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Relationships Between Cattle and Biodiversity in Multiuse Landscape Revealed by Kenya Long-Term Exclosure Experiment[☆]

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ABSTRACT

On rangelands worldwide, cattle interact with many forms of biodiversity, most obviously with vegetation and other large herbivores. Since 1995, we have been manipulating the presence of cattle, mesoherbivores, and megaherbivores (elephants and giraffes) in a series of eighteen 4-ha (10-acre) plots at the Kenya Long-term Exclosure Experiment. We recently (2013) crossed these treatments with small-scale controlled burns. These replicated experimental treatments simulate different land management practices. We seek to disentangle the complex relationships between livestock and biodiversity in a biome where worldwide, uneasy coexistence is the norm. Here, we synthesize more than 20 yr of data to address three central questions about the potentially unique role of cattle in savanna ecology: 1) To what extent do cattle and wild herbivores compete with or facilitate each other? 2) Are the effects of cattle on vegetation similar to those of wildlife, or do cattle have unique effects? 3) What effects do cattle and commercial cattle management have on other savanna organisms? We found that 1) Cattle compete at least as strongly with browsers as grazers, and wildlife compete with cattle, although these negative effects are mitigated by cryptic herbivores (rodents), rainfall, fire, and elephants. 2) Cattle effects on herbaceous vegetation (composition, productivity) are similar to those of the rich mixture of ungulates they replace, differing mainly due to the greater densities of cattle. In contrast, cattle, wild mesoherbivores, and megaherbivores have strongly guild-specific effects on woody vegetation. 3) Both cattle and wild ungulates regulate cascades to other consumers, notably termites, rodents, and disease vectors (ticks and fleas) and pathogens. Overall, cattle management, at moderate stocking densities, can be compatible with the maintenance of considerable native biodiversity, although reducing livestock to these densities in African rangelands is a major challenge.

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Introduction

Worldwide, rangelands that support domestic livestock production are playing an increasingly important role in biodiversity conservation (du Toit et al., 2017). In particular, shrinking wildlife habitats and declining

livestock revenues underpin changing management of rangelands toward mixed uses, especially promoting coexistence between livestock and wildlife (Niamir-Fuller et al., 2012; Reid, 2012; Chaminuka, 2013; Vetter, 2013; Western et al., 2015; Fynn et al., 2016; Ranglack and du Toit, 2016; Allan et al., 2017; Holechek and Valdez, 2018). It is clear that livestock-wildlife coexistence is problematic when livestock are inappropriately managed to the point of range degradation (du Toit and Cumming, 1999; Asner et al., 2004; Fynn et al., 2016; Coppock et al., 2017). However, less clear is the compatibility between wildlife and moderately stocked, well-managed livestock (du Toit et al., 2010, 2017; Butt and Turner, 2012; Reid, 2012; Allan et al., 2017; Crowsigt et al., 2017).

Competitive relationships between livestock and large ungulate wildlife are often assumed despite the fact that wild ungulate diets

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and habitat use often differ substantially from those of livestock. Conversely, it is unclear to what extent dietary overlap can be relied upon as a measure of competition (Scasta et al., 2016; Kimuyu et al., 2017b). Indeed, dietary overlap may be strongest when forage species are not limiting (Kilonzo et al., 2005). The more common forage species may not be the species for which ungulates compete most strongly. For example, there may be sufficient grass for all (and overlap in diet), but limiting amounts of N-rich forage (Odadi et al., 2013). We also need to better understand how livestock and wild ungulates, within a given study system, differ in their effects on habitat quality (forage and visibility) or interactively (e.g., nonadditively) influence their habitat. These effects of livestock and wildlife on habitat also can have cascading effects on multiple components of diversity, such as predators, rodents, birds, insects, and pathogens (e.g., Georgiadis et al., 2007; Pryke et al., 2016; Schieltz and Rubenstein, 2016). Yet nearly all studies of the effects of grazing herbivores on communities do not separate the effects of livestock and wildlife. Indeed, in many cases the removal of only one group is studied (typically livestock) and the potential for compensatory effects by the other group (here wildlife, which often can access livestock-exclosure plots) on the response variables is not explored and is often ignored. Alternatively, in the conservation literature, the effects of wildlife loss are often explored in either protected areas without livestock or via exclosures that remove all large ungulates, including livestock. This is problematic because outside of experimental systems the removal of large wild ungulates is not typically isolated, but rather accompanied by the addition of domestic stock. This can lead to mismatches between effects predicted via exclosures and those associated with realistic patterns of wildlife loss (e.g., Young et al., 2013, 2017). Few studies have separated the effects of livestock and wildlife on ecosystems (e.g., Jones, 1965; Veblen et al., 2016), and no fully replicated experimental manipulations of both livestock and wildlife have occurred. Here we synthesize > 22 yr of research from one such experiment, the Kenya Long-term Exclosure Experiment (KLEE), that was designed to examine interactions between cattle and wild ungulates, as well as the separate and combined effects of cattle and wildlife on their habitat. We have also crossed this design with burning treatments, although not as richly (or at as large a scale) as at Konza (Manning et al., 2017) or Kruger (Staver et al., 2017).

In a previous synthesis, we addressed the ways in which the KLEE project illuminated the effects of traditional pastoralism on savanna ecology (Riginos et al., 2012). The current review 1) explores the lessons we have learned about the role of cattle as large herbivores that differ from native wild ungulates, with which they coexist in savanna ecosystems and in many places have functionally replaced, and 2) expands our consideration of pastoral activities to review effects of modern commercial ranching practices (e.g., cattle dipping). We do not cover again here the effects of pastoral practices that dominated the previous review (e.g., bomas/corrals, tree clearing, or fire research outside of KLEE) (see Riginos et al., 2012 for a review of those topics, as well as Pringle et al., 2011; Porensky and Veblen, 2012, 2015; Veblen, 2012, 2013; Porensky and Young, 2013, 2016; Porensky et al., 2013b; Kimuyu et al., 2017a). Instead we focus here on updating and expanding our understanding of the relationships between cattle (and commercial cattle management) and biodiversity. We use KLEE's unique study design to ask three questions about the potentially unique role of cattle in savanna rangelands: 1) To what extent do cattle and wild herbivores compete with or facilitate each other in rangelands where both guilds are present? 2) Are the effects of cattle on vegetation similar to those of wildlife, or do cattle have unique effects? and 3) What effects do cattle and commercial cattle management have on other aspects of savanna ecology, and do these differ from the effects of wildlife?

Study Site and Exclosure Design

This research was carried out at Mpala Conservancy, located on the Laikipia plateau in central Kenya (0°17'N, 36°52'E; 1 800 m asl). The

study site is located within *Acacia drepanolobium* wooded grassland at an elevation of 1 800 m, on heavy clay (“black cotton”) soils. The understory is dominated by several species of perennial grasses, with a rich community of ~100 species of additional forbs and grasses (see Supplement 1 in Porensky et al., 2013a). Mean annual rainfall during the study period (1995–2017) was 600 mm/yr (range 364–1003 mm/yr), which on average falls in a weakly trimodal seasonal pattern, with a distinct dry season December–March. The area has been under various forms of cattle management for > 3 000 yr (Marshall, 1990; Marshall and Hildebrand, 2002; Prendergast, 2011; Marchant and Lane, 2014; Marchant et al., 2018), most recently (past 100 yr) as a commercial ranching operation increasingly tolerant of wildlife (i.e., active wildlife patrols, less wildlife removal and control, maintaining water sources).

The Mpala Conservancy is managed for both wildlife conservation and livestock production. Cattle are stocked at moderate densities (0.10–0.15 cattle ha⁻¹). Wild ungulates commonly found in the black cotton system include plains zebra (*Equus quagga* Gray), Grant's gazelle (*Gazella [Nanger] granti* Brooke), elephant (*Loxodonta africana* Blumenbach), steinbuck (*Raphicerus campestris* Thunberg), Grevy's zebra (*Equus grevyi* Oustalet), cape buffalo (*Syncerus caffer* Sparrman), eland (*Taurotragus oryx* Pallas), giraffe (*Giraffa camelopardalis* L.), hartebeest (*Alcelaphus buselaphus* Pallas), oryx (*Oryx gazella* beisa L.), and warthog (*Phacochoerus africanus* Gmelin) (Veblen et al., 2016). Wildlife densities in Laikipia are the second highest in Kenya, after the Maasai Mara National Reserve.

In 1995, we established the KLEE, designed to tease apart the separate and combined effects of cattle and wildlife on each other and on the savanna ecosystem that they share. The KLEE experiment uses a series of semipermeable barriers to allow access by different combinations of cattle (“C”), native mesoherbivore ungulates 15–1 000 kg (“W”: zebras, gazelles, eland, hartebeest, oryx, buffalo) and megaherbivores (“M”: elephants and giraffes). Below, we call these three classes of herbivores “guilds,” in recognition of the unique ecological positions occupied by livestock and megaherbivores (Owen-Smith, 1988), relative to mesowildlife. The experiment consists of three replicate blocks separated from one another by 70–200 m. In each block, there are six random-stratified 200 × 200 m (4-ha) treatment plots (18 total plots; 24 ha). The six treatments are 1) MWC—accessible to megaherbivores, mesoherbivore wildlife and cattle; 2) MW—accessible to megaherbivores and mesoherbivore wildlife; 3) WC—accessible to mesoherbivore wildlife and cattle; 4) W—accessible to mesoherbivore wildlife; 5) C—accessible to cattle; and 6) O—no large herbivore access (Fig. 1). One small antelope, steinbuck (< 15 kg), is able to access all experimental treatment plots (Young et al., 2005), as are rodents and hares, and most carnivores. (see Tables 1 and 2).

Herds of 100–120 mature cows (sometimes with calves) are grazed in each cattle-treatment plot for 2 hr on each of 2–3 consecutive days, typically 3–4 times per year. These grazing and herding practices reflect typical cattle management on most private and some communal properties in the region. The cattle are in an individual plot for only a few hours per year, greatly reducing the possibility that wildlife responses are due to direct avoidance of cattle. For cattle performance trials (Odadi et al., 2007, 2009, 2011b, 2013, 2017) smaller groups (5–6) comprising individuals of 2- to 3-yr-old heifers and steers were used. For full details of the basic experimental design, see Young et al. (1998) and Porensky et al., (2013a, Supplement 1). For survey methods of individual response variables, see the relevant references cited later.

In addition, we later embedded both heavy grazing and fire treatments within the KLEE design. In 2008, we assigned one 50 × 50 m subplot in each cattle treatment (C, WC, and MWC) to be grazed at a much higher level than the basic plots (which are grazed at normal ranch densities). At the end of each cattle run, we held the herd within the designated subplot for an additional 20–30 minutes. This resulted in substantially reduced residual forage and an altered community structure (see later). In Feb–Mar 2013, we burned one 30 × 30 m subplot in each of the 18 KLEE treatment plots and monitored these and paired

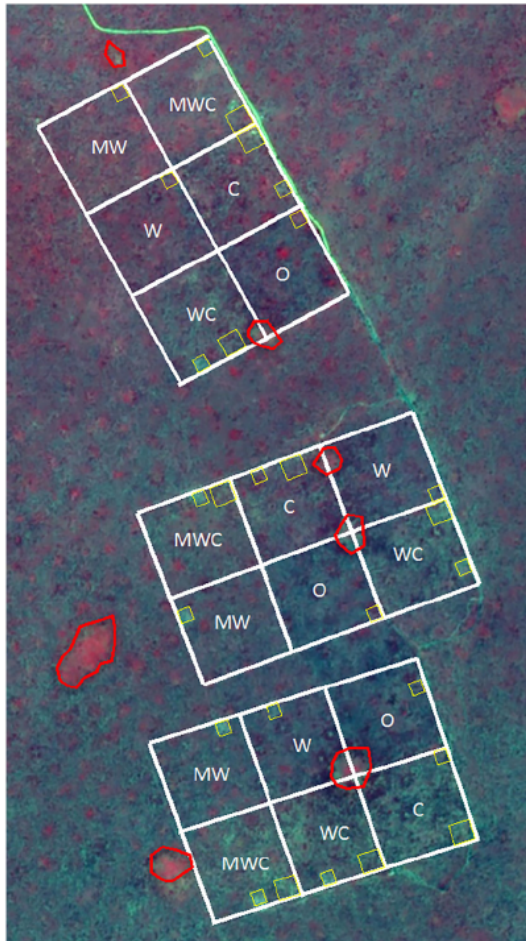


Figure 1. Satellite image of the Kenya Long-term Exclusion Experiment plots (23 May 2013) in false color. Letters in each plot represent the ungulate guild allowed: C = cattle, W = native herbivores 15–1 000 kg, M = megaherbivores, and O = no large herbivores allowed. The smaller yellow boxes indicate the locations of the Feb/Mar 2013 burns. The larger yellow boxes indicate locations of the subplots heavily grazed by cattle since 2008. The red outlines indicate the locations of anthropogenic glades.

unburned plots for animal use (dung counts and camera traps) and both understory and overstory vegetation. See Kimuyu et al. (2014) for details of the burn methodology.

Table 1
Summary of the effects cattle on of different ecosystem components. See text for details

Response variable	Effect of cattle	References
Understory vegetation	Reduce cover, shift community composition, especially during or after droughts, affect resilience	Riginos and Grace, 2008, Porensky et al., 2013a, Young et al., 2013, Veblen et al., 2016, Riginos et al., 2018
<i>Acacia drepanolobium</i>	Not fed on, but indirect facilitation via reductions in grass cover and rodent densities	Odadi et al., 2007, Riginos and Young, 2007, Riginos, 2009, Goheen et al., 2010, Maclean et al., 2011, Porensky and Veblen, 2012
Other woody species	Few effects; suppress recruitment of several species	Gadd, 2003
Net primary productivity	Increase (until high levels), reduced temporal variability	Charles et al., 2017
Glade communities	Create glades (via boma use), encourage succession, alter edge effects	Young et al., 1995, Veblen and Young, 2010, Porensky et al., 2013b
Wildlife	Reduce habitat use, but less in presence of megaherbivores, or in wet periods	Young et al., 2005, Kimuyu et al., 2017b
Rodents	Increase densities, changes in distribution	Keesing, 1998, 2000; Keesing & Crawford 2001; Goheen et al., 2010, Keesing and Young, 2014, Young et al., 2015
Snakes	Increase densities proportionately to rodents	McCauley et al., 2006
Fleas, pathogens, immune responses	Increase (mostly) proportionately to rodents	McCauley et al., 2008, Young et al., 2014, Young et al., 2017, Weinstein et al., 2017
Herbivorous insects	Effects ranging from decreases to increases, depending on taxa	Goheen et al., 2004, Huntzinger, 2005, Wilkerson et al., 2013
Spiders	Shift composition toward ground-hunting species	Warui et al., 2005
Ticks	Reduce densities (due to dipping)	Keesing et al., 2013, Keesing et al., 2018
Fire	Reduce fuel load and fire temperatures	Kimuyu et al., 2014

Key Findings

Our controlled replicated manipulations of cattle, wildlife, megaherbivores, and fire, largely crossed with each other, have revealed multiple interaction pathways in the African savanna ecosystem (Fig. 2). Many of these pathways demonstrate the myriad ways that cattle affect the ecosystem in which they live and how other ecosystem drivers affect cattle.

Do Cattle and Native Wild Ungulates Compete with or Facilitate Each Other?

Cattle Generally Suppress Both Grazing and Browsing Midsized Wildlife

Dung surveys in KLEE plots have revealed complex interactions among cattle, wild mesoherbivores, megaherbivores, rainfall, and fire (Young et al., 2005; Kimuyu et al., 2017b). In plots grazed by cattle compared with plots where cattle were excluded, there was a significant reduction in presence (measured by dung density, see Supplement) of all six wild mesoherbivore species examined (zebra, eland, oryx, hartebeest, Grant's gazelle) and also steinbuck. These patterns were already evident at a similar magnitude within 5 yr of the establishment of the exclosures (Young et al., 2005). Surprisingly, cattle suppressed species that are browsers (steinbuck) and mixed feeders that are primarily browsers (eland, Grant's gazelles), at least as much as grazers (zebra, oryx, and hartebeest). Direct avoidance of cattle is unlikely to explain this lower wildlife use because cattle are only in an individual plot < 1% of the time throughout the year. Instead, the negative effects of cattle are likely a result of reduction in both grass and forb availability. There was less forb and grass cover in plots that were accessible to cattle (see Kimuyu et al., 2017b). One interpretation is that cattle compete intensively with browsers and mixed feeders for a few valuable forb species, trumping their overall differences in dietary overlap.

These results indicate that even at moderate stocking densities, cattle usually competitively suppress most wild herbivores, including species that are primarily considered as browsers. However, this suppression is mitigated by various factors (see later), which suggest that the mechanism for such competitive interactions is much more complex than simple reductions in grass availability by cattle.

Wildlife Alter Cattle Diet and Foraging and Generally Reduce Weight Gains

Through a series of experiments, we also assessed the effects of native wild ungulates on the foraging behavior, nutrition, and performance (live weight gain) of cattle. We also measured forage availability (cover) and assessed the role of protein supplementation

Table 2
Summary of effects of different ecosystem drivers on cattle. See text for details

Driver	Effects on cattle	References
Wildlife (> 20 kg)	Shift diet Increase step rate, decrease bite rate Decrease weight gain in dry seasons, but increase weight gain in wet seasons	Odadi et al., 2007, 2011b, 2013 Odadi et al., 2009, 2013 Odadi et al., 2011a, 2011b
Megaherbivores (elephants & giraffes)	Cattle remove less grass in the presence of megaherbivores	Young et al., 2005
Fire	Increase nutrition and habitat use, but not in the presence of wildlife	Odadi et al., 2017, Odadi et al., in review
Anthropogenic glades	Increase habitat use	Veblen, 2012
Termite mounds	Increase habitat use, but less in the presence of wildlife, or in dry seasons	Odadi et al., in review

of cattle, prescribed burning, and termite mounds in influencing the interaction between wild herbivores and cattle. Wild herbivores generally affected cattle negatively, but with marked temporal (i.e., wet vs. dry seasons) and spatial (i.e., burned vs. unburned areas, and on- vs. off-mounds) variations in the magnitude and even direction of these effects (see later).

During most of the year (dry periods), wild herbivores depressed cattle performance, with cattle gaining 39–49% less weight when they shared habitat with wild herbivores (Fig. 4; Odadi et al., 2011b), indicating competition (for similar effects between elk and cattle, see Hobbs et al., 1996a, 1996b). This effect was associated with increased step rates of cattle and reductions in their bite rate, bites per step, selection and consumption of forbs (nongrasses) and the grass *Pennisetum stramineum*, and overall forage intake (Odadi et al., 2007, 2009, 2011b). These effects were mediated through reduced forage availability (cover) in the shared foraging areas.

The effects of wild herbivores on cattle bite and step rates during the dry season appear to be deleterious through reduced overall forage intake. In addition, these effects are indicative of reduced cattle foraging efficiency (i.e., higher energy expenditure relative to intake; see also Ungar and Noy-Meir, 1988; Spalinger and Hobbs, 1992; Bradbury et al., 1996), which depresses animal performance (Hart et al., 1993; D'Hour et al., 1994). The role of wild herbivores in reducing selection and consumption of *P. stramineum* by cattle also appears to be detrimental; cattle performance increased with increased selection of this grass (Odadi et al., 2011b).

Decreased selection and consumption of forbs by cattle when they forage in the same areas as wild herbivores may also be nutritionally detrimental to cattle (even though grasses represent the bulk of cattle diets). Notably, forbs generally contain higher crude protein levels than grasses (Boutton et al., 1988; Kinyamario and Macharia, 1992)

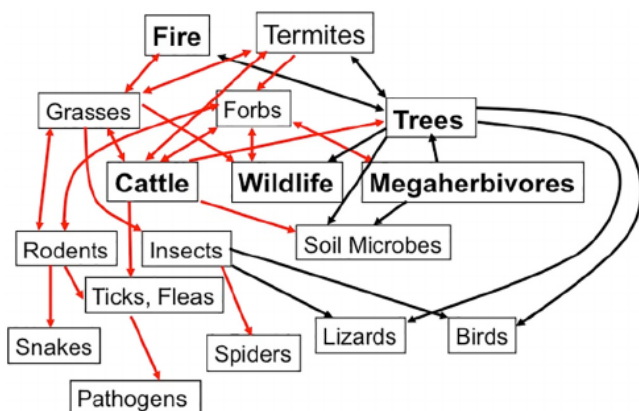


Figure 2. Demonstrated relationships between cattle and biodiversity in the Kenya Long-term Exclusion Experiment. Elements in bold represent controlled, replicated treatments (mostly crossed). Red lines represent demonstrated direct and indirect relationships related to cattle.

and may thus be nutritionally vital to cattle, especially during the dry season when nutrient content of grasses is low. Consequently, wildlife-driven reductions in forb availability and consumption by cattle during the dry season may depress cattle performance. For example, we found that when cattle were supplemented with protein during the dry season, they exhibited marked (> 76%) reductions in forb selection and consumption (see Fig. 2 in Odadi et al., 2013), signifying that such supplementation reduces the nutritional need for forbs by cattle.

Competitive Effects are Modified by Rainfall, Megaherbivores, and Fire

Whereas the findings described earlier support the long-held assumption that wild herbivores and cattle generally compete with each other for food, the story is not that simple. Suppression of both wildlife by cattle and cattle by wildlife was mitigated by rainfall, megaherbivores, and fire (see Fig. 3).

Rainfall. Although wild herbivores and cattle do compete with each other in dry periods, they at least in part compensate for this by facilitating each other in wet periods. First, the reduction in wildlife in cattle plots was less in wetter periods than in dry periods, or even reversed (Kimuyu et al., 2017b). This effect was particularly striking in zebra and steinbuck, whose presence was actually higher on average in plots grazed by cattle than plots without cattle in wet periods but lower in dry periods (see also Odadi et al., 2011a). Second, although cattle

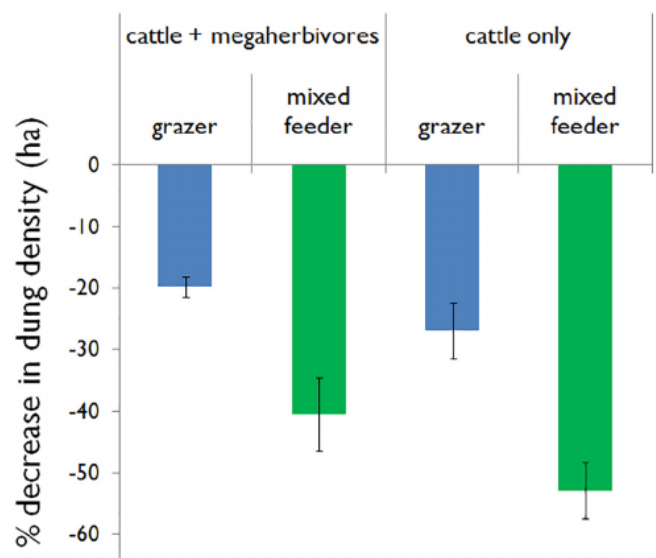


Figure 3. Reductions in habitat use (dung counts) in plots with cattle (as compared with plots excluding cattle) of native grazers (zebras, hartebeest, oryx) and mixed feeders (eating predominantly browse; steinbuck, eland, grants gazelles), both in the presence and absence of megaherbivores (elephants and giraffes). Error bars are one standard error. (Adapted with permission from Kimuyu et al. 2017b).

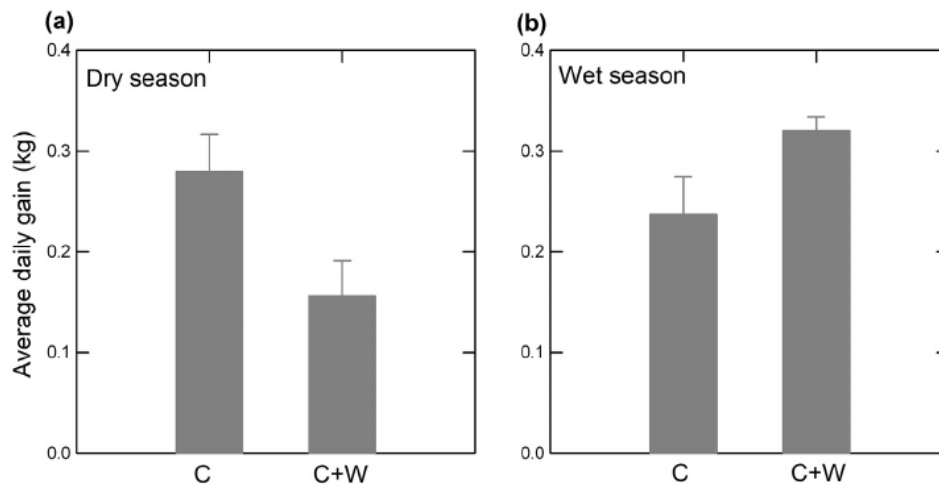


Figure 4. Cattle weight gain in the presence and absence of wildlife, during **a)** dry periods and **b)** wet periods. (Adapted with permission from Odadi et al. 2011b).

compete with wildlife during drier periods, during the wetter periods, cattle gained 34–36% more weight when they shared foraging areas with wild herbivores (see Fig. 4; Odadi et al., 2011b), a facilitative effect. It is likely that areas grazed by either cattle or wildlife are of higher productivity (Charles et al., 2017), of higher-quality (fresh) grass (Clark et al., 2000), and more diverse species composition (Porensky et al., 2013a) and therefore enhance overall quality of forage available to the other guild (Gwynne and Bell, 1968; Duncan et al., 1990), at least during wet periods when grasses tend to get “rank” and unpalatable.

Megaherbivores. The negative effects of cattle on wild mesoherbivores were also reduced in the presence of megaherbivores (both elephants and giraffes), but in practice we suspect these effects are primarily due to elephants). Without megaherbivores, cattle presence was associated with a 36% reduction in wild mesoherbivore dung density, but this reduction was only 9% in the presence of megaherbivores (Fig. 3, Young et al., 2005; Kimuyu et al., 2017b). Such an ameliorative effect may be related to indirect effects of elephants on cattle foraging behavior. As mixed feeders, elephants feed on a significant proportion of highly preferred protein-rich forbs (Young et al., 2005; Landman et al., 2013) and likely compete with both cattle and wildlife, but their suppression of cattle foraging apparently more than compensates for their direct competition with cattle. The reduction in availability of palatable forbs by elephants may negatively influence the amount of grass that cattle feed on, both slowing their bite rates and increasing their step rates (Odadi et al., 2009, 2013), leaving more grass and some nongrasses for wildlife species (Young et al., 2005). Supporting this hypothesis, feeding experiments in KLEE demonstrated that cattle receiving protein supplements feed on proportionately more grass (substantially reducing their forb consumption) than cattle whose diet has not been supplemented, especially in the dry season (Odadi et al., 2013).

An alternative hypothesis for our finding that plots with megaherbivores showed less reduction of wildlife in the presence of cattle is related to tree density. We have experimentally shown that wildlife select habitats with fewer trees, presumably because of greater predator detection (Riginos, 2015). However, although elephants have begun to reduce tree density in the KLEE plots to which they have access, these differences are as yet still small (~20%).

Fire. Competition between wild herbivores and cattle appears to be intensified in burned areas (see later) and termite mounds, both of which are nutrient-rich foraging hotspots that often attract large grazing herbivores (Sensenig et al., 2010, 2017; Brody et al., 2010; Fox-Dobbs et al., 2010; Allred et al., 2011; Eby et al., 2014; Davies et al., 2016; Odadi et al., 2017). Fire, cattle, and herbivory are known to

interact in myriad parallel and interacting ways (Bond and Keeley, 2005; Archibald and Hempson, 2016). The KLEE experiments are revealing some of the complexities of these relationships, by uniquely crossing control manipulations of all three drivers.

First, fire can shift the community toward more open habitat by killing trees, but this is dependent on the presence of elephants. Fire alone and elephants alone have small effects on tree damage, top kill, and death, but both together have strong negative effects (Okello et al., 2008; Pringle et al., 2015). The implications of this lower tree density for cattle are not yet clear (Riginos and Grace, 2008; Riginos et al., 2009).

Second, the fresh grass regrowth that arises after fires benefits cattle by increasing cattle intake, at least in the wet season. However, these benefits are greatly reduced by the presence of wildlife, which had access to the postfire forage immediately after the fire (Odadi et al., 2017). Specifically, cattle nutrient intake rates were reduced by 37–97% when cattle shared burned areas with wild herbivores, with greater detrimental nutritional consequences during dry season (see Fig. 3; Odadi et al., 2017). These effects were associated with reduced forage availability in the shared burned areas. These results suggest that prescribed burning could be applied by interspersing burns with unburned areas to minimize fire-driven negative effects of wild ungulates on cattle nutrition. Burning could also be used to draw wildlife away from valuable cattle foraging areas, such as those near available water.

As Archibald and Hempson (2016) point out, fire and cattle “compete.” Clearly, fire initially removes cattle forage, and this is why many ranchers in Laikipia have moved away using fire as a management tool (T. Young personal interviews), perhaps as rainfall patterns become less predictable (Rowell et al., 2015). Conversely, cattle compete with fire by reducing fuels loads and fire temperatures (Kimuyu et al., 2014). We still lack a more detailed cost-benefit analysis of these conflicting fire effects.

Do Cattle and Wildlife Herbivory Have Similar Effects on Vegetation?

There have been many experimental studies of the effects of cattle on vegetation, in virtually every ecosystem where cattle occur (see reviews in O'Connor, 1985; Hobbs, 1996; Augustine and McNaughton, 1998; Olf and Ritchie, 1998; Jones, 2000; Rosa Garcia et al., 2013). Much rarer are controlled experimental comparisons of the separate and combined effects of cattle and wild large mammalian herbivores, in any ecosystem. KLEE allows such comparisons with two different guilds of wildlife: mesoherbivores (15–1 000 kg) and megaherbivores (elephants and giraffes), over long periods of time (> 20 yr) and with embedded controlled burns.

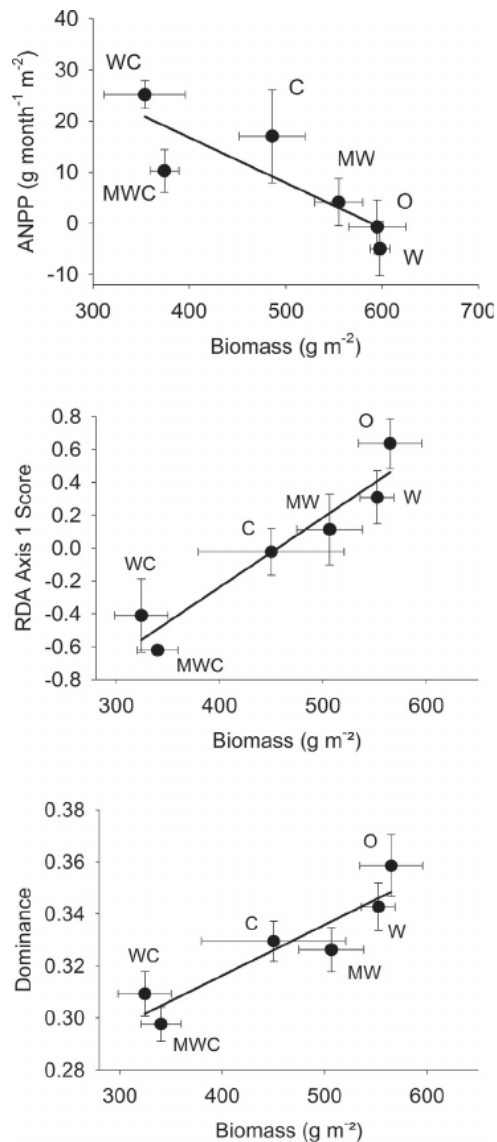


Figure 5. Residual herbaceous biomass versus **A**) ANPP, **B**) plant community composition (represented by RDA 1 score), and **C**) dominance (cover of species with single highest cover value) for herbivore treatments in Kenya Long-term Exclosure Experiment. All values are means and 1 SE of 3 reps per treatment (with each treatment value averaged over all available time steps). C = cattle allowed, W = mesoherbivore wildlife allowed, M = megaherbivores allowed, and O = all large herbivores excluded. (Adapted with permission, respectively, from **a**, Charles et al., 2017, **b**, Veblen et al., 2016, and **c**, Riginos et al., 2018).

Cattle Effects on Understory Plants are Similar to Those of Native Wild Ungulates

Consistent with research from North America (Baumgartner et al., 2015), two recent studies in KLEE show that cattle and wildlife have functionally similar effects on understory (herbaceous) plant dynamics. For the most part, differences between cattle and wildlife effects are mediated by the higher biomass and herbivory pressure of cattle relative to wildlife rather than by species- or guild-specific effects. For example, results from both productivity cage measurements and satellite normalized difference vegetation index (NDVI) demonstrated a positive relationship between mean herbaceous productivity and the amount of herbaceous biomass removed by herbivores (Charles et al., 2017; Fig. 5A). This effect was driven in particular by the presence of cattle,

which removed substantially more biomass than wild herbivores. Similarly, we found that herbaceous community composition was strongly related ($R^2 = 0.92$) to residual plant biomass, a measure of herbivore utilization (Veblen et al., 2016) (Fig. 5B). Addition of any single herbivore type (cattle, wildlife, or megaherbivores) caused a shift in plant community composition that was roughly proportional to its removal of plant biomass, suggesting that overall herbivory pressure, rather than herbivore type or complex interactions among different herbivore types, was the main driver of changes in plant community composition (for a similar example, involving cattle, elk, and deer, see Rhodes et al., 2017). The ability of cattle to reduce understory fuels and suppress fire temperatures more than wildlife (Kimuyu et al., 2014; see below) is also likely due to their greater density. However, wild versus domestic herbivores did play some functionally unique roles. For example, individual understory plant species (Veblen et al., 2016) and woody species (see “Effects of Cattle on Woody Plants” later) responded most strongly to either wild ungulates or cattle. Additionally, heterogeneity in ANPP and NDVI across both space and time were higher when cattle were present relative to the effects of wild herbivores alone, for reasons that are not clear (Charles et al., 2017).

Two other studies from KLEE have shown that the herbaceous plant community's response to drought differs between cattle and wild herbivore grazing treatments (see also Veblen and Young, 2010, and for a North American example, Hartnett et al., 1997). However, these differences again appear to be largely mediated by the greater total grazing pressure imposed by cattle and do not suggest that cattle play a fundamentally different functional role than wild herbivores in this system.

First, over the long term, we found that change in the herbaceous community was greatest during the first two rainy seasons after episodic droughts (Riginos et al., 2018). This was the case in all herbivore treatments, but when cattle were present (and especially when cattle and wildlife were both present) the direction of this short-term change was variable, leading to long-term community stability. In contrast, plots without cattle, and especially plots without cattle or wildlife, experienced more persistently directional compositional shifts in postdrought periods, such that long-term composition showed greater net change.

Second, herbaceous species richness was also higher in the first two rainy seasons after episodic droughts, but only in the presence of cattle (Porensky et al., 2013a). The combination of drought and biomass removal by large herbivores creates patches of bare ground (perhaps aided by additional trampling effects) that are colonized by (mostly annual) species that are otherwise rare (Porensky et al., 2013a). Mortenson et al. (2108) similarly found that pulsed suppression of dominant grasses increased plant species richness in a tallgrass prairie. Eldridge et al. (2018) also showed that livestock, but not native herbivores, increased species richness. Although this effect in our system was only seen in the presence of cattle, the fact that herbaceous dominance (Berger-Parker dominance) is positively correlated with total herbaceous biomass ($R^2 = 0.88$, $P = 0.005$) and negatively related with total herbivory (Fig. 3C) suggests that a greater abundance of wildlife would likely have the same effect (reducing dominance). Koerner et al., 2014 found that herbivory was also associated with decreased dominance in Konza (in the United States), but not Kruger (in Africa). Globally, there is tremendous variation in the effects of herbivory on dominance (Koerner et al. revision in review). The reason for this variation is unclear, although one explanation might be that reductions in dominance with herbivory are related to the palatability of the dominant grasses, which is consistent with our results.

In general, our work on the herbaceous plant community has revealed evidence for functional similarity between moderately stocked cattle and a diverse array of wild herbivores (albeit dominated by grazers), despite their dietary differences. However, if cattle were present at a higher stocking rate, the resultant heavy grazing would likely have negative effects on herbaceous production and species richness and would potentially cause nonlinear changes in herbaceous

community composition. Indeed, pilot surveys of KLEE subplots grazed by cattle at much higher densities since 2008 revealed a 42% reduction in herbaceous cover and significant shifts in species composition from the more palatable *Brachiaria lachnantha* (23% less relative cover) toward less palatable grasses (35% more relative cover) (Young unpublished data).

Although increases in herbaceous cover occurred quickly (Young et al. 2005), changes in community composition only began to be evident nearly 10 yr after the enclosure treatments were put in place (Veblen et al., 2016). We do not know if changes in relative composition were due to differential mortality of some species or differential recruitment under similar mortalities.

Cattle and Wildlife Have Unique Effects on Woody (Overstory) Plants

Cattle are mainly grazers in this ecosystem, but they can eat substantial nongrasses (Odadi et al., 2007). Among these are a number of woody and semiwoody plants. Cattle suppressed the growth of *Acacia brevispica*, *Lippia javanica*, and *Lycium europaeum*, an effect that was evident quickly after enclosures were put in place (Gadd, 2003), and suppressed the recruitment of these species and also *Tinnea aethiopica*, *Croton dichogamus*, *Sarcostemma viminale*, *Asparagus* spp., and *Maerua triphylla*, an effect that only became evident after several years of enclosure (Charles et al. unpublished data). Despite generally increasing bush encroachment (see review in Archer et al., 2017), cattle also suppress some woody species in other ecosystems (aspen: Kaufmann et al., 2014; oaks: López-Sánchez et al., 2014; Rhodes et al., 2017).

Conversely, although cattle apparently do not eat the dominant *Acacia drepanolobium* (Odadi et al., 2007), the experimental removal of grasses both released sapling of *A. drepanolobium* from competition and exposed the seedlings to other herbivores (Riginos and Young, 2007). The net result of these two opposing effects is a negative effect of grass removal (i.e., grazing) on *A. drepanolobium* seedlings (at least in the presence of large native herbivores). [See also the cascading effects of cattle on *A. drepanolobium* via rodents, later.] However, more intensive cattle herbivory may favor adult *A. drepanolobium* (Riginos, 2009) and the shrub *Cadaba farinosa*, likely by reducing competition with grasses (Wilkerson et al., 2013).

What Effects do Cattle and Commercial Cattle Management Have on Other Organisms?

Cattle Reduce Small Mammals (Rodents), Initiating Plant, Predator, and Pathogen Cascades

Despite the large size differences, both wild ungulates and cattle are direct competitors for forage with small mammals (see Ranglack et al., 2015). In KLEE, when either class of large ungulates were excluded, rodent abundance increased by about 50%; when both were excluded, rodent abundance (and abundance of other small mammals, such as shrews) roughly doubled (Keesing, 1998, 2000; Goheen et al., 2010; Keesing and Young, 2014, see also Long et al., 2017). These responses happened quickly after enclosures were put in place (within a year). Given that rodents themselves are important herbivores (eating half or more of forage, even with all ungulates present; Keesing, 2000), this compensatory increase in rodents following experimental removal of either cattle or wild ungulates means that much of the expected increases in forage and vegetation communities may not be realized (Keesing, 2000). The increase in rodents drives a cascade of downstream effects. This includes long-term changes to tree recruitment and likely tree density via increased predation on seeds and seedlings (Goheen et al., 2004, 2010; Maclean et al., 2011).

The increases in rodents associated with exclusion of either cattle or wildlife also drove increases in their consumers, including both snakes (McCauley et al., 2006) and mesopredator carnivores (Kimuyu unpublished data). Perhaps most directly relevant to human health and well-being, increases in rodent populations increased landscape-level abundances of many parasites that use rodents as hosts, including

fleas (McCauley et al., 2008) and ticks (Keesing et al., 2013) that often serve as vectors transmitting pathogens to other hosts. For parasites with infection patterns that are largely independent of host density, there was no increase in prevalence (proportion of hosts infected) or intensity (number of parasites per host) of infestation across treatments. However, exclusion of cattle or wildlife removal led to increases in landscape-level disease risk proportionate to the increases in rodent abundance, including for human-relevant pathogens such as *Bartonella* (Young et al., 2014). The effects of cattle or wildlife removal on parasite exposure risk may be even stronger for other groups of parasites (Weinstein et al., 2017).

Support for other invertebrate trophic cascades includes evidence that cattle reduced grasshopper biomass (Huntzinger, 2005) and sweep-netted invertebrate biomass (Ogada et al., 2008) but increased the abundance of the insect families Anthicidae and Curculionidae (Kuria et al., 2010) and increased *Colotis* butterfly densities through the positive effects of cattle on the shrub *Cadaba farinosa* (Wilkerson et al., 2013). Cattle also reduced spider species richness and altered the overall spider community, apparently mainly through increased openness in the grass canopy, which favored ground-hunting spider species over web-building species (Warui et al., 2005).

Special Case: Ticks and Cattle Dipping

East African savanna ecosystems have high densities of ticks and high diversity of tick-borne pathogens, and some of these pathogens (e.g., *Rickettsia*, *Coxiella*, and *Anaplasma*) are major regional economic and human health concerns (Cumming, 2000; Minjauw and McLeod, 2003; Parola et al., 2013; DePuy et al., 2014). It is common throughout Africa (for those who can afford it) to regularly dip cattle in order to reduce tick loads and therefore tick-borne diseases (George, 2000). While this can be effective in greatly reducing tick loads on individual dipped cattle, it also turns out to have much broader landscape-scale effects. Tick surveys of the KLEE plots reveal that plots to which (dipped) cattle had access contained greatly reduced numbers of free-living adult and nymphal ticks of *Rhipicephalus pulchellus* and adult *R. praetextatus* (Keesing et al., 2013; Allan et al., 2017). Dipping not only kills ticks attached to cattle at the time of dipping but also may kill adult and juvenile ticks that contact the cattle between dipping days (George et al., 1998).

KLEE in Broader Landscape Context

In a series of broad landscape-scale surveys, researchers compared the effects of KLEE and a nearby enclosure experiment on a different soil type (UHURU; Goheen et al., 2013) with that of other land uses, including high-intensity pastoral use, across the range of abiotic conditions (e.g., variable soil and precipitation regimes) characterizing much of Laikipia, for a suite of community-level responses (plants, mammals, and pathogens) (Young et al., 2013, 2015, 2017). In these studies, the effects of herbivores (both wild and domestic) were strongly mediated by abiotic conditions. For example, the effects of herbivores on arboreal lizard abundance (Pringle et al., 2007), rodent abundance (Young et al., 2015), and plant species richness (Young et al., 2013) tended to be more negative in low-productivity, low-rainfall environments, with the species richness pattern supported by global meta-analyses across many savanna ecosystems (Daskin and Pringle, 2016; Burkepile et al., 2017; Koerner et al. revision in review).

These landscape-scale studies also highlighted different effects of herbivores in the experimental context as compared with broader landscape context where livestock densities are often higher and rarely independent from effects on wildlife. In particular, while total herbivore density had strong effects on plant height, cover, and complexity and small mammal density in the experimental enclosure sites, there was no significant relationship between herbivore abundance and plant or small mammal responses in the broader landscape sites that were generally more human dominated. This may be because of other human impacts on these broader landscape sites, including removal of vegetation for fuel, food, or other uses.

The breakdown of the relationship between large herbivore density (both cattle and wildlife) and vegetation availability in human-dominated landscapes then interrupts some of the other cascades that have been documented. For instance, pastoral landscapes (with very high densities of ungulates) do not show the systematic decreases in small mammals (Young et al., 2015) or diseases hosted by small mammals and vectored by their ectoparasites (Young et al., 2017), as might be expected based on extrapolating data from KLEE cattle or livestock data to these natural systems. These results emphasize the potential for different responses under high-intensity grazing and associated human use compared with the more moderate-intensity livestock use approximated in most of the KLEE.

Notably, the effects of high-intensity livestock impacted the magnitude of responses but also changed the type of responses. While herbivore (wildlife or cattle) addition in the experimental enclosures tended to cause increases in the abundance of small mammals, it had very little impact on small mammal diversity or community composition. In contrast, while high-intensity livestock in human-dominated landscape use had no overall impacts on the total density of small mammals, it did have very strong impacts on diversity, richness, and composition of small mammal communities (Young et al., 2015). We would therefore anticipate that high-intensity pastoral land use conversion in human-dominated landscapes might lead to very different changes in pathogen abundance (and exposure risk) than is caused by more moderate intensity of ungulate use (as simulated in the KLEE). Consistent with this prediction, the observed effects of high-intensity pastoral land use conversion on pathogen exposure risk was, across multiple pathogens, very different than that of low-intensity grazing by large ungulates in the KLEE (Young et al., 2017).

Summary

Our experiments confirm that cattle usually compete with wild ungulates and wild ungulates usually compete with cattle, and that cattle initiate myriad trophic cascades in this savanna community. However, at moderate cattle densities, livestock production and wildlife conservation are not incompatible and our identification of multiple facilitative pathways and mitigating factors between cattle and other large mammalian herbivores (see also Augustine et al., 2011; Riginos et al., 2012) increase the windows of opportunity for coexistence and even mutual profitability (e.g., Ranglack and du Toit, 2016), within which such compatibility can occur.

Efforts aimed at enhancing compatibility between livestock production and wildlife conservation in these savanna rangelands should focus on grazing management practices that minimize competitive effects. For instance, competition for forbs during dry periods could be moderated through protein supplementation of cattle. Our findings suggest that wild herbivores are not uniformly detrimental to cattle production and that deleterious effects can be lessened through improved grazing practices. These findings raise the prospect that wildlife conservation and economic development through livestock production at moderate densities can both be achievable in these savanna rangelands.

With regard to multiple ecosystem traits (understory community composition, net primary productivity, rodent density), it appears that cattle may be essentially surrogates for the diverse mixture of wildlife species they suppress, a result consistent with the surprising result that cattle suppress habitat use of browsers at least as much as grazers. But this comes with several major caveats: 1) Cattle even at the “moderate densities” of this experiment occur at greater densities than wildlife and therefore have greater impacts. 2) In addition to all the factors that allow livestock production to maintain more cattle (predator protection, disease control, herding, boreholes), interventions such as tick dipping, fencing, and the presence of dogs (the latter two not addressed here) have both positive and negative effects on wildlife. 3) Cattle are clearly not the equivalents of wildlife in a number of ways and do not

compensate for the effects of wildlife on woody vegetation, as well as spatial and temporal variability in primary production.

One of the other striking themes of this research is how richly contextual ecological relationships are. Hardly a single pattern we describe was not significantly modified by seasonal and interannual variation in rainfall, by third-party herbivores, tree density, or various combinations of these. On the one hand, the identification of these strong modifiers in our experiment raises the specter that studies not including them may be idiosyncratic (see Vaughn and Young, 2010), and even our results are likely affected by additional, uncontrolled factors. On the other hand, the identification of these richly contextual patterns (sometimes despairingly called “confounding factors”) will likely serve to provide richer and more accurate understanding of the systems that we study and upon which we ultimately rely. The context-dependent nature of these relationships makes it difficult to assess how generalizable the specific results will be to other ecosystems, where the large herbivore assemblage and underlying ecological conditions may be quite different. However, studies that have compared herbivore removal in African savanna ecosystems with similar manipulations in North American grassland systems have found broad similarities in the trajectories of plant community changes across these ecosystems, including decreases in richness and diversity of herbaceous plant community (Eby et al., 2014). Similarly, a global meta-analysis of indirect effects of herbivores on consumer abundances shows strong evidence for a systematic suppression of consumers across a range of ecological contexts, with stronger effects in less productive environments (Daskin and Pringle 2016; Eldridge et al., 2018). While neither of these studies nor other syntheses of effects of herbivores across a range of ecological contexts in grassland or savanna communities (e.g., Borer et al., 2014, Mortenson et al 2018) are focused on differential or impacting effects of cattle and wildlife on communities, they do suggest that the effects of herbivores on savanna and grassland ecosystems are broadly similar in direction, if not magnitude, across ecological contexts, suggesting that the general conclusions may translate broadly to other ecological communities.

One of the most fundamental conclusions of the KLEE research is that *at moderate densities*, cattle production in Africa is compatible with the conservation of (and even sustainable use of) considerable biodiversity (see also Reid, 2012; Neilly et al., 2016; Schuette et al., 2016). However, it is not clear how relevant this research is in a world where livestock densities, and in particular noncattle (mainly sheep and goats, but also camels and donkeys), continue to grow beyond the ability of rangeland ecosystem to sustain them, and where wildlife outside of parks, which once represented the lion's share (70%) of wild populations (Ottichilo et al., 2000), is being eradicated by massive overgrazing and overexploitation of resources in general (Ogutu et al., 2016). Notably, comparison of our experimental plots to high-intensity pastoral use common in much of the region shows striking differences in magnitude and even direction of community-level responses (Young et al., 2013, 2015, 2017). To better address this question moving forward, the KLEE added a “heavy grazing” treatment to each of our experimental plots (since 2008, see earlier) from which we are beginning to glean information about the biodiversity effects of cattle at densities more similar to many current African rangelands. These “heavy grazing” treatments have produced shifts in community structure quite different from our moderate cattle densities.

However, there are three historical contexts in which to consider the moderate cattle densities that characterize most of the KLEE. First, until 30–50 yr ago, and apparently for thousands of years, humans and livestock in semiarid East Africa existed at densities low enough that when Europeans first penetrated beyond the coastal strip, they described with awe a landscape awash in wildlife (Reid, 2012). These low densities were maintained by “natural” but brutal processes of periodic starvation, warfare, and disease within the pastoral communities and their livestock, which the modern world has worked so hard to eradicate, and with considerable success. Second, if Africa hopes to ultimately protect its unique wildlife communities beyond postage-stamp parks in at

least some of their semiarid rangelands, it will need to be at the more moderate livestock densities approximated in the KLEE. Lastly, there are a few East African ecosystems extant where this tenuous balance between livestock and wildlife is still being maintained, like Ngorongoro in Tanzania and Laikipia in Kenya, although the future of these ecosystems is by no means secure. To the extent that they survive, they have the potential to become the touchstone “reference communities” for potential refaunation (rewilding) efforts of future generations, which both history and our research show could include both livestock and the spectacular wildlife diversity that awed the outside world over a century ago.

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Appendix A. Supplementary Data

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