CONSERVATION ECOLOGY

Cross-boundary human impacts compromise the Serengeti-Mara ecosystem

Michiel P. Veldhuis[1]*, Mark E. Ritchie[2], Joseph O. Ogutu[3], Thomas A. Morrison[4], Colin M. Beale[5], Anna B. Estes[6,7], William Mwakilema[8], Gordon O. Ojwang[1,9], Catherine L. Parr[10,11,12], James Probert[10], Patrick W. Wargute[9], J. Grant C. Hopcraft[4], Han Olff[1]

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-square-kilometer ecosystem. This spatial cascade reduced resilience in the core and was mediated by the movement of grazers, which reduced grass fuel and fires, weakened the capacity of soils to sequester nutrients and carbon, and decreased the responsiveness of primary production to rainfall. Similar effects in other protected ecosystems worldwide may require rethinking of natural resource management outside protected areas.

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, are the dominant conservation strategy worldwide (5), despite potential conflicts of interest with historic rights or the 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 the rates of both land use change and the growth of human populations can be highest near PA boundaries (13–16), and these high rates in turn accelerate edge degradation through increased livestock production, crop cultivation, and extraction of natural resources such as charcoal and bush-

meat. In regions with high human density, the sharp contrast in natural resources across PA boundaries leads to "hard edges," which exacerbate 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). Most of Earth's PAs are not fenced, raising the question of whether anthropogenic activities at the edges are increasingly compromising the ecological processes in the core. The objective of our research is to assess whether edge effects are currently undermining the ecological integrity that PAs aim to protect.
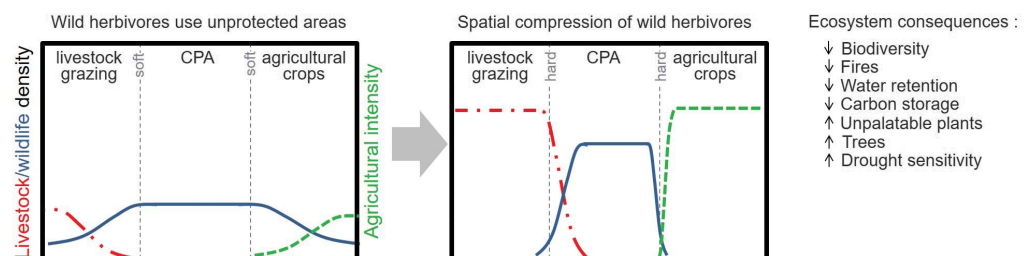
The concept of spatial compression in PAs

At low human population densities, people can extract sufficient resources and receive addi-

tional 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 PAs (CPAs) (22, 23). Unprotected areas (UPAs) can support ecotourism and harvesting of wildlife, whereas livestock keeping can create local nutrient hot spots that increase biodiversity (24, 25). This can lead to mutually beneficial relationships between people and wildlife (26) over long periods (27). However, steep increases in human populations (through population growth and/ or migration toward 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 (Fig. 1). 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 assess whether spatial compression alters the key ecological functioning of the Serengeti-Mara ecosystem in Tanzania and Kenya, one of the largest 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 management similar and complementary to that of the national parks [CPAs are International Union for Conservation of Nature (IUCN) category II] [see (31) and table S1]. The ecosystem is managed to protect the diversity of wildlife and ecological processes, foremost the migration of >2 million large herbivores, primarily wildebeest (Connochaetes taurinus),

[1]University of Groningen, Nijenborg 7, 9747AG Groningen, Netherlands. [2]Syracuse University, 107 College Place, Syracuse, NY 13244, USA. [3]University of Hohenheim, Fruwirthstrasse 23, 70599 Stuttgart, Germany. [4]University of Glasgow, Glasgow G128QQ, UK. [5]University of York, York YO10 5DD, UK. [6]Pennsylvania State University, University Park, PA 16802, USA. [7]The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania. [8]Tanzania National Parks, Arusha, Tanzania. [9]Directorate of Resource Surveys and Remote Sensing, P.O. Box 47146-00100, Nairobi, Kenya. [10]University of Liverpool, Liverpool L69 3GO, UK. [11]University of the Witwatersrand, Wits 2050, Johannesburg, South Africa. [12]University of Pretoria, Pretoria 0002, South Africa.
*Corresponding author. Email: m.p.veldhuis@gmail.com

Fig. 1. The concept of spatial compression in PAs. Unsustainable activities outside a soft-edge 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) into hard borders that effectively compress the CPA (right). Lines represent hypothesized wildlife (blue) and livestock (red) densities and agricultural intensity (green).

zebras (*Equus quagga*), and Thomson's gazelles (*Eudorcas thomsonii*) (*32*). The spatial layout of a set of PAs with different management supports this migration (fig. S1) by allowing animals free access to spatiotemporally variable forage within the CPA, adjacent PAs with sustainable resource use (PASRUs) (IUCN categories V and VI), and UPAs.

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 (figs. S2 to S6) (*31*). The human population growth rate was higher in the UPA along the western boundaries, inhabited by Sukuma and Kuria agropastoralists, than in 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 and tables S2 and S3) (*31*). The growth of the cattle population (0.9% on average per year from 2002 to 2012) was especially high in the wetter Tanzanian Mara Region, toward 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 effects, as evidenced by decreasing herbaceous vegetation green up, most notably in the PASRU (figs. S9 to S11) (*31*), and virtually no fires outside the CPA since 2005 (Fig. 2 and figs. S12 to S14) (*31*).

Expanding edge effects induce spatial compression

Data from the Narok subarea of the ecosystem 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 the Masai Mara National Reserve (MMNR) (Fig. 3, figs. S15 to S19, and tables S4 to S6) (*31*). There, human settlement and population densities have increased enormously, especially close to the CPA boundary (increased people densities inside the MMNR in Fig. 3 represent park and lodge staff, not the movement of local people living outside the reserve). The wildlife biomass inside the first 15 km of the CPA was reduced by 75% in the wet season and by 50% in the dry season from the 1970s to the 2000s. The latter declines were due largely to changes in the abundance of the Loita subpopulation of migratory wildebeest and zebras that traditionally use the MMNR as their dryseason 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 (temporary livestock enclosures) toward the borders of the CPA (figs. S20 to S25) (*31*) and even established bomas up to 10 km inside the CPA (Fig. 2). In

addition, Maasai pastoralists with bomas outside the CPA might bring their herds into the CPA on illegal multiday grazing trips, as opposed to the short, nightly grazing trips made by the agropastoralists on the west. The trend to push more livestock farther 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 decreased especially along the borders of the PASRU and in a concentrated area at the core (Fig. 4, A and B, and fig. 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 the Maswa Game Reserve, indicates that agropastoralists enter the park with their livestock on a daily basis, producing an extensive network of livestock paths (Fig. 2 and figs. S22, S23, and S27) (*31*). This coincides with a strong reduction (by >10%) in the maximum vegetation greenness [expressed as the maximum normalized difference vegetation index (maxNDVI)] within the first 7 km inside the CPA (Fig. 4, G and 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 [generalized linear model (GLM), $F_{1,14} = -5.9$, $P < 0.05$] (Fig. 4, E and F). The most severe changes in maxNDVI and fire coincide with a high density of livestock paths and (temporary) livestock corrals (bomas), suggesting that illegal livestock incursions into the PA remove vegetation biomass (Fig. 2 and figs. S10 and 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 that these areas are less intensively grazed by livestock. Along strong UPA boundaries, wildebeest increased their use close to the border, whereas in the UPAs with medium patrolling, wildebeest use increased beginning at 7 km inside the border, corresponding to the distance of livestock incursions.

The third line of evidence suggesting that livestock compete with wildlife comes from observing the response of wildebeest in the different PASRU boundaries (Fig. 4, C and D, and fig. S26) (*31*). In Narok, Kenya, where the intensity of use by wildebeest was previously highest, wildebeest utilization has declined up to 15 km inside the CPA, whereas along the border with the Loliondo Game Controlled Area (LGCA), the decreased use stretches only a few kilometers inside. Most notably, utilization in
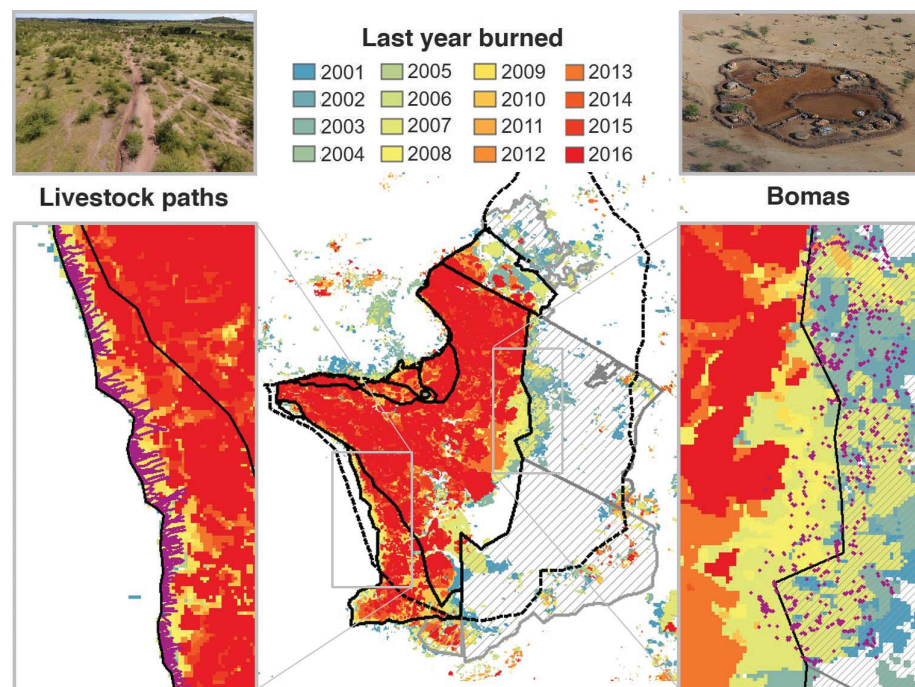

Fig. 2. Spatial compression of burned area in the GSME. Different colors represent the last year each pixel burned between 2001 (blue) and 2016 (red) as visualized by using the Moderate-Resolution Imaging Spectroradiometer (MODIS) burned-area product. Magnifications show the same map overlaid with livestock paths (left) and bomas (right). Solid black lines represent borders of CPAs. Gray hatched areas are PASRUs inhabited by people and grazed by livestock. The black dashed line is the boundary of the GSME that represents the area formerly used by the migratory wildlife.
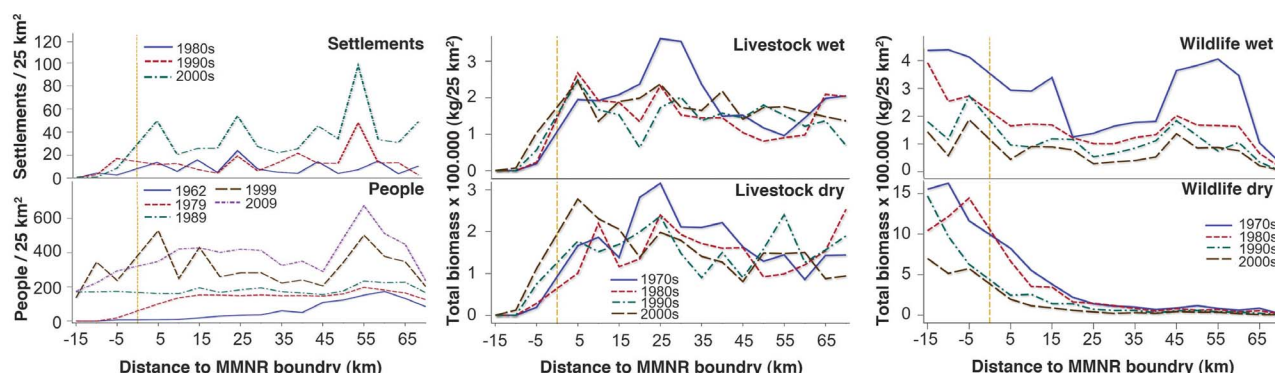
Fig. 3. Spatial expansion of humans and livestock and the compression of wild herbivores over multiple decades. Wildlife and livestock trends shown for both the wet (top) and dry (bottom) seasons. Density estimates are plotted against the distance to the border of the MMNR, covering the first 15 km inside the MMNR and 70 km 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 far into the MMNR.

Fig. 4. Changes in wildebeest occupancy, fire, and vegetation greenness in the border regions of the CPAs. Wildebeest utilization between 1999 and 2007 and between 2008 and 2017 (**A** and **C**), the mean areas burned between 2001 and 2005 and between 2011 and 2016 (**E**), the mean maxNDVI between 2001 and 2005 and between 2011 and 2016 (**G**), and the change between the two periods (**B**, **D**, **F**, and **H**) as a function of the distance to the border for three different border types: those between the CPA and a PASRU with medium border control against illegal activities (PASRU medium) (blue line), a UPA with strong border control (UPA strong) (red line), and a UPA with medium border control (UPA medium) (orange line). (C) and (D) show the same information as that for the PASRU (blue lines) in (A) and (B) but now split up for the three different PASRU areas. The black lines in (B), (F), and (H) represent the overall weighted mean. Data cover both the Tanzanian and Kenyan sides of the ecosystem.

the Ngorongoro Conservation Area (NCA) increased in recent years. There are multiple explanations for these contrasting effects among the different PASRUs. First, the NCA has lower human and livestock population densities than the LGCA and Narok (figs. S4, S5, and 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 the NCA is further reduced because of 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 the NCA (*35*), suggesting that 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 displacement of wildlife away from the dry-season range in Narok and toward the northern Serengeti and the western corridor (fig. S26) (*31*) and increasing wildebeest utilization in the UPAs with strong and medium border control (except in the first 7 km) (Fig. 4, A and B).

Consequences for the ecological functioning of the CPA

In addition to the severe effects of human disturbance in the border regions of the CPA, our data suggest that these compression effects (Figs. 2 to 4) spatially cascade to modify ecosystem pro-

cesses over the entire CPA, not just the boundary. The intensity of grazing (by wildlife) measured at eight long-term grazing exclosure (LTGE) sites, each with three pairs of ungrazed (exclosure) and control (unfenced) plots, across the SNP (48 plots in total) (fig. S12) (*31*) has increased by 16% between 2001 and 2016 (~1.1% per year) (Fig. 5A and fig. S28A) (*31*). A GLM with plot pairs as subjects (blocks) and year and September-to-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, whereas the maxNDVI decreased by 8% on average, from 0.78 to 0.71 (Fig. 5, B and C). Wildebeest formerly spent the longest time on the Serengeti plains, in the central Serengeti,
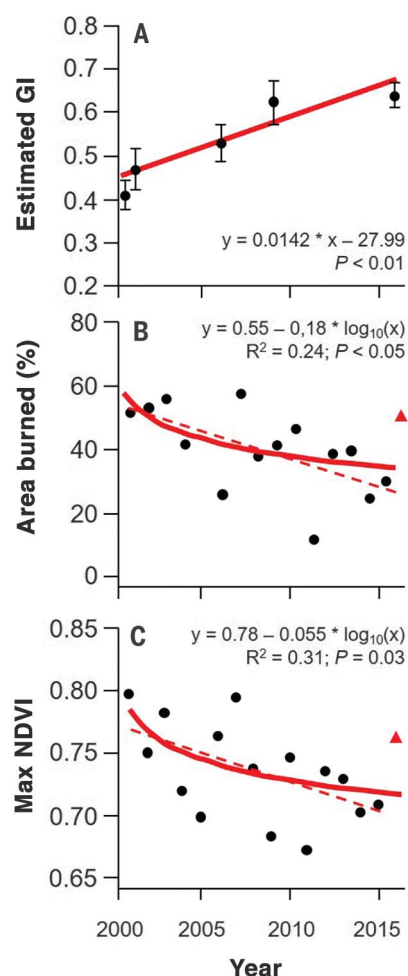
Fig. 5. Changes in grazing intensity, burned area, and maxNDVI between 2001 and 2016 for the entire area designated as a CPA. (**A**) The grazing intensity (GI) (mean ± SE), measured through herbivore exclosures, increased by 1.08% per year on average. (**B**) The area burned decreased by 40% in 16 years' time (solid red line). (**C**) The maxNDVI decreased by 8% in 16 years' time. The burned area and maxNDVI increased in 2016 (red triangles) because of management actions in the eastern SNP. Excluding this data point results in a stronger correlation and more explained variation (dashed red lines) [area burned = 0.53 − (0.017 × years), coefficient of determination $R^2 = 0.38$, $P = 0.01$; 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 to 2017 in the Serengeti LTGE experiment (eight 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 the mean grazing intensity across all sites in 2001 to 2008 (blue) and 2009 to 2016 (red). (**A**) The 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 Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) satellite–estimated rainfall across eight sites in 2001, 2002, and 2006 (blue circles) ($n = 21$) and at seven sites in 2009 and six sites in 2016 (red circles) ($n = 13$). Slopes are significantly different ($P < 0.04$). (**B**) Changes in SOC in each grazed plot from 2001 to 2008 (blue circles) ($n = 24$) and 2009 to 2017 (red triangles) ($n = 21$). (**C** to **E**) Effects of excluding herbivores in plot pairs (control–exclosure measure) at different mean grazing intensities (measured in 2006 and 2009) on (C) the percentage of cover with N-fixing plants, both grasses and legumes (open circles) and low-palatability forb species (closed circles); (D) root biomass; and (E) the production of hyphae of arbuscular mycorrhizal (AM) fungi.

and in 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 biomasses of plants living on poorer-quality soils (figs. S26E and S28B). Increased use of such areas inside the CPA would be expected when herbivores are displaced from preferred grazing sites in Narok and the LGCA, as they are the only
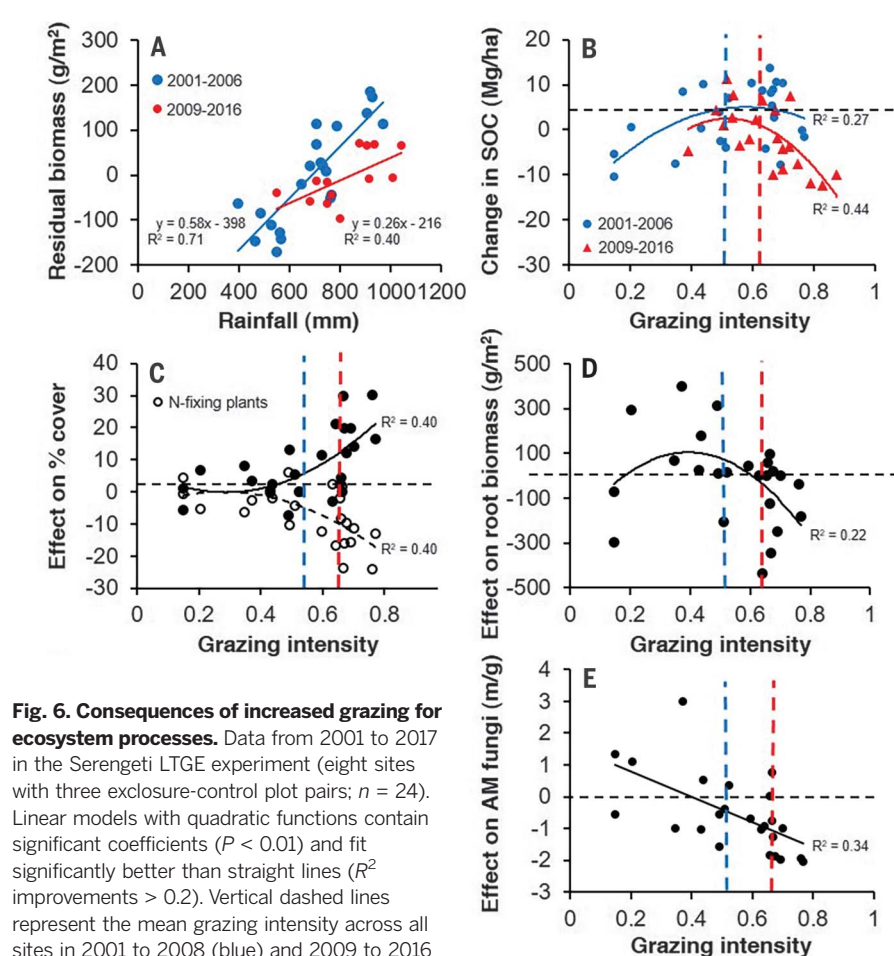
other areas with permanent water. These changes in wildebeest use, grazing intensities, the area burned, and maxNDVI in the core ecosystem cannot be explained by changes in wildebeest population numbers (fig. S29 and table S8) (*31*) or decreasing rainfall (*36*) (figs. S30 and S31) (if anything, there was a trend of increasing rainfall). Changes occurred simultaneously with the increased human dominance outside the CPA and in its boundary areas and together provide strong evidence that ecological function is changing at the core of an ecosystem because of the compression of wildlife.

It is unclear why this habitat compression has not resulted in an observable decline in wildebeest numbers, as 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 and S31) (*31*) has resulted in sufficient primary productivity to

support the current densities of wildebeest. Alternatively, the wildebeest population may not be near carrying capacity or may not yet have reached a new equilibrium (*37*). Whereas 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 for other demographic components, such as birth rates or juvenile survival. Overall, the future effects 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 show that plant biomass in grazed areas in the CPA depended much less on annual rainfall in the

period from 2009 to 2016 than over the same range of rainfall variation during the period from 2001 to 2006 (GLM year × rainfall interaction, χ^2 = 5.31, $P < 0.03$) (Fig. 6A and 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 multiyear dynamics of soil organic carbon (SOC) (0- to 30-cm depth) in grazed plots reveal a significant unimodal response to grazing intensity (Fig. 6B), with negative changes at higher grazing intensities [>0.55, calculated as 1 − (biomass outside an exclosure)/(biomass inside the exclosure)]. This response suggests that the increased grazing intensities due to a "squeeze" effect decrease 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 of C/ha between 2009 and 2017 (6 of 21 plots; 28.3%) compared with the number that did so between 2001 and 2008 (14 of 24 plots; 58.6%) (χ^2 = 4.01, $P = 0.04$).

Other data from the LTGE experiment suggest three different ecosystem responses that may explain why compression and increased grazing intensity would yield lower resilience and carbon storage. First, higher grazing intensities were significantly associated with higher percentages of cover with largely unpalatable forbs and lower cover with known N-fixing species, including legumes, in grazed plots (Fig. 6C) (40). Second, as indicated by a significant quadratic regression model, higher grazing intensities shifted the effects of grazers on root biomass significantly ($P < 0.01$), from positive to negative (Fig. 6D). Third, the effects of grazers on the production of hyphae by arbuscular mycorrhizal fungi, plant symbionts important for phosphorus uptake, shifted from positive to negative as grazing intensity increased ($P < 0.01$) (Fig. 6E) (41). These relationships suggest that the higher grazing intensities associated with habitat compression may weaken mutualistic relationships that assist nutrient acquisition (Fig. 6, C and E) and increase belowground carbon inputs (Fig. 6, D and 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 (GSME) (42). These changes may signal future degradation in the CPA similar to what has already happened in human-dominated community areas.

The way ahead

Today, wildlife compete with cattle for grass, generating a conflict both in 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. Whereas 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 effects 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 ecosystems whose PA boundaries were established on the basis of 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 new strategies for improving the ecological integrity of fragmented ecosystems as well as for preserving the last remaining places where these large-scale migrations persist.

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 the mutual agreement of local people and regional or national governments are likely the way forward. This will require continually monitoring both the ecological integrity and societal trends in the surroundings of PAs; building more trust with local communities that they will keep sharing in the benefits of natural resource conservation; and ensuring that livestock numbers, settlement, and cropland expansion in the direct vicinity of CPAs do not go beyond a point where they impair the key structure and functioning of the underlying socioecological system.

REFERENCES AND NOTES

1. B. Worm et al., Science 314, 787–790 (2006).
2. G. M. Mace, K. Norris, A. H. Fitter, Trends Ecol. Evol. 27, 19–26 (2012).
3. M. Loreau et al., Science 294, 804–808 (2001).
4. D. Tilman, D. Wedin, J. Knops, Nature 379, 718–720 (1996).
5. J. E. M. Watson, N. Dudley, D. B. Segan, M. Hockings, Nature 515, 67–73 (2014).
6. T. O. McShane et al., Biol. Conserv. 144, 966–972 (2011).
7. K. R. Jones et al., Science 360, 788–791 (2018).
8. T. H. Ricketts et al., Proc. Natl. Acad. Sci. U.S.A. 102, 18497–18501 (2005).
9. C. A. Runge et al., Science 350, 1255–1258 (2015).
10. C. N. Jenkins, K. S. Van Houtan, S. L. Pimm, J. O. Sexton, Proc. Natl. Acad. Sci. U.S.A. 112, 5081–5086 (2015).
11. I. D. Craigie et al., Biol. Conserv. 143, 2221–2228 (2010).
12. R. DeFries, A. Hansen, B. L. Turner, R. Reid, J. Liu, Ecol. Appl. 17, 1031–1038 (2007).
13. G. Wittemyer, P. Elsen, W. T. Bean, A. C. O. Burton, J. S. Brashares, Science 321, 123–126 (2008).
14. L. Naughton-Treves, J. Alix-Garcia, C. A. Chapman, Proc. Natl. Acad. Sci. U.S.A. 108, 13919–13924 (2011).
15. A. B. Estes, T. Kuemmerle, H. Kushnir, V. C. Radeloff, H. H. Shugart, Biol. Conserv. 147, 255–263 (2012).
16. K. S. Andam, P. J. Ferraro, K. R. E. Sims, A. Healy, M. B. Holland, Proc. Natl. Acad. Sci. U.S.A. 107, 9996–10001 (2010).
17. R. Woodroffe, S. Thirgood, A. Rabinowitz, "The impact of human–wildlife conflict on natural systems," in People and Wildlife, Conflict or Co-existence? R. Woodroffe, S. Thirgood, A. Rabinowitz, Eds. (Cambridge Univ. Press, 2005), pp. 1–12.
18. M. J. Somers, M. W. Hayward, Eds., Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes? (Springer, 2012).
19. C. Packer et al., Ecol. Lett. 16, 635–641 (2013).
20. J. O. Ogutu, N. Owen-Smith, H. P. Piepho, B. Kuloba, J. Edebe, Biodiversity Conserv. 21, 1033–1053 (2012).
21. B. Phalan, M. Onial, R. E. Green, Science 333, 1289–1291 (2011).
22. M. Y. Said et al., J. Nat. Conserv. 34, 151–164 (2016).
23. J. O. Ogutu, Open Conserv. Biol. J. 7, 11–26 (2013).
24. C. Riginos et al., Pastoralism 2, 10 (2012).
25. V. Vuorio, A. Muchiru, R. S. Reid, J. O. Ogutu, Biodiversity Conserv. 23, 3219–3240 (2014).
26. K. Homewood, W. A. Rodgers, Maasailand Ecology: Pastoral Development and Wildlife Conservation in Ngorongoro, Tanzania (Cambridge Univ. Press, 1991).
27. H. Olff, J. G. C. Hopcraft, in Serengeti III: Human Impacts on Ecosystem Dynamics, A. R. E. Sinclair, C. Packer, S. A. R. Mduma, J. M. Fryxel, Eds. (Univ. of Chicago Press, 2008), pp. 95–134.
28. S. L. Lewis, D. P. Edwards, D. Galbraith, Science 349, 827–832 (2015).
29. J. S. Brashares, P. Arcese, M. K. Sam, Proc. R. Soc. London Ser. B 268, 2473–2478 (2001).
30. J. O. Ogutu, H. P. Piepho, H. T. Dublin, N. Bhola, R. S. Reid, J. Zool. 278, 1–14 (2009).
31. Materials and methods are available as supplementary materials.
32. A. R. E. Sinclair et al., Conserv. Biol. 21, 580–590 (2007).
33. B. Butt, A. Shortridge, A. M. G. A. WinklerPrins, Ann. Assoc. Am. Geogr. 99, 309–334 (2009).
34. S. A. R. Mduma, A. R. E. Sinclair, R. Hilborn, J. Anim. Ecol. 68, 1101–1122 (1999).
35. W. O. Odadi, M. K. Karachi, S. A. Abdulrazak, T. P. Young, Science 333, 1753–1755 (2011).
36. G. S. Bartzke et al., PLOS ONE 13, e0202814 (2018).
37. J. M. Diamond, Proc. Natl. Acad. Sci. U.S.A. 69, 3199–3203 (1972).
38. D. Rentsch, C. Packer, Oryx 49, 287–294 (2015).
39. R. M. Holdo et al., PLOS Biol. 7, e1000210 (2009).
40. M. E. Ritchie, R. Raina, Pedobiologia 59, 233–241 (2016).
41. J. R. Propster, N. C. Johnson, Plant Soil 388, 21–34 (2015).
42. S. N. de Visser, B. P. Freymann, H. Olff, J. Anim. Ecol. 80, 484–494 (2011).
43. S. Thirgood et al., Anim. Conserv. 7, 113–120 (2004).
44. R. DeFries, K. K. Karanth, S. Pareeth, Biol. Conserv. 143, 2870–2880 (2010).
45. G. Harris, S. J. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, J. Berger, Endanger. Species Res. 7, 55–76 (2009).
46. M. P. Veldhuis, M. E. Ritchie, J. O. Ogutu, T. A. Morrison, C. M. Beale, A. B. Estes, W. Mwakilema, G. O. Ojwang, C. L. Parr, J. Probert, P. W. Wargute, J. G. C. Hopcraft, H. Olff, Data for "Cross-boundary human impacts compromise the Serengeti-Mara ecosystem," Dryad (2019); doi:10.5061/dryad.b303788.
47. African BioServices, Serengeti Squeeze – Interactive Maps; https://arcg.is/01CjXW.

Science

Cross-boundary human impacts compromise the Serengeti-Mara ecosystem

Michiel P. Veldhuis, Mark E. Ritchie, Joseph O. Ogutu, Thomas A. Morrison, Colin M. Beale, Anna B. Estes, William Mwakilema, Gordon O. Ojwang, Catherine L. Parr, James Probert, Patrick W. Wargute, J. Grant C. Hopcraft and Han Olff

Threats to the Serengeti
　　　　Protected areas are an important tool for conserving biodiversity and ecosystem functioning. But how well do these areas withstand pressure from human activity in surrounding landscapes? Veldhuis　*et al.* studied long-term data from the Serengeti-Mara ecosystem in East Africa. Human activities at boundary regions cause animals to concentrate in the core of the protected area, which eventually reduces soil carbon storage and nitrogen fixation rates and increases vulnerability to extreme droughts. Similar patterns are likely for many, if not all, large protected areas.
　　　　Science, this issue p. 1424

ARTICLE TOOLS	http://science.sciencemag.org/content/363/6434/1424
SUPPLEMENTARY MATERIALS	http://science.sciencemag.org/content/suppl/2019/03/27/363.6434.1424.DC1
REFERENCES	This article cites 65 articles, 13 of which you can access for free http://science.sciencemag.org/content/363/6434/1424#BIBL
PERMISSIONS	http://www.sciencemag.org/help/reprints-and-permissions

Use of this article is subject to the Terms of Service