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Goheen, JR, Augustine, DJ, Veblen, KE et al. (18 more authors) (2018) Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments. Annals of the New York Academy of Sciences, 1429 (1). pp. 31-49. ISSN 0077-8923

https://doi.org/10.1111/nyas.13848

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Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments

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African savannas support an iconic fauna, but they are undergoing large-scale population declines and extinctions of large (>5 kg) mammals. Long-term, controlled, replicated experiments that explore the consequences of this defaunation (and its replacement with livestock) are rare. The Mpala Research Centre in Laikipia County, Kenya hosts three such experiments, spanning two adjacent ecosystems and environmental gradients within them: the Kenya Long-term Exclosure Experiment (KLEE; since 1995), the Glade Legacies and Defaunation Experiment (GLADE; since 1999), and the Ungulate Herbivory Under Rainfall Uncertainty experiment (UHURU; since 2008). Common themes unifying these experiments are (1) evidence of profound effects of large mammalian herbivores on herbaceous and woody plant communities; (2) competition and compensation across herbivore guilds, including rodents; and (3) trophic cascades and other indirect effects. We synthesize findings from the past two decades to highlight generalities and idiosyncrasies among these experiments, and highlight six lessons that we believe are pertinent for conservation. The removal of large mammalian herbivores has dramatic effects on the

ecology of these ecosystems; their ability to rebound from these changes (after possible re-faunation) remains unexplored.

Keywords: competition, extinction, extirpation, fire, herbivore exclusion, mutualism, Laikipia, predation, resilience, trophic cascade, wildlife loss

Introduction

Semiarid rangelands cover 26% of the earth's surface, and 68% of these are tropical[1]. They support tens of millions of people raising livestock, and are home to the vast majority of the world's large (>5kg) mammal species. The iconic exemplars of this biome are in Africa, where they cover half the continent, support most of its livestock economies, and house the greatest abundance and diversity of large mammals anywhere on Earth[2]. Large mammals in Africa may be representative of similar communities that existed in other grassland and savanna communities on other continents as recently as 15,000 years ago (North and South America), 40,000 years ago (Australia) and 250,000 years ago (Eurasia); such faunas have likely shaped the evolution and ecology of species and communities that have residual effects even today[3-5].

Laikipia County in central Kenya is at once exceptional and typical. Like many African savannas, Laikipia County contains private and communal lands where livestock production and other agricultural activities are the primary source of livelihood. Unusually, however, wildlife in Laikipia has increased in recent years. Currently, Laikipia hosts the second largest population of elephants in Kenya (after Tsavo National Park), as well as the second densest community of large mammalian species (after Maasai Mara National Reserve)[6,7]. Additionally, Laikipia houses one of the world's only increasing populations of African wild dogs, remains the stronghold for the globally-endangered Grevy's zebra, and contains four sanctuaries for black rhinos.

Background and Motivation for the KLEE, GLADE, and UHURU Experiments

Nearly 25 years ago, Milchunas and Lauenroth[8] published a comprehensive synthesis of the effects of large mammalian herbivores on plant communities and ecosystem processes. They concluded that variation among systems in precipitation and in evolutionary history of grazing are the primary drivers of variation in ecosystem responses to herbivore removal. Their synthesis relied heavily on exclusion experiments conducted in temperate rangelands, with only a handful of experiments from tropical rangelands.

In the 25 years since this publication, we initiated three parallel long-term experiments at the Mpala Research Centre in Laikipia County, Kenya (Table 1) that have since provided new insights to the overarching question that Milchunas and Lauenroth[8] originally posed: what drives variation in the way that large mammalian herbivores influence plant communities and ecosystem processes? Throughout this contribution, we distinguish between wild, large mammalian herbivores ("wild LMH") and livestock, using simply "LMH" to encompass both. Our experiments occur in tropical savannas characterized by the longest evolutionary history of herbivory by wild LMH, in addition to a >4,000-year history of grazing and browsing by livestock[9]. The three experiments are within 20 km of each other; two experiments occur on red sandy soils, while the third occurs on black cotton soils (Table 1). Here, we report on the similarities and differences in the effects of LMH on two adjacent savanna ecosystems as revealed in these three sets of experiments, with particular attention to six lessons we believe to be particularly relevant to conservation in the 21st century.

Laikipia encompasses diverse soils, elevations, and vegetation, where flat plains on volcanic soils dominated by *Acacia drepanolobium* savanna transition to a lower plateau on metamorphic rocks dominated by *Acacia mellifera, A. etbaica*, and *A. brevispica* bushland with a discontinuous grass understory[10,11]. Throughout this paper, we distinguish between (a) black cotton soils (Pellic Vertisols), that occur on the flat plains in the south and west (hereafter, the "black cotton ecosystem"); and (b) red sandy soils (Ferric and Chromic Luvisols) that occur on lower, dissected terrain to the north and east[10] (hereafter, the "red soil ecosystem"). These soils differ dramatically in texture, with black cotton averaging 50% clay and 24% sand[12], and red sands averaging 15% clay and 74% sand[13]. In our study area, transition zone between the two soil types occurs at elevations of 1740–1800 m ASL.

In the black cotton ecosystem, understory is characterized by relatively continuous and homogeneous cover of four dominant bunchgrasses, and species turnover is low. A single woody species, *A. drepanolobium*, dominates the overstory (Table 1). In contrast, understory in the red soil ecosystem consists of a heterogeneous mosaic of bare soil patches (1–25 m in diameter) interspersed with an understory layer dominated by bunchgrasses beneath diverse woody plant canopies and stoloniferous grasses between canopies[13,14]. Black cotton soils primarily occur in the less dry southern portions of Laikipia (MAP > 550 mm), the red soils span a south-north rainfall gradient (440–640 mm on MRC). Although understory biomass declines by ~50% across this gradient[14,15], species composition and spatial heterogeneity distribution remain largely similar[15].

The Mpala Research Centre and Conservancy hosts three separate sets of exclusion experiments—KLEE, GLADE, and UHURU—each replicated multiple times (Table 1). Each experiment was established primarily to test different aspects of LMH ecology, although all employ large ($\geq$0.5 ha) exclusion fences. Together, they provide a powerful platform for the analysis of the effects of LMH on vegetation, other savanna herbivores, and trophic cascades.

The Kenya Long-term Exclosure Experiment (KLEE; established 1995) examines the separate and combined effects of three guilds of wild and domestic LMH on community and ecosystem processes in the black cotton ecosystem[12]. Additional (crossed) factors include anthropogenic glades (nutrient-rich hotspots derived from abandoned livestock corrals), controlled burns, and manipulation of cattle densities.

The Glade Legacies and Defaunation Experiment (GLADE; established 1999) examines the effects of all large herbivores combined, with paired exclosures on the typically nutrient-poor sandy soils and on nutrient-rich patches created by glades (mostly treeless areas derived from abandoned livestock corrals)[14]. One emphasis of this project is the interaction between soil nutrients and LMH. It is situated in the red soil ecosystem.

The Ungulate Herbivory Under Rainfall Uncertainty experiment (UHURU; established 2008) tests the effects of three size-specific guilds of wild LMH on understory plants, overstory plants, and small mammals along a strong rainfall gradient[16]. It too occurs within the red soil ecosystem.

Below, we synthesize six lessons from KLEE, GLADE, and UHURU that we believe are particularly pertinent to conservation of savanna ecosystems: (1) context-dependence of patch dynamics; (2) effects of wild LMH on understory and overstory plants; (3) indirect effects, with particular emphasis on trophic cascades; (4) context-dependence of mutualisms; (5) functional compensation by cattle for wild LMH; and (6) cattle enhance ecosystem heterogeneity and can coexist with wildlife, despite competitive relationships. Although these experiments consist of relatively large plots[17], they are carried out spatial scales (one to four hectares) that constrain the ecological questions we can directly address. We can examine both functional and numerical responses of plants, invertebrates, rodents, and perhaps some birds to different herbivory treatments. We cannot examine numerical responses of larger (>10 kg) herbivores or mammalian carnivores. However, we can examine functional responses of large mammalian herbivores, and perhaps some carnivores (‘Do they spend more time foraging in certain plots?’), from which we may estimate numerical responses on a larger spatial scale.

Lesson #1: Rates of Recovery of Plant Communities From Grazing Differ Between Savanna Ecosystems.

In semiarid rangelands, intense, chronic herbivory can shift the spatial distribution of vegetation and is a precursor to desertification (including the creation and expansion of bare ground)[18,19]. The spatial distribution of vegetation differs markedly between the understory communities on black cotton versus red soils. After 5 years of LMH exclusion through KLEE, complete closure of the understory canopy occurred in the black cotton ecosystem (Figure 1). From Years 5-17 in GLADE, control plots (i.e., those to which LMH had access) varied from 33–99% cover, while full exclusion plots fluctuated between 61–99% cover, depending upon annual rainfall. In contrast to the black cotton ecosystem, the red soil ecosystem is characterized by patches of bare soil that covered ~40% of the study areas of both GLADE and UHURU at the onset of both experiments (Figure 1a). Here, LMH exclusion increased biomass and productivity within existing vegetated patches for the first two years of the GLADE experiment[11], whereas bare patches declined slowly and linearly, at a rate of ~1.6% per year, over a 17-year period following LMH exclusion. Most notably, cover of bare patches on the red soils required 17 years of LMH exclusion to reach levels comparable to grazed savanna on black cotton soils (Figure 1a).

Although both ecosystems have a long evolutionary history of herbivory, they exhibit different levels of resilience to LMH. In the black cotton ecosystem, herbivory is important in maintaining both productivity[20] and plant diversity, the latter by creating gaps that allow forbs and sub-dominant grasses to coexist[21]. In contrast, and on red soils, LMH exclusion does not trigger closure of the understory canopy, even after 17 years. Here, the difference in response times between vegetated patches (increasing within 2 years) versus bare patches (requiring >17 years for full closure of the understory canopy), suggests that the red soil ecosystem exists as a mosaic of two alternative stable states[15,22], where vegetated patches represent a resilient state similar to the black cotton ecosystem. In contrast, bare patches of sealed soil may represent an alternative state that requires longer time frames or active intervention to recover from historic levels of herbivory[23]. This interpretation hypothesizes that grazing over the past century, potentially in concert with fire suppression following European settlement, induced the formation of a mosaic of bare patches and woody vegetation clusters, but the existence and time frame of such a grazing effect has not been measured.

Comparison across GLADE and UHURU provides further insights to the role of LMH in bare patch recolonization by herbaceous vegetation. Within GLADE, the extent of bare patches declined linearly in exclusion plots over the first 16 years, suggesting that bare patches are not a permanent stable state, but rather can be eventually restored simply through alleviation of herbivory. However, this process is sufficiently slow that exclusion of all LMH for this period of time may not be feasible for pastoralists that rely on livestock for their livelihoods.

While exclusion plots in both UHURU and GLADE recovered slowly over time, dynamics in control (grazed) plots varied among experiments. For most control plots, understory cover remained large unchanged through time. However, in the southern (mesic) level of the

UHURU experiment, understory vegetation in plots grazed by wild LMH has steadily shifted from dominance of bare patches to densely vegetated patches at a rate similar to the exclosures (Figure 2). This result suggests that under some conditions, restoration of bare patches may be possible even in the presence of wild LMH. The southern level of UHURU receives the highest rainfall (average of ~640 mm annually). Further, and in contrast to GLADE, grazed plots within UHURU were not used by cattle, the most abundant species of LMH at Mpala. Reduced grazing pressure in UHURU compared to GLADE (where cattle graze the control plots), combined with enhanced plant productivity due to greater rainfall inputs (compared to northern levels of the UHURU experiment) and soils with greater water holding capacity (compared to KLEE), may explain the relative rapid recovery of the understory layer measured within the wettest level of UHURU.

In sum, our results demonstrate that resilience (and, more generally, responses to LMH) are contingent on a suite of factors, including topo-edaphic conditions, rainfall, and LMH abundance. Across a range of rainfall on red soils, LMH have the potential to maintain the system in a two-phase mosaic of bare and vegetated patches. We suggest that the ability of red soils to impede infiltration and generate runoff underlies variation in this response to grazing, in contrast to black cotton soils where water-holding capacity is uniformly high. Ultimately, such differences in soil hydrology may determine how quickly savanna communities can respond to changes in grazing.

Lesson #2: Wild LMH Drive Understory and Overstory Dynamics.

Across KLEE, GLADE, and UHURU experiments, shifts in species composition of understory vegetation occurred at a slower rate than shifts in biomass. During the first decade after LMH exclusion in KLEE, control and LMH exclusion plots remained similar in the relative abundance of dominant grasses and forbs. Community structure only began to diverge after 10 years of LMH exclusion, and continued along a trajectory of continuous, linear divergence in species composition between 10-19 years[24]. Changes to community composition were correlated with the amount of plant biomass consumed by herbivores, suggesting that wild and domestic herbivores similarly maintain community structure (in controls) relative to their relative abundances[24]. In KLEE, a subordinate palatable grass species has come to dominate inside the total herbivore exclosures. This grass is *Brachiaria lachnantha*, and one of the grasses it displaced is *Pennisetum stramineum*, a species common on nutrient enriched sites on black cotton soils. These community shifts associated with herbivore exclusion may reflect long-term shifts in limiting resources, as unconsumed plants are subject to greater light limitation and soil nutrients are increasingly bound in litter and standing dead vegetation. These responses to grazing are similar to patterns reported for mesic grasslands of North America and southern Africa, which also have a long co-evolutionary history of grazing by LMH[25,26].

In the red soil ecosystem, species composition of understory vegetation also remained relatively unchanged during the first 3 years of LMH exclusion despite increased productivity[15]. Over this same period of time, existing vegetated patches within each exclosure became denser and more productive, and began to expand into adjacent bare areas[14]. Long-term compositional shifts have not yet been analyzed quantitatively, but appear to involve the increased abundance of stoloniferous grasses as they colonized bare patches, and decreased productivity of bunchgrasses beneath woody plant communities, as shading and competition with woody plants becomes more intense (e.g. Figure 3; photos from Google Earth).

Trees and other woody plants drive various aspects of savanna structure and function, and have been the subject of intense research[2,27]. The results from KLEE, GLADE, and UHURU demonstrate strong effects of LMH on woody plants at three different ontogenetic stages, sometimes interacting with fire. First, LMH reduce seed production of dominant woody species in all three experiments, including *A. drepanolobium* in KLEE[28], *A. etbaica, A. brevispica, A. mellifera,* and *A. nilotica* in GLADE[29], and *Solanum campylacanthum* and *A. brevispica* in UHURU[30,31]. Second, wild LMH can slow or prevent the recruitment of saplings into adult size classes, and reduce densities of at least some species of woody plants[31-34]. Third, wild LMH increase mortality rates of all species in both sapling and adult size classes[27,34,35]. Woody encroachment after the loss of LMH therefore results from a combination of all three mechanisms, which can collectively lead to increases of woody cover of an order of magnitude or greater.

In all three experiments, LMH exclusion eventually resulted in more woody individuals. These differences occur in both recruiting size classes and among mature woody plants (older than the exclosures), and often took several years to manifest[27,36,37]. For *A. drepanolobium* trees in KLEE, a reduction through time of mature woody plants outside exclosures suggests a non-steady state of the ‘control’ treatments. Elephants have been increasing steadily throughout the study period[38], and it may be more appropriate to think of these experiments as much as studies on controlled increases as controlled exclusions, at least with regard to elephants.

In contrast to the relatively slow effect of LMH exclusion on woody plants in the black cotton ecosystem, the release of suppressed woody individuals on red soils was often dramatic even in the first 1-3 growing (wet) seasons, with increases in size of woody individuals[16,39]. In contrast to understory plants (where responses are related to overall grazing pressure; see above), both the release from suppression and the increase in recruitment of woody individuals were often specific to both the woody plant species and the herbivore guild excluded. Over a decade, the combination of sapling release, reduced woody plant mortality, and increased growth rates of existing woody individuals generated a much larger response of woody cover and biomass to LMH exclusion on red versus black cotton soils[39], likely due to a combination of greater palatability of woody plants and higher abundances of browsing, wild LMH on the red soil[32,40].

Although the two ecosystems differ in the magnitude of LMH effects on woody plant abundance, they exhibit commonalities over the long term on composition of woody plants. In the black cotton ecosystem, dramatic changes in woody species composition occurred in LMH exclosures, where many previously rare species prospered within the previously *A. drepenolobium*-dominated savanna[32,33]. In the red soil ecosystem, the woody plant community was co-dominated by multiple woody species at the start of the GLADE and UHURU experiments. Over the next decade, these species continued to coexist in LMH exclosures (with additional increases in some previously rare species), while browsing by impala enhanced dominance by *A.* etbaica in control plots[41]. On both soil types, wild LMH promote dominance by a single species of woody plants that invests heavily either in mechanical defenses (straight and recurved thorns in *A. etbaica*), or a combination of mechanical and biotic defenses (straight thorns and ants in *A. drepanolobium*). Further, our experiments show that across all topo-edaphic conditions and the precipitation gradient, LMH play an important role in suppressing the development of dense, woody thickets, which in turn enhances forage production for livestock and reduces predation risk for wild grazers[41-44].

Lesson #3: LMH Play Central Roles in Trophic Cascades and Other Indirect Effects.

Carnivore-initiated cascades. Indirect effects occur when one species (the initiator) alters the abundance or traits of another (the receiver) by altering the abundance or traits of a third species (the transmitter) with which both the initiator and receiver interact[45]. The 'green world hypothesis[46] invigorated ecology by proposing that top predators indirectly benefit plants by suppressing herbivore populations, in what came to be known as a trophic cascade (Figure 4a). Implicit in the original formulation of this idea is that cascading interactions triggered by herbivore populations should be relatively weak in ecosystems with intact predator assemblages. However, as pointed out by Paine[47], this expectation may not hold in ecosystems dominated by very large herbivores that consume vast quantities of plant biomass, and that may partially escape top-down control[48,49]. Insights from the KLEE, UHURU, and GLADE experiments have provided evidence for both predator- and LMH-initiated cascades, demonstrating that they are not mutually exclusive and that both types have transformative effects on savanna communities and ecosystems.

Much evidence for indirect effects has been derived from studies of relatively small and short-lived species, often under the semi-controlled conditions of mesocosm experiments[50]. These studies provide a translational framework to understand how larger, free-living organisms interact. Efforts to explore, measure, and elucidate these links are aided by the application of rigorous experimental methods to food-web ecology[51].

Research from the GLADE and UHURU experiments has paralleled a proliferation of studies demonstrating where, when, and how large mammalian carnivores can indirectly benefit plants. By selectively excluding different guilds of wild LMH, the UHURU experiment has identified several ecological relationships involving large carnivores, two species of wild LMH (dik-dik and impala), and overstory and understory plants. For example, restoration of one of the world's most endangered large carnivores, the African wild dog, has been celebrated as a conservation milestone[52]. The return of African wild dogs reduced the abundance of their primary prey (dik-dik) by about 30%[36]. Although dik-dik reduce growth of their preferred food plants (*A. mellifera*), the restoration of wild dogs did not cause a compositional shift in the woody plant community. This may be because rainfall increased during wild-dog extirpation, obscuring any facilitation by wild dogs on woody plants[36]. The experimental exclusion of dik-dik, coupled with the fortuitous recolonization of wild dogs after the construction of the GLADE experiment but before the construction of the UHURU experiment, was crucial in identifying the mechanistic pathways most sensitive to the indirect effects of wild dogs[36,51]. That wild dog recolonization did not trigger a trophic cascade via suppression of dik-dik reminds us that trophic cascades are not a foregone conclusion. Indeed, the buffering of indirect effects are common in food webs comprised of smaller fauna[50]; an emerging challenge for ecologists is to understand why indirect effects attenuate or amplify across trophic levels involving large mammals.

One clue to understanding the outcome of trophic cascades lies not within the ecology of large mammals themselves, but in the evolutionary response of plants to herbivory. Specifically, plant defenses – thorns, spines, chemicals, and symbiotic ants – redirect trophic flows across species, space, and time. For example, impala avoid bushy areas where they are vulnerable to predation, thereby concentrating their foraging efforts in safer, open areas[41; see also 42,43]. These open areas or "glades" – a product of traditional pastoralism – are surrounded by thorny trees. Beyond this thorny ring, tree communities comprise a greater proportion of species lacking large thorns. Using the UHURU experiment, Ford et al.[41] isolated the effects of herbivory by impala from those of other wild LMH to show that impala suppressed the abundance of less-thorny tree species, but not the thorniest ones. In sum, risk of predation causes impala to avoid densely wooded areas, thereby resulting in less thorny tree communities where their predators hunt.

Through GLADE and UHURU, we chose to focus on trophic interactions—and the potential for trophic cascades—involving impala and dik-dik. We targeted these two species of wild LMH for two reasons. First, elephant, impala, and dik-dik populations dominate the wild LMH community at Mpala, accounting for over 85% of the biomass density (average kilograms per square kilometer) of wild LMH. Although elephants attain higher biomass densities than impala or dik-dik, populations of all three wild LMH consume equivalent amounts of energy based on allometric equations for field metabolic rates[16]. Thus, all three species should be particularly influential in shaping the abundance and distribution of plants across the landscape. Second, because their massive size typically prevents predation and thus top-down control of their populations by carnivores[49,54], we assumed that any trophic cascades in this landscape would not be routed through elephants. We therefore explored pathways for trophic cascades that involved (smaller) impala and dik-dik, based on a combination of their ecological dominance and the potential for their populations to be limited top-down.

Outcomes of trophic cascades involving smaller-bodied, wild LMH (dik-dik) and medium-sized wild LMH (impala) contrast with theoretical predictions. Shurin and Seabloom[53] predicted that trophic cascades were more likely with smaller-bodied prey (or larger predator : prey size ratios), partly because smaller-bodied prey might incur more total mortality from predation[54]. We believe the limited evidence for this prediction reflects compensation for the loss of dik-dik by other browsing ungulates following wild dog restoration[36], and the constraints that territoriality imposes on the ability of dik-dik to shift their activity to areas of low perceived predation risk[55] (as impala do).

From the wolves of Yellowstone to the dingoes of Australian deserts, evidence for trophic cascades have helped raise the profile of carnivore conservation. For the most part, evidence for trophic cascades involving large carnivores has relied on correlative and observational methods[41,51]. However, such methods have limited power to establish mechanistic cause-and-effect inferences, and challenges in interpreting correlative results have mired ecologists in debates over causation and the role of trophic cascades in conservation. The long-term, replicated, and semi-controlled nature of field experiments provide a powerful tool to resolve these debates.

Herbivore-initiated cascades.

The Laikipia exclosure experiments have played a fundamental role in the discovery that LMH exert a diverse range of indirect effects on smaller consumers[14,35,56-59]. Keesing[60-62] showed that the exclusion of large herbivores in KLEE led to a rapid and sustained doubling of small-mammal abundance. Subsequent research in UHURU has revealed a pattern that is congruent with, and of similar magnitude to, Keesing's results[14,63,64]. These effects appear to stem chiefly from exploitation competition: the release of herbivorous and omnivorous rodents from competition for food[62]—especially seeds, which are the primary food for the dominant small-mammal species, and the production of which is suppressed by ungulate herbivory[28,29]. It is plausible that a release of small mammals from avian predation inside the more thickly vegetated exclosure plots might also have contributed to the net doubling of rodent density, and this possibility has not yet been tested directly. However, the appeal of this hypothesis is dampened by the observation that snake abundance also doubles inside exclosures[65] (Figure 4b), suggesting that any release from aerial predators might be at least partially offset by a corresponding increase in terrestrial predators. Moreover, the abundance and diversity of birds also increased in the KLEE megaherbivore (elephant and giraffe) exclosures, apparently in response to increased availability of food and perches[66], suggesting that any increase in the availability of antipredator refuges in the absence of LMH might be offset by an increase in the number of foraging avian predators. Finally, giving-up densities—a surrogate for time spent in artificial food patches[67]—do not differ significantly between exclosure plots and paired controls in the UHURU experiment, implying that perception of risk by small mammals is unaltered by large-mammal exclusion[68] (Figure 5).

The increase in small-mammal density inside exclosures propagates even further throughout the food web (in addition to increases in snakes, see above), leading to increased ectoparasite abundance and the risk of tick- and flea-borne diseases[69-71] (Figure 4b), as well as of rodent-borne macroparasitic helminths[72]. The rate of seed predation by rodents in UHURU increased nearly tenfold when megaherbivores were excluded, and increased by another 50% when antelopes (primarily dik-dik and impala) and zebra were excluded[30]. Similarly, and in some (but not all) years, seedling predation of trees more than doubled inside exclosures[56,73,74], with ramifications for tree demography[35]. In these cases, as with the increases in snake and bird abundance inside KLEE, the exploitation competition between ungulates and smaller herbivores lengthens into a multi-trophic pathway.

In addition to trophic pathways, LMH initiate indirect effects via ecosystem engineering, especially with respect to woody-plant assemblages. The heterogeneous distribution of large herbivores across savanna landscapes, as well as differences among those species in forage preferences and diet composition[75], influences the relative density of woody-plant cover[76-79] and spatial patterns in the primary productivity, community composition, and traits of trees[32,41,76]. Elephants are particularly potent architects, owing to their ability to topple trees and splinter large branches, which shapes understory plant communities[80] and creates habitat for small animals[81,82] (Fig. 4c).

Notably, the strengths of these herbivore-initiated indirect effects are variable in space, in ways that seem to be explained at least in part by underlying differences in primary productivity. Exclusion of wild LMH systematically increases population size structure and abundance of a common understory shrub, *Hibiscus meyeri*, as rainfall increases[83]. Exclusion of (acaricide-treated) cattle increased abundances of nymphal and adult ticks[84], an effect borne out across entire landscapes[85]. Lizards and arthropods occurred at higher density inside LMH exclosures, but the magnitude of this response was far greater in the relatively low-productivity GLADE exclosures than in the higher-productivity KLEE exclosures[76]. Similarly, the strength of the response of rodents and ticks to wildlife decline decreased with increasing rainfall[71]. These results might have been influenced to some extent by confounding differences in plant species composition and other environmental attributes that co-vary with this productivity in Laikipia; however, a global meta-analysis showed both that LMH generally suppress the abundance and species richness of diverse small-consumer taxa and that these indirect effects are generally stronger (i.e., more negative) at low-productivity sites[86].

In sum, although there is evidence for positive indirect effects of some species of LMH (especially elephants) on some consumer taxa at local scales, the net effect of LMH removal is generally to increase the abundance of a diverse range of small consumers. A next frontier in this research program is to ascertain how well these results from hectare-scale experimental manipulations scale up to predict the consequences of genuine defaunation. Our work has shown that the answer depends upon how defaunated landscapes are used, because the replacement of wild LMH with livestock can at least superficially maintain many of the direct and indirect effects of the former[63].

Lesson #4: LMH affect ant-acacia and pollination networks

Cooperative partnerships among species, known as mutualisms, play important roles in the structure and function of African savanna ecosystems. Below-ground, termites engage in fungal or endosymbiotic associations to break down cellulose, while plants may partner with mycorrhizal fungi or rhizobial bacteria to obtain key nutrients. Above ground, some acacia trees are protected by defensive ants, and many savanna plants rely on pollinators for reproduction. Research from both the KLEE and UHURU experiments has revealed how LMH can exert unexpected and powerful indirect effects on the structure and dynamics of some of these mutualist guilds. For example, the loss of wild LMH can change a species from a mutualist to a competitor. Work on an understory shrub in UHURU, *Hibiscus meyeri*, shows that neighboring plants conceal *H. meyeri* from wild LMH, thereby reducing herbivory and increasing its fitness. By contrast, following wild LMH loss, neighboring plants decrease its fitness, presumably by competing for water and other resources[87]. LMH can also affect plants' investment in mutualisms. For example, work within KLEE revealed that the loss of wild LMH from the black cotton ecosystem triggers a breakdown in the mutualism between *A. drepanolobium* and its defensive ant partners[88]. In the decade following wild LMH exclusion, acacia trees reduced their investment in both the housing (swollen spine domatia) and food (extrafloral nectar) they provide to ant symbionts[89], shifting the balance of competition from dominance by a highly defensive and beneficial ant partner (*Crematogaster mimosae*) that depends strongly on these plant-provided resources, to dominance by a non-defending ant species (*C. sjostedti*) that does not rely upon these resources. The shift from mutualistic to non-defending ant species, in turn, reduced growth and increased mortality of the host acacia trees[88]. Paradoxically, the loss of wild LMH that feed on these acacias results in a slower growth and reduced survival of individual trees, mediated by a complex interaction cascade that links large browsers, plants, and insects. The KLEE experimental framework allowed us to tease apart this network of interactions, and to infer the powerful role wild LMH have played this widespread defensive mutualism.

The impact of wild LMH loss on savanna mutualisms isn't necessarily negative. For example, working in the UHURU experiment, Guy et al.[90] examined how the exclusion of LMH affects networks of plants and their pollinators. In the absence of all LMH, plant communities had higher floral diversity and abundance, and were visited by a more diverse and abundant group of pollinators. These more diverse communities, in turn, formed interaction networks that were more generalized, more nested, and were characterized by higher interaction diversity – all properties which tend to stabilize plant-pollinator communities, and make them more robust to the extinction of member species[91-95]. By feeding on plants, wild LMH suppress plant reproduction (see above), leading to lower floral and pollinator abundance, and more specialized and less robust pollination networks. Here, the (relatively) large scale experimental framework provided by UHURU allowed researchers to demonstrate the surprising and strong indirect effects that wild LMH can exert on mutualisms within African savannas.

Lesson #5: Cattle Can Compensate for the Loss of Wild LMH, to Some Degree.

In many savannas and grasslands, the loss of wild LMH occurs in conjunction with the addition of livestock to the system. Livestock often are kept at higher abundances (higher stocking rate, or more total animal-days per year) than wild LMH, and are often a more continuous presence than more nomadic or migratory wild LMH (even in nomadic pastoral systems). In considering these effects, it is important to distinguish among (a) the effects of loss of a specific guild or species of wild LMH without replacement by domestic herbivores; (b) the loss of wild LMH with equivalent replacement by livestock herbivory; and (c) loss of wild LMH, in which livestock are replaced at higher stocking rights than wild LMH.

The three experiments differ in if and how livestock are manipulated. In GLADE, cattle are included or excluded along with wild LMH (all LMH excluded or all LMH allowed). In UHURU, cattle were discouraged from visiting any of the plots, which may explain grass colonization of bare spots even in UHURU control plots (see above). The KLEE experiment, with its uniquely separate manipulation of wildlife and cattle, was designed to test scenario (a) and scenario (c) (although in the latter case cattle are stocked at what is considered a “moderate” rate, except for “heavy grazing” subplots).

In KLEE, the loss of particular species or guilds of LMH is less important to the dynamics and composition of understory vegetation than the total herbivory exerted by all LMH (see above). In other words, cattle can largely compensate for the loss of wild LMH in affecting understory vegetation. Results from both productivity experiments and satellite normalized difference vegetation index (NDVI) demonstrated a positive relationship between understory productivity and the amount of understory biomass removed annually by herbivores (the inverse of residual biomass)[20] (Figure 6a). Cattle increase understory productivity because biomass removal stimulates productivity, and they remove more understory biomass than wild LMH. Additionally, understory composition and dominance were strongly related to residual plant biomass, a measure of herbivore off-take[24] (Figures 6b and 6c). Finally, understory composition also varied along a gradient of total herbivory, such that the exclusion of all LMH led to the greatest change in the understory community[96].

Species richness of understory plants is highest immediately (first two years) after episodic droughts in the presence of cattle[97]. The combination of drought and biomass removal by cattle creates gaps in the understory layer that otherwise are uncommon in black cotton soils (see above). When rains follow a drought, bare patches are colonized by species that are otherwise rare[97]. Therefore, and conversely, the loss of LMH allows more dominance and less plant diversity in this system.

In summary, data from KLEE on understory plants has revealed evidence for functional similarity between moderately-stocked cattle and wild LMH. These results suggest that the loss of all LMH would change understory dynamics substantially, but that cattle, at moderate stocking rates, may largely compensate for wild LMH loss, at least in terms of understory composition and productivity.

Lesson #6: Cattle Enhance Heterogeneity and can Coexist with Wild LMH.

Throughout much of sub-Saharan Africa, cattle are contained each night in temporary corrals (bomas), and are accompanied by herders while foraging each day. After abandonment (at intervals of weeks to months), bomas develop into ecosystem hotspots characterized by high nutrient concentrations and unique plant community composition[98-101]. On both the red soil and black cotton ecosystem, abandoned bomas develop into highly productive, treeless ‘glades’ supporting nutrient-enriched grasses. Furthermore, glades on black cotton soil are ringed by unusually high densities of large trees which provide important structural and compositional heterogeneity in a landscape that is otherwise quite homogenous[100]. Glades attract both domestic and wild large herbivores[101,102] and also support higher abundances of other wildlife[79].

Work from KLEE and GLADE suggests that antelopes (primarily impala) and zebra contribute to the long-term maintenance of glade hotspots, while megaherbivores dampen glade-associated heterogeneity. In KLEE, antelopes and zebra reinforced landscape heterogeneity over time by maintaining glades in an early successional state. Cattle and megaherbivores, on the other hand, accelerated succession via preference for the palatable, early successional grass species, *Cynodon plectostachyus*[103]. Finally, both caging and clearing improved tree survival and growth inside glades, indicating that wild browsers help to maintain glades in a treeless state over the long-term[97]. Within the red soil ecosystem, *Cynodon plectostachyus* dominates the short-statured grazing lawns on glades, even in the face of intense grazing pressure[13]. The resistance of these glades to grazing contrasts with grazing-induced reductions in herbaceous productivity on the surrounding nutrient-poor red soils[13]. Further, antelopes reinforce glade persistence by consuming nutrients from the surrounding bushland and preferentially bedding (and depositing nutrients) in glades[41]. This net input of nitrogen to glades is sufficiently large on an annual basis to offset other pathways of gaseous N loss from glades, and maintain their nutrient-enriched status[13]. This nitrogen effect in the black cotton soils is reinforced by increased termite mounds densities. Together, these results emphasize that different guilds of wild LMH have different effects on the persistence of glade hotspots and the landscape heterogeneity they provide; in particular, evidence suggests that loss of antelopes and zebra would lead to more rapid degeneration of these hotspots, while loss of megaherbivores would promote maintenance of glade hotspots. Furthermore, these findings illustrate how management changes resulting in the loss of bomas from these ecosystems could dramatically alter their structure and function.

Interactions between cattle and wild LMH are largely context-dependent; negative effects occur primarily during dry periods while less negative or even positive effects ensue during wet periods. The presence of wild LMH reduces cattle performance, at least during dry periods[104, see also 105]. Competition between cattle and wild LMH appears to be intensified in burned areas and on termite mounds (W.O. Odadi, unpublished data), both of which are nutrient-rich foraging hotspots that attract high concentrations of LMH[106-110]. Supplementing cattle with protein appears to partially moderate competition for forbs between cattle and wild LMH[111].

While wild LMH compete with cattle during dry periods, they can facilitate cattle during wet periods; weight gains of cattle increase in areas accessible to wild LMH[104]. This pattern is mediated through enhanced forage quality and associated improved cattle diet quality in areas where wild LMH also graze. This facilitative effect appears to be largely attributable to zebras, whose removal of 'rank' grass allows regrowth of higher quality forage[112].

Taken together, these findings indicate that the interaction between cattle and wild LMH are more complex than previously assumed. The nature and magnitude of these interactions are modified by various factors including weather conditions, presence or absence of megaherbivores, prescribed burning, termite mounds and nutritional management of cattle. Overall, these findings suggest that cattle (*at moderate densities*) and wild LMH are not uniformly detrimental to each other, and that deleterious effects can be lessened through improved grazing management and enhanced conservation of wild LMH.

A Final Note on the Role of Fire in East African Savannas: Interest in the interactions between fire and herbivory in structuring savanna ecosystems has increased in recent decades. In 2013, we introduced a series of fire treatments in each of the 18 KLEE plots, allowing us to test how fire interacts with different guilds of LMH. Plots associated with more diverse combinations of LMH burned less severely, suggesting that additional guilds of LMH may successively dampen the effect of burning[113]. While the negative effects of cattle and wild ungulates on fire temperatures are associated with reduction in understory fuel loads, the effects of megaherbivores result from reductions of tree cover and therefore in fine woody debris[113]. This is in contrast to the model prediction that megaherbivores, by reducing tree cover, facilitate understory growth and thereby promote more intense fires[114]. As is the case in most other savanna ecosystems, trees within KLEE rarely form canopies dense enough to inhibit understory growth. On the contrary, there tends to be denser understory beneath tree canopies underneath short trees, such that cattle may partly compensate for the loss of wild LMH by reducing the herbaceous, but not woody, fuels.

One major gap in our knowledge is the role of fire-grazer interactions in the red soil ecosystem. The extent of bare soil patches in this ecosystem often suppresses fire spread, but where grass and fuel continuity increase, opportunities may increase for prescribed fire applications on these soils as well.

Closing

Large mammalian herbivores have profound effects on ecosystems, and their loss may lead to alternative stable states very different from those that once existed. Ecosystems that have lost their large mammals in the last 10,000-250,000 years are likely to represent a new baseline, with no historic (or prehistoric) analog [3,5,115]. Livestock (in our case cattle) may compensate for these losses in some aspects of their impact on the herbaceous community, but not the woody community.

Efforts to translate the ecology of the 'small and controlled' to the 'large and wild' are not merely conceptual contributions to generality in ecology[116]; they also provide a means to revalue conservation priorities and public perceptions of wildlife. As Hutchinson opined over a half century ago in "Homage to Santa Rosalia"[117]:

> "…I cannot refrain from pointing out the immense scientific importance of obtaining a really full insight into the ecology of the large mammals of Africa while they can still be studied under natural conditions. It is indeed quite possible that the results of studies on these wonderful animals would in long-range though purely practical terms pay for the establishment of greater reservations and National Parks than at present exist."

Hutchinson was among the pioneers in articulating this linkage between the basic science of community ecology and conservation – especially in East Africa. We have established and maintained a series of (relatively) large scale, long-term experiments with the dual purpose of revealing how large mammals impact community structure and ecosystem function of semiarid rangelands, and of providing insights relevant to conservation of these increasingly imperiled ecosystems. We hope that this work inspires future generations of ecologists and conservation biologists working in these grand ecosystems.

Acknowledgements

We thank Nick Georgiadis, Maggie Kinnaird, Mike Littlewood, Dino Martins, and other staff at the Mpala Research Centre. We thank Gilbert Busienei, Marissa Dyck, Brandon Hays, Stephen Kinyua, Simon Lima, and Jackson Lima for assistance with the UHURU experiment. The UHURU experiment was supported by NSF DEB grants 1355122, 1457691, 1547679, and 1556728, an NSERC Research Tools and Instruments grant, and the University of Wyoming. The KLEE research was carried out under Government of Kenya research clearance permit No. NCST/RCD/12B/012/42. We would like to thank Frederick Erii, John Lochikuya, Mathew Namoni, Jackson Ekadeli, Steven Ekale, and Patrick Etelej for their invaluable assistance in the field. The KLEE exclosure plots were built and maintained by grants from the James Smithson Fund of the Smithsonian Institution (to A.P. Smith), The National Geographic Society (Grants 4691-91 and 9106-12), The National Science Foundation (LTREB DEB 97-07477, 03-16402, 08-16453, 12-56004, and 12-56034) and the African Elephant Program of the U.S. Fish and Wildlife Service (98210-0-G563) (to T.P. Young, C. Riginos, and K.E. Veblen).

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Figure Captions

Figure 1. Changes in the abundance of (A) bare patches, and (B) densely vegetated herbaceous patches within the KLEE (black cotton) and GLADE (red soil) experiments in central Laikipia, Kenya. The black cotton ecosystem is flat and underlain by high-clay vertisols (50% clay, 24% sand), while the red soil ecosystem is gently sloping and underlain by aridisols (15% clay, 74% sand). At each site, we placed pin frames in a systematic grid (n = 30 frames per plot on black cotton; 144 frames per plot on red soil) across each study plot (n = 3 grazed and 3 ungrazed plots on each soil type), and then calculated the percent of frames within a plot in which the 0 – 2 out of 10 pins contacted vegetation (bare patches) and the percent of frames in which 8 – 10 pins contacted vegetation (densely vegetated patches). On black cotton, densely vegetated patches increased rapidly following grazer removal, reaching nearly 100% (full canopy closure) in the first 5 years. In contrast, a large proportion (~40-45%) of the study plots on red soil initially consisted of bare patches, which in the ungrazed treatment were slowly recolonized by grasses over time. After 17 years, the ungrazed red soil plots attained a similar percentage of bare soil and densely vegetated patches as the grazed black cotton plots.

Figure 2. Changes in the abundance of bare and densely vegetated herbaceous patches in 4 exclosure experiments in central Laikipia, Kenya. Study sites are all located on gently sloping terrain and are distributed along a north-south rainfall gradient. At study sites with red sandy soils, bare patches declined (and densely vegetated patches increased) over time in ungrazed compared to grazed plots across the entire rainfall gradient. In contrast, at one study site with red sandy soil and high rainfall, both the grazed and ungrazed plots underwent a large decline in

bare patches (and corresponding increase in densely vegetated patches) over the first 8 years of the experiment.

Figure 3. Examples of changes in spatial pattern of vegetation cover over time on sandy red soils (left panels) versus black cotton soils (right panels) in response to large herbivore exclusion. In each panel, the red square shows the location of fencing that excludes all mammalian ungulate herbivores, and the blue squares show two paired 50 x 50 m areas with and without herbivores for the specified time period. In the gently sloping, red sands, herbivores have maintained a 2-phase mosaic of bare patches and vegetated patches, while herbivore exclusion led to near-complete contraction of bare patches by year 16. In contrast, black cotton soils supported homogenous vegetation cover both in the presence and absence of herbivores throughout the experiment. On the sandy soils, woody cover increased substantially and linearly over time, while on clay soils, woody cover increased more slowly, with thickening not evident until >15 years of herbivore exclusion.

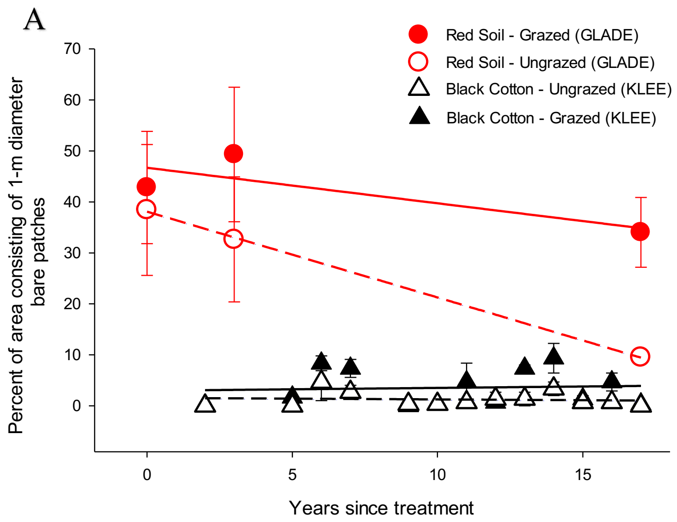
Figure 4. Trophic cascades and indirect effects of LMH on smaller consumers. Solid black arrows signify flows (transfers of energy, utilization, state changes); dashed arrows signify indirect effects (blue, positive/facilitative; red, negative/inhibitory). (a) Classical trophic cascade, in which carnivores indirectly benefit plants by suppressing herbivores. (b) Extended trophic cascade, also known as 'trophic ricochet'[118] or 'trophic bounceback'[119]. Here, exploitation competition between large and small herbivores (1) leads to a negative indirect effect of large herbivores on snakes (3), ticks (4), and lizards (2) that feed on small herbivores. (c) Indirect

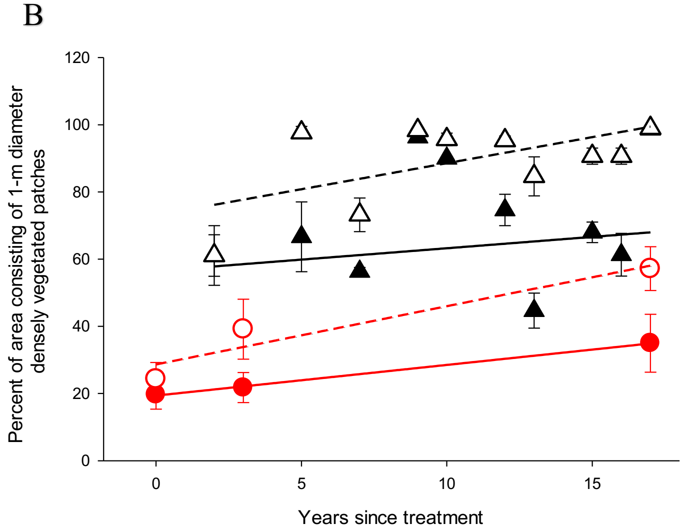
effects via ecosystem engineering. Here, elephants induce a state change in trees by damaging them while foraging, which increases habitat quality for arboreal geckos (5).

Figure 5. Giving-up densities (GUDs) collected from artificial food patches (seed trays) following the long rains (July 2016) and at the end of the dry season (March 2017) from the UHURU experiment. Error bars are +/- standard deviation. GUDs that share a letter are not statistically significant (rank sum tests). Small mammals do not perceive risk differentially between large-mammal exclusion and open control plots (Kruskal-Wallis H = 8.01, P<0.01), although GUDs are lower in open plots following the long rains, which likely is reflective of higher densities during this time period.

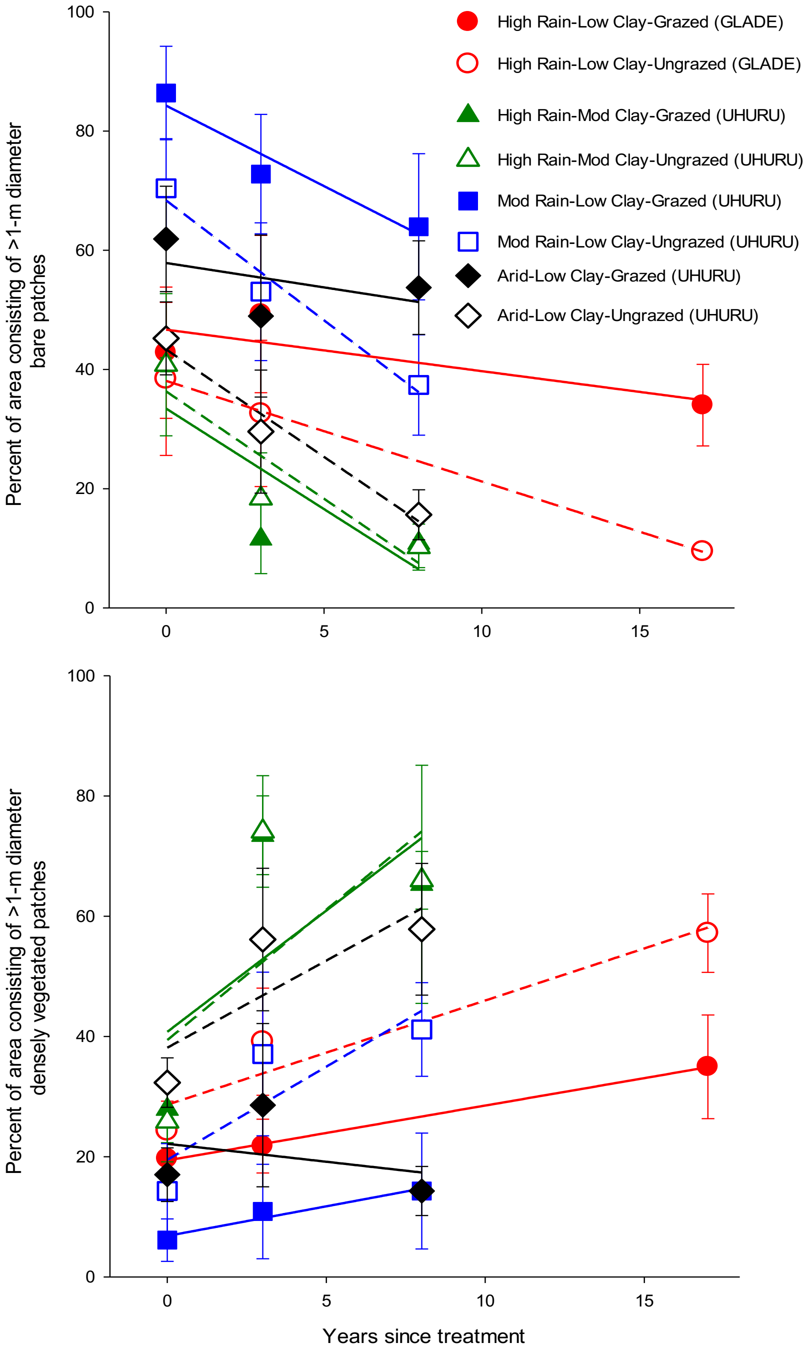
Figure 6. Residual herbaceous biomass (inversely related to biomass offtake) vs. (A) ANPP and (B) plant community composition (represented by RDA 1 score) in KLEE. All values are means and 1 SE of 3 reps per treatment (with each treatment value averaged over all available time steps). C = cattle allowed, W = mesoherbivore wildlife (antelopes and zebra) allowed, M = megaherbivores allowed, and O = all LMH excluded. a, b, and c reprinted, respectively, from Charles et al. 2017, Veblen et al. 2016 and Riginos et al. revision.

Figure 1


A
Red Soil - Grazed (GLADE)
Red Soil - Ungrazed (GLADE)
Black Cotton - Ungrazed (KLEE)
Black Cotton - Grazed (KLEE)
Percent of area consisting of 1-m diameter bare patches
70
60
50
40
30
20
10
0
0
5
10
15
Years since treatment


B
Percent of area consisting of 1-m diameter densely vegetated patches
120
100
80
60
40
20
0
0
5
10
15
Years since treatment

931 **Figure 2**



932
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Figure 3

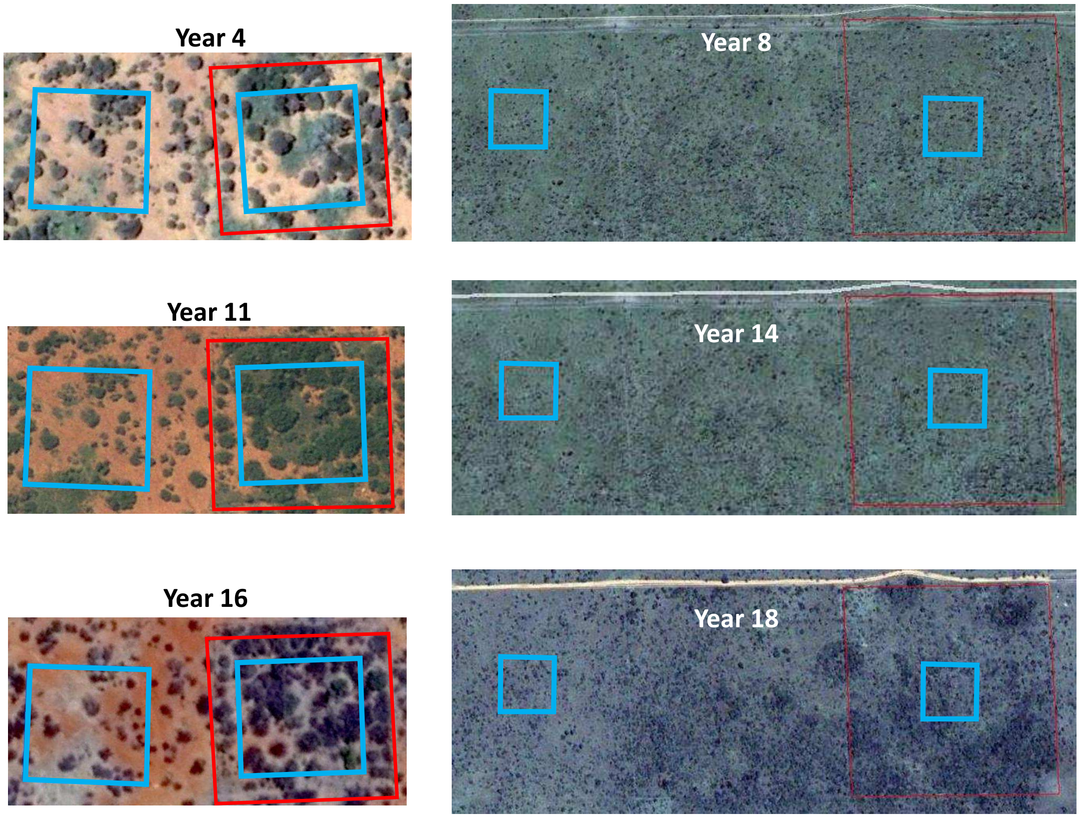

Figure 4

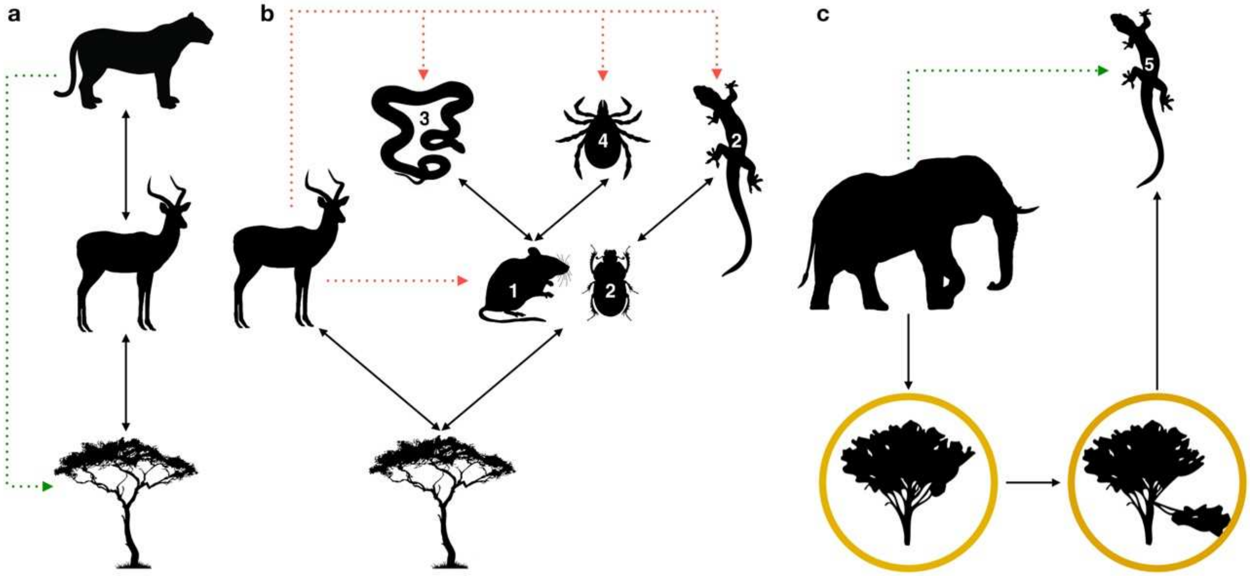

Figure 5

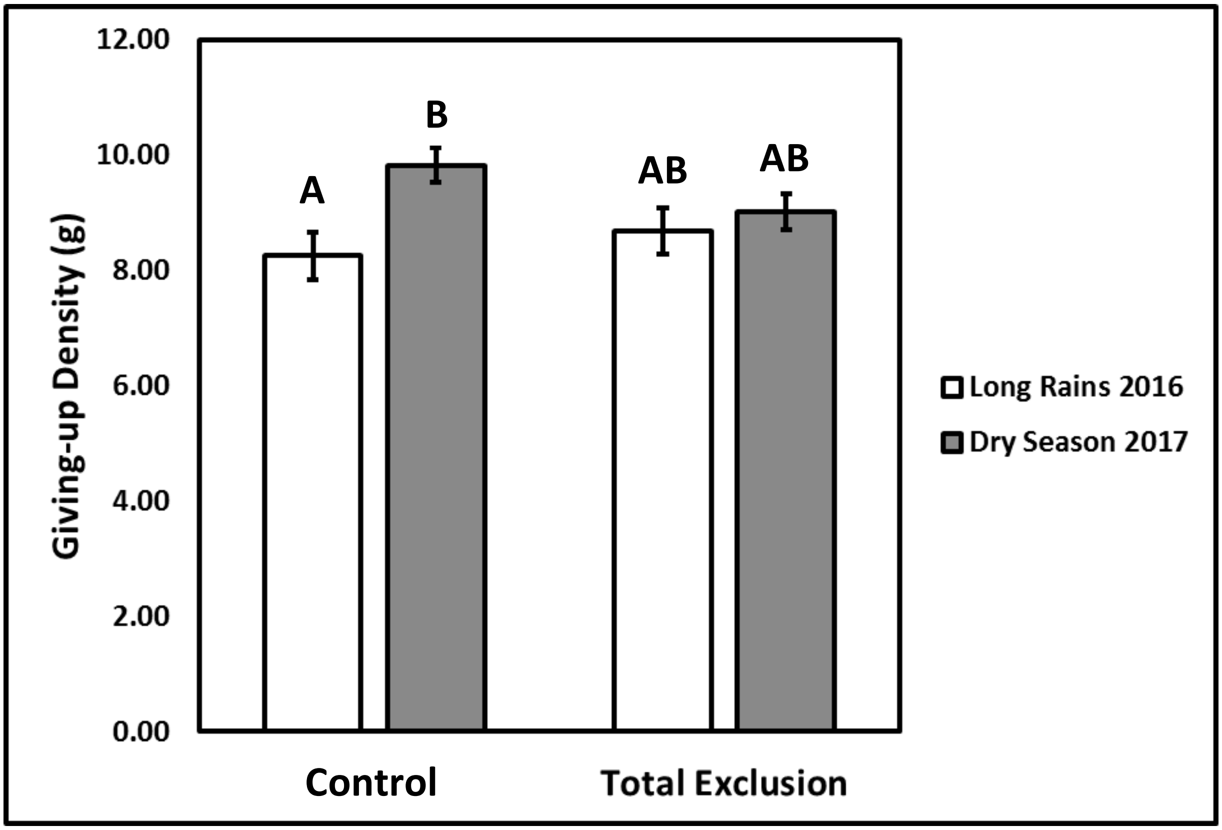
12.00
10.00
8.00
6.00
4.00
2.00
0.00
Giving-up Density (g)
A
B
AB
AB
Control
Total Exclusion
Long Rains 2016
Dry Season 2017

Figure 6

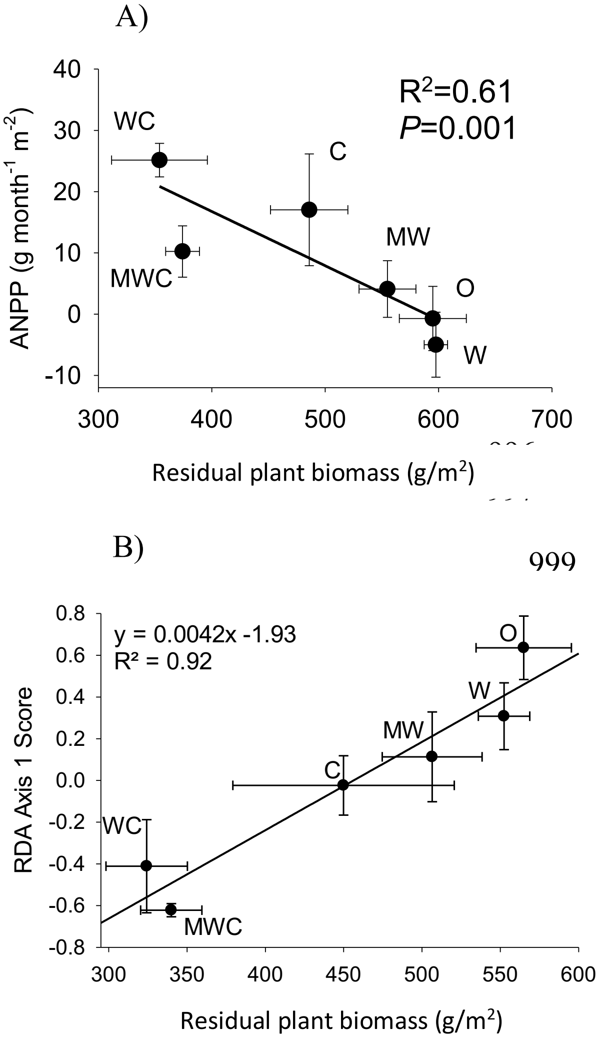
A)
R²=0.61
P=0.001
WC
C
MW
MWC
O
W
ANPP (g month⁻¹ m⁻²)
40
30
20
10
0
-10
300
400
500
600
700
Residual plant biomass (g/m²)
B)
y = 0.0042x -1.93
R² = 0.92
O
W
MW
C
WC
MWC
RDA Axis 1 Score
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
300
350
400
450
500
550
600
Residual plant biomass (g/m²)

Table 1. Characteristics of the three Laikipia exclosure experiments.

	KLEE	**UHURU**	**GLADE**
Principal Investigators	Truman Young, Corinna Riginos, Kari Veblen, Duncan Kimuyu, Wilfred Odadi	Jacob Goheen, Robert Pringle, Todd Palmer	David Augustine, Mahesh Sankaran, Jayashree Ratnam
Locations	36°52'E, 0°17'N	36°89'E, 0°28'N (southern plots) 36°91'E, 0°40'N (central plots) 36°87'E, 0°48'N (northern plots)	36°89'E, 0°28'N (southern plots) 36°91'E, 0°40'N (central plots)
LMH guilds excluded	1) none (control) 2) megaherbivores 3) LMH >20kg 4) cattle (crossed)	1) none (control) 2) megaherbivores 3) LMH >20kg 4) all LMH	1) none (control) 2) all LMH
# LMH treatments	Six	Four	Two
Date established	1996	2008	1999
Plot size	200 x 200m	100 x 100m	70m x 70m
Replicates	3 blocks (replicates) x 6 treatments	3 rainfall sites x 3 blocks (replicates) x 4 treatments	3 sites (replicates) x 2 features (glade vs woodland) x 2 treatments
Mean annual rainfall (2000-15)	615 mm	640 mm (south) to 440 mm (north)	640 mm (south) to 540 mm (north)
Slope	Flat	1-2%	1-3%
Soil type	Black cotton clay (Pellic Vertisol)	Red sandy clay loam (Ferric and Chromic Luvisols)	Red sandy clay loam (Ferric and Chromic Luvisols)
% Clay, Silt, Sand	50, 26, 24	10-27, 51-73, 17-22	15, 11, 74
Unique features	Livestock (two levels); controlled burn sub-plots; glades	Rainfall gradient; exclusion of small (5-10kg) ungulates	Glades
Dominant woody species	*Acacia drepanolobium*	*Acacia mellifera, A. etbaica, A. brevispica*	*Acacia mellifera, A. etbaica, A. brevispica*
Dominant grasses	*Pennisetum stramineum, Bracharia lachnantha, P. mezianum, Themeda triandra*	*C. dactylon, Pennisetum stramineum, Digitaria macroblephara (milanjiana?)*	*Digitaria milanjiana, Cynodon dactylon, Pennisetum stramineum*
Dominant native ungulates	Plains zebra, Grant's gazelle, hartebeest, giraffe	Impala, dik-dik, elephant	Impala, dik-dik, elephant

Less abundant native ungulates	Elephant, Grevy’s zebra, eland, buffalo, oryx	Plains zebra, Grevy’s zebra, eland, waterbuck, giraffe	Plains zebra, Grevy’s zebra, eland, waterbuck, giraffe
Dominant livestock species	Cattle	(Cattle largely excluded)	Cattle
Publications (#)	69	18	14