	0.641309	-4.05	<0.0001	ZINB	Logistic
Wildebeest	Wet	Inf_Dist*decade 1980s	ZeroModel	1980s	1	-0.218737	0.060383	-3.62	0.0003	ZINB	Logistic
Wildebeest	Wet	Inf_Dist*Dist*decade 1970s	ZeroModel	1970s	1	-0.007567	0.002644	-2.86	0.0042	ZINB	Logistic
Wildebeest	Wet	Inf_Dist*Dist*decade 1980s	ZeroModel	1980s	1	0.00398	0.001104	3.61	0.0003	ZINB	Logistic
Wildebeest	Wet	Inf_Dist*Dist*decade 1990s	ZeroModel	1990s	1	-0.0003	0.000113	-2.64	0.0082	ZINB	Logistic
Wildebeest	Wet	_Alpha	Internal		1	2.206308	0.136439	16.17	<0.0001	ZINB	Logistic
Cattle	Both	Intercept	Model		1	6.708102	0.055938	119.92	<0.0001	ZINB	Logistic
Cattle	Both	decade 1990s	Model	1990s	1	-0.213581	0.105099	-2.03	0.0421	ZINB	Logistic
Cattle	Both	Inf_Intercept	ZeroModel		1	-1.022067	0.122687	-8.33	<0.0001	ZINB	Logistic
Cattle	Both	Inf_decade 1990s	ZeroModel	1990s	0	-240.597647	.	.	.	ZINB	Logistic
Cattle	Both	Inf_Dist*decade 1990s	ZeroModel	1990s	0	-15.027878	.	.	.	ZINB	Logistic
Cattle	Both	Inf_Dist*Dist*decade 1970s	ZeroModel	1970s	0	-0.000629	.	.	.	ZINB	Logistic

Cattle	Both	Inf_Dist*Dist*decade 2000s	ZeroModel	2000s	1	-14.857691	18.868601	-0.79	0.431	ZINB	Logistic
Cattle	Both	_Alpha	Internal		1	2.025176	0.098899	20.48	<0.0001	ZINB	Logistic
Sheep and goats	Both	Intercept	Model		1	7.293816	0.129953	56.13	<0.0001	ZINB	Logistic
Sheep and goats	Both	decade 1970s	Model	1970s	1	-0.759663	0.186923	-4.06	<0.0001	ZINB	Logistic
Sheep and goats	Both	decade 1980s	Model	1980s	1	-1.093346	0.185041	-5.91	<0.0001	ZINB	Logistic
Sheep and goats	Both	decade 1990s	Model	1990s	1	-0.976482	0.185221	-5.27	<0.0001	ZINB	Logistic
Sheep and goats	Both	Inf_Intercept	ZeroModel		0	-2118.3008	.	.	.	ZINB	Logistic
Sheep and goats	Both	Inf_decade 1980s	ZeroModel	1980s	0	-1343.416946	.	.	.	ZINB	Logistic
Sheep and goats	Both	Inf_Dist*Dist*decade 1970s	ZeroModel	1970s	0	-2648.905303	.	.	.	ZINB	Logistic
Sheep and goats	Both	_Alpha	Internal		1	4.45757	0.189031	23.58	<0.0001	ZINB	Logistic

Table S5. Trends in livestock and wildlife densities in Mara Reserve (CPA), Mara Conservancies (PASRU) and Narok Community Areas (UPA) between 1977 and 2016.

		Mara Reserve (CPA)			Mara Conservancies (PASRU)					Narok Community Areas (UPA)				
Resident Species	Season	Population size in 1977-1978	Population size in 2016	%Change in population size between 1977-1978 and 2016	Population size in 1977-1978	Population size in 2005	Population size in 2016	%Change in population size between 1977-1978 and 2016	%Change in population size between 2005 and 2016	Population size in 1977-1978	Population size in 2005	Population size in 2016	%Change in population size between 1977-1978 and 2016	%Change in population size between 2005 and 2016
Cattle	Both	2494	28756	1052.9	66157	76713	92606	40	20.7	580794	628512	526041	-9.4	-16.3
Sheep and goats	Both	1646	20967	1173.9	67350	104776	195013	189.6	86.1	416179	717402	887360	113.2	23.7
Donkeys	Both	29	119	305.2	2144	674	668	-68.8	-0.8	15650.6	12003.1	10279.1	-34.3	-14.4
Thomson's gazelle	Both	24279	4926	-79.7	29698	10071	7051	-76.3	-30	66711.6	19119.5	7603.8	-88.6	-60.2
Grant's gazelle	Both	879	2079	136.4	3569	2175	1631	-54.3	-25	18408.5	8803.7	3595.6	-80.5	-59.2
Impala	Both	18316	2308	-87.4	26913	12248	7752	-71.2	-36.7	68263.7	23498	7094.8	-89.6	-69.8
Warthog	Both	3850	516	-86.6	1491	372	285	-80.9	-23.3	4395.1	487.2	402.3	-90.8	-17.4
Waterbuck	Both	1086	315	-71	332	108	81	-75.7	-25.5	3456.3	98.3	54.3	-98.4	-44.8
Topi	Both	20204	4031	-80	10742	2671	1667	-84.5	-37.6	10097.4	3268.3	1244.1	-87.7	-61.9
Hartebeest	Both	3167	472	-85.1	3715	502	249	-93.3	-50.5	5856.8	1069.6	324.9	-94.5	-69.6
Wildebeest	Dry	477561	174269	-63.5	162409	35625	23481	-85.5	-34.1	134514	65071.4	60589.6	-55	-6.9
Wildebeest	Wet	7667	10289	34.2	7924	2570	1969	-75.1	-23.4	115794	33921.4	20751.3	-82.1	-38.8
Burchell's zebra	Dry	58227	46358	-20.4	21006	8541	5501	-73.8	-35.6	40817.5	26179.9	27687.6	-32.2	5.8
Burchell's zebra	Wet	16636	29269	75.9	11268	7953	8232	-26.9	3.5	40278.1	33448.2	14653.8	-63.6	-56.2
Eland	Both	1322	528	-60	704	363	311	-55.9	-14.3	3427.6	816.6	310.3	-90.9	-62
Buffalo	Both	22122	4799	-78.3	4545	926	592	-87	-36	16998.8	1322.6	716.6	-95.8	-45.8
Giraffe	Both	1311	200	-84.7	2139	660	408	-80.9	-38.1	6019.2	1541.3	792.5	-86.8	-48.6
Elephant	Both	1421	847	-40.4	381	442	425	11.6	-3.8	592.8	1187.7	1264.1	113.2	6.4

Table S6. Tests of three linear hypotheses comparing similar regression coefficients for the ZINB models for the 1970s and 1980s (Test0 and Test1) and the full ZINB regression models for the 1970s and the 1980s (Test2).

Species	**Test Label**	**Test**	**Test Type**	**Statistic**	**Pr > ChiSq**
Buffalo	Dist_Decade_1970s-Dist_Decade_1980s = 0	Test0	Wald	7.518825	0.0061
Buffalo	Dist_Decade_1970s-Dist_Decade_1980s = 0	Test0	L.R.	7.562645	0.006
Buffalo	Dist_Decade_1970s-Dist_Decade_1980s = 0	Test0	L.M.	7.862879	0.005
Buffalo	Inf_Dist_Decade_1970s-Inf_Dist_Decade_1980s = 0	Test1	Wald	0.654118	0.4186
Buffalo	Inf_Dist_Decade_1970s-Inf_Dist_Decade_1980s = 0	Test1	L.R.	0.666487	0.4143
Buffalo	Inf_Dist_Decade_1970s-Inf_Dist_Decade_1980s = 0	Test1	L.M.	0.66146	0.416
Buffalo	Dist_Decade_1970s = 0, Dist_Dist_Decade_1980s = 0, Inf_Decade_1980s = 0, Dist_Decade_1970s-Dist_Decade_1980s = 0, Inf_Dist_Decade_1970s-Inf_Dist_Decade_1980s = 0	Test2	Wald	90.87512	<0.0001
Buffalo	Dist_Decade_1970s = 0, Dist_Dist_Decade_1980s = 0, Inf_Decade_1980s = 0, Dist_Decade_1970s-Dist_Decade_1980s = 0, Inf_Dist_Decade_1970s-Inf_Dist_Decade_1980s = 0	Test2	L.R.	75.23483	<0.0001
Buffalo	Dist_Decade_1970s = 0, Dist_Dist_Decade_1980s = 0, Inf_Decade_1980s = 0, Dist_Decade_1970s-Dist_Decade_1980s = 0, Inf_Dist_Decade_1970s-Inf_Dist_Decade_1980s = 0	Test2	L.M.	206.9255	<0.0001

Test Type: Wald= Wald; L.M.=Lagrange multiplier; L.R.=likelihood ratio.
Test0: Tests the hypothesis that the linear slopes for the count part of the ZINB model for the 1970s and the 1980s are equal.
Test1: Tests the hypothesis that the linear slopes for the zero-inflated part of the ZINB model for the 1970s and the 1980s are equal.
Test2: Tests the hypothesis that the full ZINB regression models for the 1970s and the 1980s are not different. Note that the intercepts for the two parts of the ZINB model are not considered since they are the same for the ZINB models for the 1970s and 1980s as shown in Table S4. This test shows that the two curves for the 1970s and the 1980s are indeed statistically highly significantly different based on all the three types of statistical tests.

Table S7. Generalized Linear Models analysis of grazing intensity associated with each of 24 plot-pairs, as influenced by variation among 8 sites, rainfall in the previous six months, and year.

Variable	X2	df	P
(Intercept)	7.641	1	.006
Site	18.598	6	.005
Pair	1.367	2	.505
RAIN	8.074	1	.004
Year	7.694	1	.006
Site * Year	18.548	6	.005
RAIN * Year	8.045	1	.005
Dependent Variable: GI = 1 - Biomass Unfenced/Biomass Fenced for each plot pair, total N=24 Model: (Intercept), Site, Pair, RAIN, Year, Site * Year, RAIN * Year, X2 = Wald Chi-square, RAIN is Rainfall in the previous six months prior to sampling			

Table S8. Serengeti wildebeest census data from 1957 to 2015. Data from Conservation Information Monitoring Unit of the Tanzania Wildlife Research Institute.

Year	Wildebeest Estimate (10^9)	Standard Error
1957	0.1900000	0.0000010
1961	0.2633620	0.0000010
1963	0.3561240	0.0000010
1965	0.4391240	0.0000010
1967	0.4832920	0.0000010
1971	0.6927770	0.0288250
1972	0.7730140	0.0766940
1977	1.4400000	0.2000000
1978	1.2489340	0.3546680
1980	1.3379790	0.0800000
1982	1.2087110	0.2719350
1984	1.3378790	0.1381350
1986	1.1463400	0.1338620
1987	1.1839660	0.1283719
1991	1.2217830	0.1772400
1994	0.9172040	0.1736320
1999	1.2969440	0.3000720
2000	1.2452220	0.1449340
2006	1.2391640	0.2635360
2009	1.2722330	0.0662610
2015	1.3267090	0.1326709

Table S9. Generalized Linear Models analysis of site grazed biomass as a function of early (2000-2006) versus late (2009-2016) periods during the study, with rainfall and grazing intensity as covariates.

Variable	X2	df	P
(Intercept)	12.924	1	.000
Period	4.975	1	.026
RAIN	7.626	1	.006
GI	10.096	1	.001
Period * GI	7.554	1	.006
Period * RAIN	4.429	1	.032
Dependent Variable: Biomass Model: (Intercept), Period, RAIN, GI, Period * GI, Period * RAIN X2 = Wald Chi-square, GI is Grazing Intensity, RAIN is Rainfall in the previous six months prior to sampling, period is 2000-2006 or 2009-2016.			