

# Ecological Importance of Large Herbivores in the Ewaso Ecosystem

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**ABSTRACT.** Large ungulate herbivores are widely considered to be functionally important components of African savannas, but this belief is based largely on what is known about their direct interactions (as consumers of plants and food for predators). Their indirect interactions, both as key consumers within food webs and as “engineers” of habitat structure, are less well understood. Here we review the results of nearly 15 years of experimental research at Mpala Research Centre (Laikipia, Kenya), focusing primarily on the indirect effects of ungulates on the abundance, distribution, and diversity of other species. We highlight several broad conclusions: (1) ungulate exclusion increases densities of plants and many small consumers; (2) the strength of these indirect effects is context dependent and may vary systematically along environmental gradients; (3) impacts of different ungulate species vary both quantitatively and qualitatively. Although some of the observed effects of ungulate exclusion were predictable, others were surprising. These insights are obliquely relevant to management, but there remains a mismatch between the kinds of information most interesting to academics on the one hand and most useful to land managers on the other. We conclude by identifying some areas of likely convergence between questions of basic and applied importance.

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## INTRODUCTION

Much early research on African savanna ecosystems focused on the natural history and population dynamics of particular wildlife species. Pioneering work on conspicuous species such as elephants (Laws et al., 1975), buffalo (Sinclair, 1977), lions (Schaller, 1972), and hyenas (Kruuk, 1972) helped lay the foundation for studies that illuminated relationships between herbivores and plants and between predators and prey (e.g., McNaughton, 1976, 1978; Hilborn and Sinclair, 1979). Recently, synthetic works have drawn on this knowledge to paint more complete pictures of entire ecosystems (Scholes and Walker, 1993; Sinclair and Arcese, 1995; du Toit et al., 2003).

As a result, we now know a great deal about the biology of large mammals in African savannas: what they eat, how they eat it, what eats and what parasitizes them, and, increasingly, how their activities affect vegetation communities and other key landscape attributes. Most of these processes fall into the category of what ecologists call direct interactions—immediate physical contact and/or exchanges of energy between species. But such direct exchanges represent only a fraction of the total number of interspecific interactions in an ecosystem since each direct interaction creates the potential for numerous indirect interactions. Indirect effects occur when a direct interaction between two species influences a third species in some meaningful way (Abrams et al., 1996). One well-known example from African ecosystems involves the Serengeti ungulate migrations, where grazing by wildebeest (*Connochaetes taurinus*) prevents grass senescence, enhances productivity, and therefore determines the subsequent pattern of grazing by Thomson's gazelles (*Gazella thomsonii*) (McNaughton, 1976).

Typically, however, indirect interactions are difficult or impossible to observe in real time. To take just one example, detecting system-wide indirect effects of lions on grasses via their suppressive effects on grazers might require years of observation and experimentation. Partly for this reason, indirect effects remain poorly understood relative to direct ones. Nevertheless, ecological studies over the past 40 years have shown repeatedly that indirect interactions are powerful determinants of the abundance, distribution, and diversity of organisms in many types of ecosystems and that they are frequently even more important in these respects than direct interactions (Paine, 1966, 1980; Wootton, 1994; Menge, 1995; Abrams et al., 1996; Schmitz et al., 2000; Ripple and Beschta, 2004).

Thus, we cannot understand any ecosystem or predict the likely consequences of perturbing it without characterizing the most important interaction chains within it. Indirect interactions help define the emergent patterns and properties of all ecosystems, including how many species it supports, how many individuals of each species, where these individuals occur, and how they behave. Indirect interactions can also define characteristics of savannas at very broad scales, such as the relative balance of trees and grasses and the amount of carbon stored in the ecosystem (Holdo et al., 2009). Even seemingly straightforward direct interactions, such as the impact of ungulates on plants, are often mediated by cryptic indirect effects (as we will describe below) (Goheen et al., 2010).

Studying the indirect effects of large mammals in African rangelands is appealing for several reasons, some

esoteric and some more pragmatic: it allows us to test general hypotheses about ecological organization; it may enable us to predict the consequences of wildlife declines and extinctions (or, conversely, wildlife translocations and reintroductions); and at least in theory, it can provide insights about how best to manage landscapes simultaneously for wildlife conservation and livestock production.

Many advances in our understanding of the functional importance of large mammals in savanna landscapes have emerged from the past 15 years of research at the Mpala Research Centre and Conservancy in Laikipia, Kenya (an area under constant but relatively low-intensity human use). Much of this work has utilized a series of large-scale (0.5–4 ha) experimental plots that employ electric fences of different designs to selectively exclude different kinds of large mammals, allowing investigators to assess the responses of plant and small-animal communities. There are two ways to view this research. One is as an effort in experimental “community disassembly” for the purpose of basic understanding. The other is as a simulation of extinction: if the declining trends in many wildlife populations continue, what are the likely consequences for biodiversity and ecosystem functioning? In the remainder of this chapter, we summarize salient findings from this body of work and discuss ways in which future research might speak more directly to conservationists and land managers.

## METHODS

Mpala Research Centre supports several large-mammal exclusion experiments (“exclosures”). The oldest is the Kenya Long-term Exclosure Experiment (KLEE), located in the southwestern corner of Mpala Ranch on black-cotton vertisol (“clay”) soils (Young et al., 1998). This experiment was established in 1995 and uses electric wires at different heights along with visual barriers to selectively exclude cattle, “megaherbivores” (elephants and giraffes), and all other large ungulates (>15 kg) from three replicated sets of 4 ha plots, allowing researchers to isolate the impacts of each of these groups. The high clay content of these recent volcanic soils impedes infiltration and drainage and causes pronounced shrinking and swelling with changes in water content. At least partly for these reasons, the clay soils of Mpala are highly productive but low in diversity and evenness of almost every group of organisms *except* large mammals: a single tree (the whistling thorn, *Acacia drepanolobium*) makes up ~97% of the overstory (Young et al., 1997), five dominant grasses constitute ~90% of the understory (Riginos and Young,

2007), the pouched mouse (*Saccostomus mearnsi*) represents 75% of all rodent captures (Keesing, 1998), etc.

Another experiment, comprising only two treatments (total exclusion plots surrounded by 3 m tall electric fences along with unfenced “control” plots), was established by David Augustine in 1999 (Augustine and McNaughton, 2004). This experiment is located in red sand soil and includes three replicated sets of exclusion (70 × 70 m) and control plots in ordinary bushland and another three in nutrient-rich treeless glades (abandoned cattle enclosures called “bomas”; Young et al., 1995). The sand soils are older and coarser and contain fewer nutrients than the clay soils; they are less productive but support more heterogeneous and diverse biotic communities than the clay soils. Further details on the design of these experiments and the sampling strategies of studies conducted within them can be found in the original sources cited throughout this chapter.

## RESULTS

### INFLUENCE OF UNGULATES ON POPULATION DENSITIES OF OTHER SPECIES

Perhaps the most straightforward prediction from these experiments was that standing plant biomass would increase in the absence of ungulates. In general, this prediction has been supported, although the net effects of ungulates on plants are not straightforward (Figure 1). In sand soil bushland, woody plants responded rapidly and dramatically to ungulate exclusion: after three years, *Acacia* leaf density and biomass were lower by 60% and 80%, respectively, in unfenced plots relative to ungulate enclosures (Augustine and McNaughton, 2004). Likewise, live aboveground grass and herb biomass was greater in ungulate exclusion than control plots in both bushland and glade sites, although these effects were contingent on rainfall: in a low-rainfall year grazers reduced aboveground productivity regardless of soil nutrient availability, whereas in a wetter year grazers reduced productivity in bushland but *increased* productivity in nutrient-rich glades (Augustine, 2002).

Plant responses to ungulate exclusion in black-cotton clay soils have been more muted. After a decade, plots without wildlife exhibited no substantial increases in the density, cover, or biomass of the whistling thorn tree (*Acacia drepanolobium*) (Okello, 2007; Pringle et al., 2007; Ogada et al., 2008; Augustine et al., 2011 [this volume]). Changes in grass and forb cover materialized slowly, with no appreciable difference between the experimental

treatments during the first two years of the experiment (Keesing, 1998). By the sixth year of the experiment, grass density was 28% greater in cattle exclusion plots than in plots with cattle, while forb density was 8% greater in plots from which only megaherbivores had been excluded (this latter change is attributable to elephants since giraffes do not eat forbs) (Young et al., 2005).

There are several potential explanations for this difference in plant community response between the two soil types, and these factors might be operating singly or in conjunction with one another. The greater productivity in clay soils relative to sands might contribute to this result since, with all else equal, plants in high-productivity environments can compensate more rapidly for each unit of production lost to herbivores (Chase et al., 2000; Pringle et al., 2007). Differential ungulate activity levels across soil types would also influence the relative magnitude of effects in different sites. Moreover, some of the dominant plants in clay soils are exceptionally well defended, most notably the whistling thorn, which is protected by both large thorns and symbiotic ants. Recent research by Goheen and Palmer (2010) shows that ants effectively defend trees against elephants, which reduces the impact of elephants on tree density at the landscape scale. Moreover, the removal of large herbivores precipitates a shift in the structure of this ant community; specifically, an ant species that weakly defends its host trees gains dominance over a more aggressively defending species (Palmer et al., 2008). Because trees occupied by the poorly defending species are more likely to die, the shift toward this species in the absence of ungulates may, counterintuitively, increase tree mortality. Finally, the removal of large mammals causes a dramatic increase in the density of rodents (see below). Rodents are efficient predators upon whistling thorn seeds and seedlings (Figure 1), which means that reduction in browsing of *Acacia* by large mammals (which largely affects resilient mature trees) is offset by increased mortality of juvenile tree stages due to mice (Goheen et al., 2010). Thus, although more seeds are produced by trees in the absence of large browsing mammals (Goheen et al., 2007; Young and Augustine, 2007), fewer are able to establish.

A second set of predictions involved the responses of small consumers. Since many small mammals consume vegetation, Keesing (1998, 2000) tested the hypothesis that rodent populations would be released from competition and increase in plots without large herbivores. Years of trapping within the clay soil KLEE plots have shown a sustained doubling of the dominant rodent species in the black-cotton community, the pouched mouse, *S. mearnsi* (Keesing, 1998, 2000; Goheen et al., 2004; McCauley et

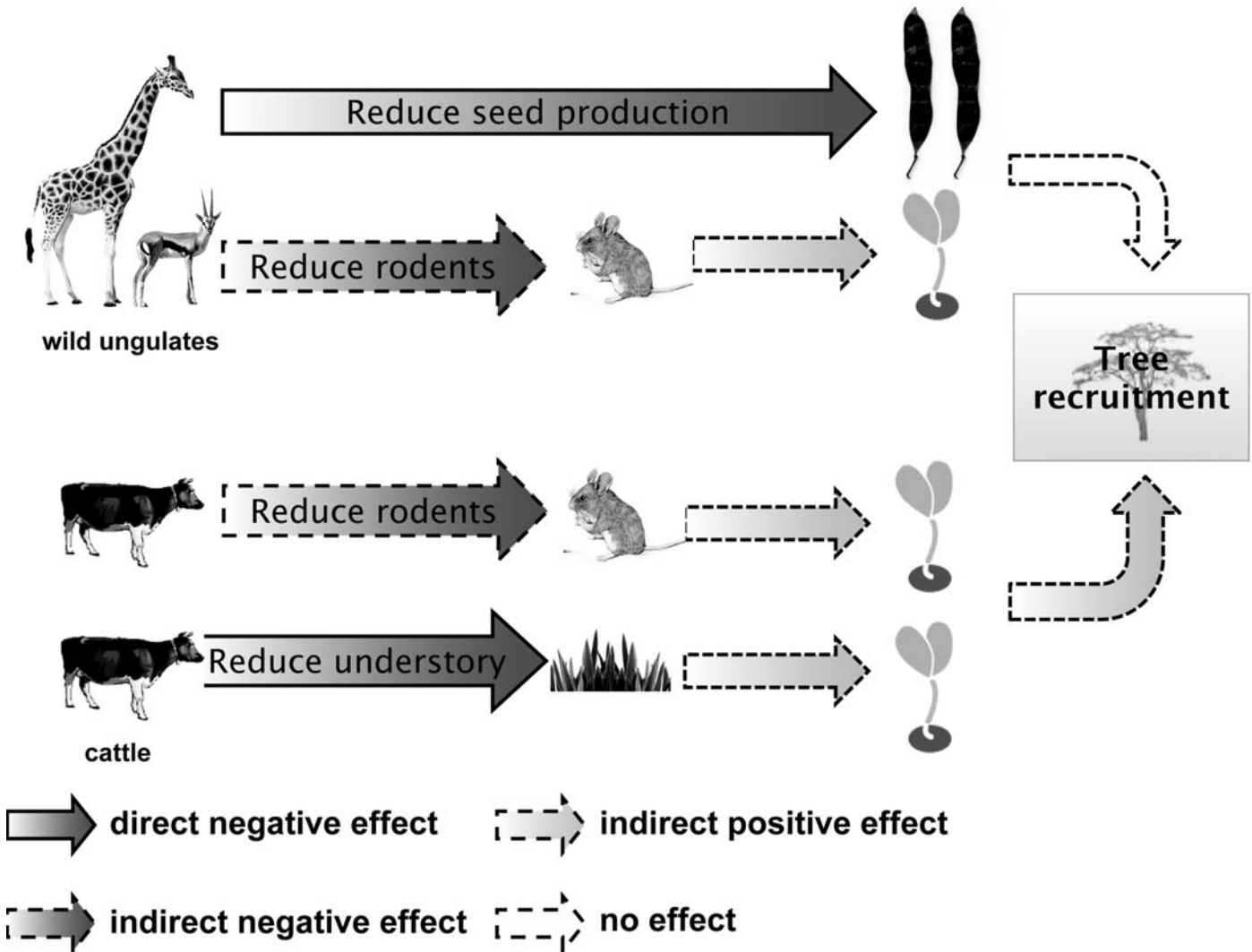


FIGURE 1. Direct and indirect effects of wild and domestic ungulates on *Acacia* establishment. Browsers such as giraffes and gazelles (pictured) directly suppress seed production. However, this negative effect is cancelled by the positive indirect effects of browsers' suppressing rodents, which depredate seedlings. Cattle, in contrast, suppress rodents and grasses, leading to positive net effects on tree establishment. Reprinted, with permission, from Goheen et al., 2010.

al., 2006). This increase occurred before any detectable difference in the amount of grass cover (Keesing, 1998), suggesting two things. First, it is unlikely that mice became more abundant simply because they were better concealed from predators, a conclusion further supported by the fact that mouse survivorship rates were similar in areas with and without large herbivores (Keesing, 2000). Second, as discussed above, mice might be consuming plant biomass in ungulate removal plots before it can accumulate, providing one explanation for the relatively mild shifts in vegetation cover documented in KLEE. Consistent with this

interpretation, Keesing (2000) installed small rodent exclosures within the larger ungulate exclosures and found that plant biomass in these smaller ungulate- and rodent-free plots increased by 50%.

Predators and parasites of mice have also responded to ungulate removal. Nineteen months of sampling in KLEE's total-exclusion and control plots revealed that rodent-eating sand snakes (*Psammophis mossambicus*) were roughly twice as abundant within the exclosures (McCauley et al., 2006). The number of fleas (Siphonaptera) that parasitize mice increased as a linear function of mouse density, also



leading to a near doubling, on average, of flea density in ungulate exclusion plots (McCauley et al., 2008).

In contrast to the consistent results for mice and their predators and parasites, studies of free-living insect populations have yielded variable results that defy easy explanation. Ogada et al. (2008) sampled arthropods within the clay soil KLEE plots and found that cattle suppressed grass-dwelling arthropods (captured in sweep nets) whereas megaherbivores (elephants and giraffes only) suppressed ground-dwelling arthropods (captured in pitfall traps). Goheen et al. (2004) used both pitfall traps and sweep nets and found that true bugs (Hemiptera) increased more than twofold in total-exclusion plots but that beetles (Coleoptera) and grasshoppers (Orthoptera) did not respond detectably. Several years later, Pringle et al. (2007) used the same sampling methods in both KLEE and the sand soil exclusion plots and found that only beetles increased significantly following ungulate removal, again by nearly twofold on average, but with much stronger responses in sand soils than clay soils (Figure 2). Thus, insect responses, when detected, tend to be in the same direction (greater in the absence of ungulates), but the responses are not always detected and vary spatially, temporally, and taxonomically. The lack of clarity regarding the impacts of large herbivores on insect populations may stem in part from inadequate taxonomic resolution in these studies (in which insects were identified only to order) and/or from insufficient sampling duration or repetition. It is also possible that arthropod populations respond much more strongly to abiotic climatic variables such as precipitation than to shifts in the biotic variables influenced by large mammals.

Among the arboreal fauna, Pringle et al. (2007) found that densities of the Kenya dwarf gecko (*Lygodactylus keniensis*) increased in the absence of ungulates, by about 60% on average, because of increases in the availability of both prey (insects) and habitat (trees). As was the case with the beetles and trees studied by Pringle et al. (2007), the response of geckos to ungulate exclusion was more dramatic in sand soil than clay soil habitats (Figure 2). One potential explanation, as mentioned above, is that this variability in effect size was related to productivity, with stronger effects in lower-productivity areas (i.e., where rainfall is low or soils are poor). Although this hypothesis is consistent with evidence that grassland plants are more sensitive to herbivory in low-productivity areas (Chase et al., 2000), the existence of multiple confounding factors across the two soil types means that further testing is required. A novel ungulate exclusion experiment (UHURU, see below), which is replicated across a rainfall gradient, is now underway and will shed light on the context dependence of ungulate effects.

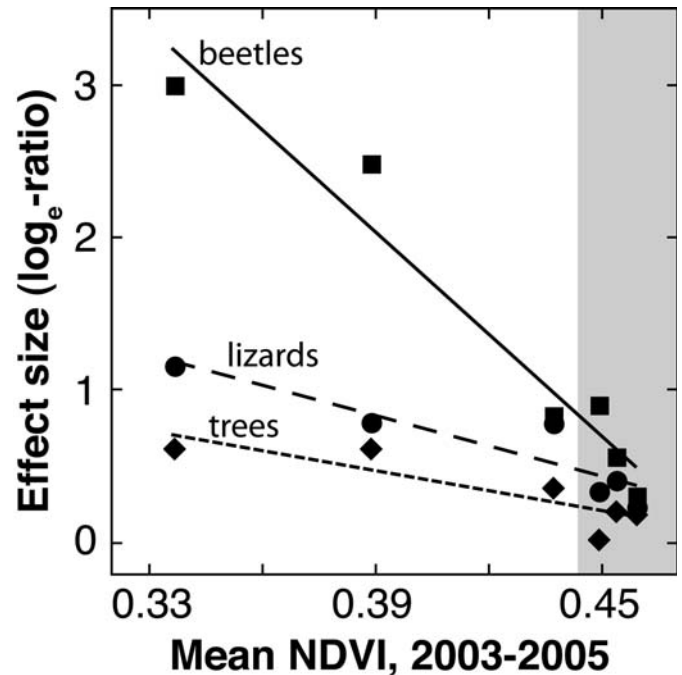


FIGURE 2. Spatial variation in the strength of ungulate effects across six pairs ungulate exclusion and control plots. The strength of the experimental effect of ungulate exclusion on the densities of trees (diamonds), beetles (squares), and lizards (circles) is negatively related to the normalized difference vegetation index (NDVI), a commonly used proxy for primary productivity. Effect size is calculated as the natural logarithm of the ratio of each variable in the enclosure versus the control plot at each site. White background indicates three relatively low-productivity sites on red sand soils, and gray indicates three relatively high-productivity sites on black clay soils. Redrawn from data in Pringle et al. (2007).

Intriguingly, the negative indirect effects of ungulates on geckos in general concealed a positive effect of elephants in particular. Elephant browsing alters tree structure, often creating splintered crevices, which geckos use for shelter (Pringle, 2008). As a result, geckos were most abundant where there were no ungulates whatsoever, but where ungulates were present, geckos were more numerous in areas with elephant-damaged trees. This finding underscores the importance of physical, “ecosystem-engineering” effects on habitat structure and illustrates two additional points: not all ungulates are equivalent in the effects that they exert on other species, and some species may simultaneously exert positive and negative indirect effects on other species via distinct pathways. Thus, in making difficult management decisions about individual wildlife species—for example, whether to reduce or augment elephant

populations—comparisons of treatments that exclude *all* ungulates versus open-access controls may not be particularly informative, since they do not allow experimenters to discern the impacts of individual species.

#### EFFECTS ON BIODIVERSITY

Many fewer studies have addressed how ungulate removal influences community composition and biodiversity. Theoretical arguments suggest that forces promoting disturbance and habitat heterogeneity, such as large herbivores, should enhance diversity (Ritchie and Olff, 1999), but there are currently insufficient data to allow a compelling test of this proposition in the Ewaso ecosystem.

The few studies that have compared community composition across different ungulate exclusion treatments have revealed complex and context-dependent effects. Huntzinger (2005) studied grasshoppers. In sand soil glade habitats, grasshopper biomass increased dramatically following the exclusion of ungulates from red soil glade habitat. In the clay soil KLEE plots, total grasshopper biomass did not differ between plots with and without cattle, but the number of grasshopper individuals was actually slightly *higher* where cattle were present. This seemingly counterintuitive result arose from differential responses within the grasshopper community: two small-bodied species increased in abundance while a medium-sized species decreased. Hence, cattle facilitate some grasshopper species while suppressing others, which may result from structural impacts of cattle on the architecture of the herbaceous layer.

Invertebrate predators also exhibited subtle responses to changes in the large-mammal community. Warui et al. (2005) sampled spiders in the KLEE plots and found that native ungulates did not influence total spider diversity. Cattle, however, decreased the diversity of the spider community as well as the abundance of the three most common species. One species of jumping spider (Salticidae), in contrast, increased in abundance where cattle were present. Because cattle decreased herbaceous cover and because spider diversity was positively correlated with relative vegetation cover, Warui et al. (2005) proposed that cattle indirectly affect spiders via their effects on vegetation structure. It is also possible that spiders suffered from reductions in their insect prey (Goheen et al., 2004; Pringle et al., 2007; Ogada et al., 2008). However, these studies of grasshoppers and spiders seem to suggest that for many arthropod communities the structural attributes of the grass layer may be at least as important as food availability.

Finally, Ogada et al. (2008) showed that elephants and giraffes significantly reduced total bird activity and the diversity of insectivorous birds in the 4 ha KLEE plots, whereas native ungulates in general depressed the diversity of granivorous birds. Again, multiple causality is likely: removal of elephants and giraffes increased the canopy area of subdominant tree species (i.e., species other than *A. drepanolobium*), providing a greater number of perches and less exposure to predators, whereas enhanced seed production in ungulate-free plots may have attracted granivores.

#### IMPLICATIONS FOR MANAGED LANDSCAPES

Several studies have revealed effects of ungulate exclusion that may be relevant for the maintenance of productive rangelands. For example, Sankaran and Augustine (2004) showed that ungulates indirectly suppressed the abundance of microbial decomposers in red soil glade and bushland habitats by decreasing the input of plant matter to the soils. Because these decomposers play a pivotal role in the breakdown of organic matter such as dead plants, dung, and animal carcasses, reductions in ungulate biomass could reduce rates of nutrient cycling, a key ecosystem function with important economic ramifications.

Another example involves behavioral interactions among native and domestic ungulates. Grazing wildlife such as zebra may sometimes compete with cattle for food (Odadi et al., 2007). As described above, the KLEE plots independently manipulate the presence of cattle, megaherbivores, and all other wildlife. Young et al. (2005) reported data suggesting that the strength of competition between cattle and zebra depended upon whether elephants were present. The presence of cattle caused zebra to forage elsewhere (but not vice versa). However, this effect was significantly weaker in plots accessible to elephants, perhaps because of changes in the composition of the herbaceous layer. Cattle feed readily on certain forbs, and elephants reduced forb cover by 33% in this experiment. Young et al. (2005) hypothesized that cattle may feed less in plots accessible to elephants because of lower forb availability, which may then make these plots more attractive to grazing zebra.

Evidence from other African savanna systems suggests that ungulates are an important link between the biosphere and the climate. In the Serengeti ecosystem of northern Tanzania, vaccination of cattle against the rinderpest virus in the late 1950s led to the eradication of the disease among the native grazers of Serengeti National Park (Dobson, 1995). The resulting four- to fivefold expansion of the wildebeest population between 1960 and

1980 reduced fuel loads and fires, which, in turn, increased woody cover. This shift from an open grassland to a more heterogeneous savanna doubled the amount of carbon stored in trees, switching the Serengeti from a net source of carbon to the atmosphere to a net sink (Holdo et al., 2009). Thus, this chain of indirect effects involving large herbivores determines a key ecosystem function with major implications for climatic change.

## DISCUSSION

### CONCLUSIONS AND GAPS IN BASIC KNOWLEDGE

The work summarized above helps to illuminate the ecological structure of the Ewaso ecosystem and suggests several broad conclusions. In general, the removal of large herbivores has a net positive effect on the densities and/or activity levels of other populations, although not all species respond. Taxa increasing in density, biomass, or local habitat usage following removal of large ungulates include woody and herbaceous plants, small mammals, lizards, snakes, and at least some species of birds and arthropods. The ecological interpretation of these results seems straightforward: the large-mammal guild represents a very large warm-blooded biomass, which is maintained by the consumption of vast quantities of plant material. The reduction or elimination of large mammals from the system frees that primary production for use by other consumers (and, by extension, the consumers of those consumers), either as energy or as habitat.

However, the mechanisms underlying these net effects may be complex and counterintuitive, necessitating some caution in extrapolating the results. For example, although tree density is higher on average in ungulate exclusion plots than in control plots, ungulates actually *facilitate* tree seedling establishment and survival by suppressing herbivorous rodents and competing grasses (Goheen et al., 2004, 2010; Riginos, 2009). In the special case of the whistling thorn tree, aggressive ant defenders also limit the impacts of mammalian herbivory. Likewise, arboreal geckos are suppressed by the ungulate community at large but facilitated by structural impacts of elephant on trees (Pringle et al., 2007; Pringle, 2008). Indeed, most of the experimental effects documented to date are likely to have multiple causes, although only for trees have these been systematically and experimentally untangled (Goheen et al., 2004, 2010; Riginos and Young, 2007; Riginos, 2009).

An obvious conclusion, but one whose implications may often be overlooked, is that different large-herbivore species are not ecologically equivalent. A thousand

kilograms of zebra does not equal a thousand kilograms of elephant or a thousand kilograms of cattle. Each species eats different sets of plants in different ways, and each therefore exerts a unique impact on the broader system. The distinction between predominantly grazing and predominantly browsing species is one example, but there are many ecologically important differences between species within these loosely defined guilds: body size, water requirements, and, in the case of elephants, the ability to uproot mature trees. The effects of altering livestock density are likely to be particularly pronounced, in part because humans shield domestic animals from many factors that control wildlife populations: drought, food shortage, and predation (Hairston et al., 1960). Thus, livestock may continue to exert strong ecological influence even at times when other large-herbivore populations are declining and in circumstances (e.g., drought) when the rest of the community may be least resilient to their impacts.

Finally, the relative ecological importance of large herbivores is variable in space. Pringle et al. (2007) showed that the indirect effects of ungulates on the densities of trees, beetles, and arboreal geckos varied in strength across a gradient in soil type and rainfall. Because the magnitude of these effects were negatively related to productivity (Figure 2), the authors hypothesized that productivity may modulate the strength of herbivore impacts. Studies elsewhere (Larson et al., 2008; Asner et al., 2009) have yielded at least partial support for this notion. However, multiple factors confounded the comparison of effects across soil types.

To better understand both the modulating influence of environmental context and the differential effects of different native ungulate species, J. R. Goheen, R. M. Pringle, and T. M. Palmer (unpublished) initiated a novel ungulate exclusion experiment in September 2008. Ungulate Herbivory Under Rainfall Uncertainty (UHURU) was designed to focus on the effects of three particularly abundant and influential wildlife species: dik-dik (*Madoqua kirkii*), impala (*Aepyceros melampus*), and elephant (*Loxodonta africana*). Thus, the experiment includes a treatment that excludes all mammals larger than hares (*Lepus* spp.), another that allows dik-dik but excludes impala and all larger species, and a third that excludes elephant and giraffes only. A fourth treatment is unfenced and accessible to all wildlife (but not to livestock, which are kept out by herders). Each plot is 1 ha (100 × 100 m), and each type of plot is replicated three times in the northern, central, and southern parts of the Mpala Conservancy (all on red sand soils), with precipitation increasing ~80% from north to south. This experiment will reveal potential

interactions between herbivory and precipitation regimes, and planned warming treatments may also reveal how important ecosystem variables like soil carbon storage will vary as global temperature increases.

What is most striking in reviewing these studies is how much we still do not know. It is odd how few studies have addressed the effects of ungulate exclusion on community diversity, especially with respect to grass and forb communities. There is a similar paucity of data about the influence of large herbivores on basic ecosystem functions such as decomposition and nutrient-cycling rates. Even the influence of ungulates on primary productivity has received little study, and no attempt has been made to understand how the impacts of herbivores on plants scale up to determine levels of carbon sequestration and storage (cf. Holdo et al., 2009). The role of predators is likewise poorly understood. Studies in the Yellowstone ecosystem of North America have shown that the reintroduction of wolves in the mid-1990s has profoundly affected the landscape by altering the behavior and physiology of elk (Ripple and Beschta, 2004; Creel et al., 2007). Similar processes may be at work in the Ewaso ecosystem, with the apparent recent recovery of many predator species on properties in Laikipia since the 1990s (Georgiadis et al., 2007a, 2007b), but no data exist with which to evaluate this possibility. Finally, there has thus far been a bias in this research toward questions that are academically interesting but dubiously useful from the perspective of day-to-day landscape management, an issue that we address in the following section.

#### RECONCILING BASIC AND APPLIED INTERESTS

At the most ethereal level, it can be argued that preserving any complex system in working order—from automobiles to ecosystems—requires a functional understanding of how that system works and what its different parts actually do. The studies that we synthesize above, which paint an increasingly complex picture of how ungulates shape the abundance, distribution, and diversity of other species in savannas, are certainly an effort in this direction. On a slightly more pragmatic level, the information generated by these studies should be considered when managing large-herbivore populations. Harvesting, culling, contraception, translocation, and reintroduction of ungulates are all common practices (van Aarde et al., 1999; Georgiadis et al., 2003; Tambling and du Toit, 2005; Druce et al., 2006; Hayward et al., 2007a, 2007b; Whitman et al., 2007). These actions are always expensive and often contentious (e.g., Landeman, 1978; Pimm and van Aarde, 2001), and it therefore seems prudent to know how such deliberate

manipulations are likely to affect biodiversity and ecosystem processes. Understanding the direct and indirect effects of elephants in particular (i.e., how ecosystem properties change as a function of elephant abundance) may inform the emotionally charged issue of elephant management. The indirect effects of elephants have received little formal study. Given the high stakes of elephant management and control programs, this is an area where rigorous experimental data are surprisingly few.

These issues aside, very different imperatives drive academic science, on the one hand, and land management, on the other. The reward structures in most parts of academia (including the large grants necessary to finance major research efforts) demand advances at the “forefront” of scientific theory (wherever that might be at the time). Many rangeland management issues are widely considered (rightly or wrongly, and with definite exceptions) to fall outside the narrow boundaries of modern ecology’s leading edge. This situation can lead to frustration on behalf of both local stakeholders (“Why are researchers spending so much time and money on projects with no immediate practical benefit?”) and researchers (“Why won’t managers and community members look at the ‘big picture’ of interconnected parts?”).

From the perspective of the research community, there are at least two ways to help resolve this dilemma. One is to identify research questions that simultaneously meet both needs: to extend the frontiers of ecology and to address issues that genuinely matter to managers and pastoralists. (This suggestion is not to diminish the importance of research questions that are more purely basic or more purely applied but merely to point out that all of these things are compatible.) Each of the concerns most commonly cited by those who raise livestock or manage multiuse landscapes in the Ewaso ecosystem dovetails in some way with issues currently considered exciting by academic ecologists and ecological economists: the relationship between climate and plant (i.e., forage) production, the potential for competition between native and domestic herbivores, the behavior and population dynamics of large carnivores, the transmission and management of infectious diseases, the determinants of range quality, the market price of livestock, and strategies for generating alternative revenue streams, such as from tourism.

We provide just a few examples relevant to the topic of this chapter. As discussed above, early research in KLEE showed that small mammals and their potentially disease-bearing ectoparasites doubled in the absence of ungulates. The logical next steps, some of which are currently under investigation by McCauley, Keesing, and



colleagues, are to understand whether this shift actually alters the prevalence of disease in humans and domestic animals and to what extent this is true in landscapes where livestock have completely replaced native ungulates. The effort to address these questions links recent intensive efforts in disease ecology with very real problems encountered in managed landscapes. Another example, being addressed by Goheen's research group, is to understand how both wild and domestic ungulates might be better managed to limit predation on the latter (or similarly, how common wild ungulates might be managed to minimize depredation of rare ones). This research fuses long-standing academic interest in issues such as "apparent competition" (Holt, 1977) with the goal of enabling coexistence of people and predators and/or the stabilization of rare and declining wildlife species such as hartebeest (Georgiadis et al., 2007a, 2007b). Rangeland quality, from the perspective of livestock production, is largely a product of factors that have long intrigued "basic" biologists and that are determined in part by the abundance and community composition of ungulates, such as the relative abundance of trees and grasses. Along similar lines, an ecological-economic quantification of how the relative abundance of native wildlife influences per hectare profitability of single-use and multiuse landscapes would be warmly received both by managers and by academics in the thriving hybrid discipline of "ecosystem services." Finally, there is enormous interest within academia in projecting the biological impacts of ongoing climatic change. Such changes, including shifts in rainfall regime, will determine the quantity, quality, and spatial distribution of forage over the coming century, but they remain poorly understood.

None of these research efforts, however conclusive their results might be, will yield the desired objective of linking basic science to conservation without another element, which is to aggressively disseminate results and their implications to nonscientists while simultaneously being forthright about the limits of current knowledge in informing range management. Obviously, experimental results will never be applied as long as they remain confined to scientific journals; perhaps less obviously, yet even more importantly, nothing destroys respect for science more efficiently than hypotheses passed off as certainties in an effort to influence decisions.

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