In African savannas, are donor and trophic control of ungulate prey coupled by apparent competition?

Authors:

Nicholas J. Georgiadis[1], Justine A. Becker[2], Adam T. Ford[3], Douglas N. Kamaru[4], Jacob R. Goheen[4]

1. 4718 SW Pendleton St., Portland OR 97221 (independent researcher)
2. Department of Ecology, Montana State University, Bozeman, MT, USA
3. Department of Biology, University of British Columbia, 1177 Research Road, Kelowna, British Columbia, V1V 1V7, Canada
4. Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa, USA

Contact and Corresponding Author: Nicholas J. Georgiadis (nicogeo@uw.edu)

Open Research Statement

Data used to derive Figure 2 were originally published in graphic form in Georgiadis et al. (2007b), and are provided as numerical values in the Supplementary Information for this manuscript as Table SI 1. A subset of data from the database published by Daskin and Pringle (2018), which were used to perform the analysis described in Table 2, is provided in Dryad: http://datadryad.org/share/vTtYm0p8erwl8RozWe4I7L04lGfTZ0SyALojeQhI660

Artificial Intelligence (AI) Policy Statement

During preparation, and at multiple points in developing the manuscript, AI tools *Undermind* and *ChatGPT* were used to 1) Reference discovery: targeted questions (over 70 in total) were submitted to *Undermind* to identify relevant literature concerning specified ecological concepts, models, and case studies. 2) Summarize: *ChatGPT* was used to generate summaries of selected published papers, which were then checked against original sources. These tools were used iteratively across the manuscript, particularly in sections synthesizing theory and empirical case studies, to help ensure coverage and correct interpretation of relevant literature. All interpretations, arguments, and conclusions are our own.

Key words and phrases:

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Abstract

Understanding how donor (bottom-up) and trophic (top-down) modes of population control shape food web structure and dynamics has long been a major goal of ecology, yet consensus about mechanisms is lacking. Two prevalent patterns hint at generality in mechanisms that shape predator-prey communities. First, within communities, herbivore biomass declines and plant biomass increases in the presence of predators, regardless of ecosystem productivity, evoking a trophic cascade. Second, across communities, predator biomass density increases sublinearly with prey biomass density, a ‘power law’ which often is assumed to arise from donor control. We show how both patterns can emerge simultaneously, using data from ungulate assemblages in African savannas. Within three savannas where mechanisms underlying trophic dynamics are understood (the Greater Serengeti ecosystem, Kruger National Park, and the Laikipia highlands), prey biomass is dominated by one or a few ungulate species that are donor controlled, yet they support most of the predators. The same predators also consume less abundant prey species that are trophic controlled. In effect, donor and trophic control of prey are coupled by generalist predators via ‘non-reciprocal apparent competition’ (NRAC). Within 56 African savannas where ungulate biomass densities but not dynamics are known, mean ungulate biomass rankings resemble those of Serengeti, Kruger, and Laikipia, and are therefore consistent with the hypothesis of NRAC. Under NRAC, total prey biomass declines within systems because trophic-controlled prey are suppressed by predators. Among systems, power law patterns emerge from the dynamics of dominant prey that are donor controlled. Given that coupled donor and trophic control can occur wherever there are generalist predators, NRAC is a candidate mechanism contributing to the prevalence in nature of both trophic cascades and predator-prey power laws.

Introduction

Understanding how donor (bottom-up) and trophic (top-down) modes of population control shape food web structure and dynamics has long been a focus of empirical and theoretical ecologists (Hairston et al. 1960, Oksanen et al. 1981, Fretwell 1987, Power 1992), yet consensus about mechanisms is lacking. Two sets of macroecological patterns provide clues about food web structure and function. First, a meta-analysis of studies that manipulated donor and trophic control in real ecosystems – by adding nutrients and removing predators, respectively – revealed that herbivore biomass declines and plant biomass increases in the presence of predators, regardless of ecosystem productivity (Borer et al. 2005). This suggests that trophic control (via trophic cascades) is prevalent in nature. Second, across diverse ecosystems, herbivore biomass density increases as a sublinear function of primary productivity (McNaughton et al. 1989), and predator biomass density increases as a sublinear function of prey biomass density (Carbone and Gittleman 2002, Hatton et al. 2015, Perkins et al. 2022). Such power laws can arise from models driven either by donor control (Hatton et al. 2015, Salahshour 2023) or by trophic control (Mazzarisi et al. 2025), but it is not clear which of these models best reflect real food webs. We address how both macroecological patterns can arise and persist within and among ecosystems.

Barbier and Loreau (2019) envisioned such macroecological patterns as representing two distinct but complementary domains of food web theory. The first, which they called the ‘dynamical paradigm’, emphasizes interactions among species, such as between predators and prey, and seeks to understand how effects of predators cascade downwards in food webs. The second, which they called the ‘energetic paradigm’, seeks to understand how energy flows upwards in food chains, and how allometric scaling (*sensu* Hatton et al. 2015) emerges from environmental and physiological processes. As a first step towards unifying the energetic and dynamical paradigms, Barbier and Loreau (2019) proposed a model that, in its basic form, features four trophic levels, each behaving as a single entity comprising the sum of within-level biomass. This linear food chain is either donor controlled with levels stacked like a stepped pyramid, or trophic controlled with biomass totals alternating in size between sequential trophic levels. Transition between donor- and trophic-controlled versions of the model depends partly on the strength of predation, relative to the strength of density dependence within prey.

In addition to linear food chains, real food webs feature a variety of trophic motifs, such as omnivory and intraguild predation (e.g. Bascompte and Melián 2005), with donor and trophic control operating simultaneously within and across levels. Modeling these interactions is challenging, but Wollrab et al. (2012) showed that equilibrium dynamics of donor and trophic control depend on only two properties: the length of component food chains and the presence of a generalist top predator. In their classification of food chain types, 'branched' chains become 'looped' if two or more branches are coupled at the apex by a generalist predator, thereby enabling indirect effects among prey, mediated by predators (Wollrab et al. 2012).

Within food webs, apparent competition (Holt 1977) can be the most frequent type of indirect effect (see, e.g., Table 3 in Bascompte and Melián 2005). Apparent competition rarely features explicitly in multi-layer model food webs (for example, the term apparent competition does not appear in Barbier and Loreau (2019), although their model can be extended to include it). However, stabilizing effects of apparent competition have been widely explored in two-level systems (Holt and Lawton 1994, Holt and Bonsall 2017). In the simplest (1-predator, 2-prey) models, stability depends on key processes such as the shape of a predator's functional response (Lou et al. 2025). In a 1-predator, n-prey system with a linear functional response, Seno (2025) proved that apparent competition has a globally stable equilibrium (i.e., an equilibrium to which all solutions converge, regardless of initial conditions), with numerically dominant prey exhibiting higher ratios of recruitment to predation rates, while other prey with lower ratios are numerically subordinate or may go extinct. In addition, theoretical models and empirical evidence have suggested that prey switching, which affects the shape of functional responses, can contribute to food web stability by dampening population oscillations and preventing predator-prey cycles (e.g., Van Baalen et al. 2001, Saha and Samanta 2021, Prokopenko et al. 2022, Archibald et al. 2023, Kamaru et al. 2024; but see Hopcraft et al. 2005). The stabilizing properties of apparent competition might therefore help to explain the prevalence of generalist predators in nature (Closs et al. 1999).

Typically, apparent competition is asymmetric because multiple prey species are unlikely to be affected identically by the predators they share (Holt 1977). Asymmetry becomes extreme when populations of one or more prey species are negatively affected by shared predators, while populations of other prey species are not affected. Chaneton and Bonsall (2000) referred to this as 'non-reciprocal apparent competition' (herein referred to as NRAC). Chaneton and Bonsall (2000) found that NRAC operated in 76% of a putatively random sample of 34 terrestrial and freshwater food webs. Given the prevalence in their sample, they inferred that non-reciprocal indirect effects are prevalent in nature. This is plausible, given that NRAC occurs when one or more prey species that share predators escapes trophic control to become donor controlled.

However, Chaneton and Bonsall (2000) did not consider the potential for NRAC to couple donor and trophic control.

The central theme of our synthesis is that donor and trophic control are coupled by NRAC. We believe that the significance of this process has been overlooked in food web theory, perhaps due to mathematical intractability, and under-reported in empirical studies of food webs, perhaps because its diagnosis is onerous, requiring knowledge of how each prey species in a community is controlled. We assessed the prevalence of NRAC in large-mammal assemblages in African savannas.

Savanna mammal assemblages have featured prominently in food web studies because they are relatively intact (Fløjgaard et al. 2022), they have a linear trophic structure (Figure 1), and the component species are sufficiently large (>~10 kg) to be censused reliably. Herbivore and carnivore abundances have been quantified across many localities to reveal consistencies in community structure (e.g. Hatton et al. 2015). Temporal dynamics of herbivore (i.e., wild ungulate) populations have been sufficiently monitored in three well-studied locales to support the inference that donor control of abundant species was coupled with trophic control of less abundant species by NRAC (Georgiadis et al. 2007a). We present evidence suggesting that savanna ungulate communities are shaped by predation, and infer that NRAC operates widely in savannas. We show that NRAC can simultaneously produce the patterns described by Borer et al. (2005) and by Hatton et al. (2015). Since there is nothing functionally unique about savanna food web dynamics, we conclude that there is potential for NRAC to occur wherever there are generalist predators, providing a candidate mechanism contributing to the prevalence of trophic cascades and predator-prey power laws in nature.

Donor and trophic control in African savannas

Early comparisons of ungulate biomass density and primary production within and among savannas affirmed that resources – rainfall and nutrients – underlie producer and consumer dynamics. Evidence included positive relationships between mean annual rainfall and plant biomass density (Deshmukh 1984), rainfall and ungulate biomass density (Coe et al. 1976, East 1984, Fritz and Duncan 1994), rainfall and herbivory (McNaughton et al. 1989), and primary production and ungulate biomass (Coe et al. 1976). Subsequently, predator (i.e., large carnivore) and prey (i.e., wild ungulate) biomass densities were shown to be correlated, both within (Hayward et al. 2007) and among savannas (Hatton et al. 2015). The generality and consistency of these correlations led to broad acceptance that, from plants to apex predators, savanna communities are strongly donor controlled.

In contrast, evidence for trophic control of prey was initially scarce, rarely featuring in early studies on wild ungulates (reviewed by McNaughton and Georgiadis 1986, but see Sinclair 1985). Foundational work on the behavior and population biology of large carnivores (e.g., Kruuk 1972, Schaller 1972) preceded emergent properties of multi-predator, multi-prey food webs (Ford and Goheen 2015, Allen et al. 2019, Atkins et al. 2019, Montgomery et al. 2019). Trophic control may also have been overlooked because predation is often challenging to qualify either as contributing to additive mortality, or as compensatory mortality that would otherwise have been caused by starvation or disease (but see Sinclair and Arcese 1995a). These reasons do not imply that trophic control of savanna ungulate assemblages is weak; rather, impacts of large carnivores on their ungulate prey simply had not been quantified. Still, there was a prevailing view that predation did not rival primary production as a principal driver of population dynamics for African ungulates. This perception applied to ungulate populations elsewhere, leading Sinclair and Krebs (2002) to conclude that "food supply drives changes in large-mammal populations and top-down processes rarely intervene". They listed predation as one of three secondary processes capable of modifying or overriding donor control (the others were intraspecific sociality and stochastic events).

One year later, Sinclair et al. (2003) reported that a subset of the ungulate species in the Greater Serengeti Ecosystem (Tanzania and Kenya) was trophic controlled. Since then, evidence has accumulated that the same is true of two other well-studied savannas, Kruger National Park in South Africa (Du Toit et al. 2003) and the Laikipia region of northern Kenya (Georgiadis et al. 2007a, Georgiadis et al. 2007b, Georgiadis 2011). Much of what is known about the mechanisms underlying the dynamics of savanna ungulates comes from these three ecosystems.

Greater Serengeti Ecosystem, Tanzania and Kenya

Serengeti is defined by its iconic wildebeest (*Connochaetes taurinus*) migration. Following the eradication of rinderpest (an exotic viral disease introduced via domestic ruminants; Sinclair 1977) in 1962, the migratory wildebeest population irrupted from ~250,000 to stabilize at 1.0-1.5 million, ultimately to be limited by food availability and density-dependence (i.e., donor control) during the dry season (Mduma et al. 1999). Such profusion was likely driven by extensive grasslands and seasonal rainfall patterns that closely matched the resource requirements of wildebeest (Hopcraft et al. 2015). In addition, their migratory lifestyle and synchronous breeding satiates predators at the time when calves are at their most vulnerable (Estes and Estes 1979, Holdo et al. 2009). The result is a high annual birth rate and high calf survival (compared to non-migratory wildebeest in the same system; Ndibalema 2009), allowing wildebeest to proliferate and maintain their numerical dominance.

By contrast, topi (*Damaliscus lunatus*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus africanus*), and especially migratory plains zebra (*Equus burchelli*; hereafter “zebra”) were likely controlled by predation (Sinclair 1985, Grange et al. 2004, Hopcraft et al. 2010), while the evidence was less conclusive for non-migratory wildebeest (Sinclair et al. 2003, Hopcraft et al. 2010, Ndibalema 2009), Thomson's gazelle (*Eudorcas thomsonii*) and Grant's gazelle (*Nanger granti*; Sinclair 1985). Additional evidence of trophic control for numerically subordinate prey was reported by Sinclair et al. (2003) following a human-caused perturbation in northern Serengeti, where, from 1981 to 1986, predators (lions *Panthera leo*, hyenas *Crocuta crocuta*, and jackals *Canis* spp) were suppressed by illegal snaring that targeted migratory wildebeest. During this interval, smaller-bodied ungulates, including oribi (*Ourebia ourebi*), Thomson’s gazelle, impala, warthog, and topi increased in abundance, only to decline again when snaring abated and predators recovered. Across the international border with Kenya, where snaring was less severe, there was no corresponding change in the abundance of these species. Thus, a key feature of ungulate population dynamics in Serengeti is the contrast between donor control of numerically dominant migratory wildebeest, and trophic control of mostly smaller, less abundant ungulates.

Kruger National Park, South Africa

Population monitoring of wild ungulates over multiple decades revealed complex modes of control (Owen-Smith and Mills 2006, Owen-Smith and Mills 2008) that varied subtly within and among prey species. Species that maintained high abundance (giraffe *Giraffa camelopardalis,* impala, wildebeest, and zebra) over time were most consistently affected by a combination of density dependence and rainfall (i.e., donor control), and were minimally affected by predation. Lion numbers varied with the abundance of zebra, wildebeest, and buffalo (*Syncerus caffer*; Mills et al. 1995), but the degree of trophic control of these abundant wild ungulates changed with rainfall (Owen-Smith and Mills 2008) over seasonal and decadal time spans (Gertenbach 1980, Mills et al. 1995). During wet phases, lion diets featured more wildebeest and zebra and fewer buffalo, but the reverse was true during dry phases (when anthrax may also have contributed to buffalo declines; Huang et al. 2022). Thus, zebra, wildebeest, and buffalo were all primary prey (i.e., the numerically dominant species that comprised the bulk of lion diets) at different times. When the relative abundance of primary prey declined—independently of lion abundance—lions killed greater proportions of alternative prey, including giraffe, greater kudu (*Tragelaphus strepsiceros*), waterbuck, and warthog (Owen-Smith and Mills 2008).

Eland (*Taurotragus oryx*), greater kudu, tsessebe, waterbuck, and warthog were generally trophic controlled, although populations of each were sensitive to drought. Roan (*Hippotragus equinus*) and sable (*H. niger*) declined steeply following an increase in lion predation driven by an influx of zebra and wildebeest to human-installed water points (Harrington et al. 1999), providing evidence for apparent competition (Owen-Smith et al. 2011). Overall, the roles of donor and trophic control were more nuanced than in Serengeti, possibly because prey relative abundance in Kruger was more equitable. Each species of wild ungulate was regulated by a unique combination of donor and trophic control that was modulated by rainfall (Owen-Smith 2015, Ogutu and Owen-Smith 2005).

Laikipia, Kenya

In the Laikipia region of northern Kenya, the abundance of wild and domestic ungulates changed when land use shifted from beef production (up to the mid-1980s) to wildlife conservation (1990 onwards). It was intended that wildlife would generate income for landowners, initially by consumptive use, and later from ecotourism (Georgiadis et al. 2007b). From the mid-1950s to mid-1980s, wild ungulates perceived to compete with cattle (*Bos indicus*) – principally zebra – were lethally suppressed or excluded from many private holdings, as were large carnivores. The suppression of wild ungulates mostly ceased in the mid-1980s, allowing their populations to grow to the highest recorded levels in 1990-1991 (Georgiadis 2011). Zebra abundance increased five-fold to dominate the biomass density of wild ungulates. Several years later, lethal control of large carnivores also abated, allowing lions, hyenas (*C. crocuta*, *Hyaena hyaena*), leopards (*Panthera pardus*) and wild dogs (*Lycaon pictus*) to recover over the following decade (Frank 2011, Woodroffe 2011, Bauer et al. 2015, Frank 2023). In essence, this staggered restoration of prey and then predators provided another perturbation yielding insights about the impact of large carnivores on a wild ungulate assemblage that initially was donor controlled.

As predator populations recovered across Laikipia, zebra, Grant's gazelle, and impala maintained high abundances, with zebra numbers depending on lagged rainfall and zebra density

(Georgiadis et al. 2003, Georgiadis et al. 2007b). In contrast, hartebeest (*Alcelaphus buselaphus*), waterbuck, Thomson's gazelle, eland, buffalo, and to a lesser extent giraffe, all declined. An assessment of nine hypotheses concluded that trophic control was the most plausible cause for these population declines (Georgiadis et al. 2007a): only predator restoration, by itself, explained the synchrony, lagged timing, and extended declines of wild ungulates with such disparate food and habitat preferences (Georgiadis et al. 2007a; Figure 2, Table 1). Predation shaped the ungulate assemblage by decreasing the biomass density of many species, thereby promoting dominance by zebra (and to a lesser extent Grant's gazelle and impala), reducing community evenness (Figure SI 1). By the early 2000s, the biomass density of wild ungulates in Laikipia had declined by ~60% (Figure 2).

Coincident with the return of large carnivores to Laikipia, two parallel studies revealed support for the hypothesis of trophic control. Ford et al. (2015) documented a ca. 33% decrease in the density of Guenther's dik-dik (*Madoqua guentheri*), the primary prey of wild dogs, following the recovery of wild dogs in the mid-2000s. Dik-dik were trophic controlled, as their densities were better explained by energetic demands of the wild dog population than by density dependence or rainfall. In a second study, population growth of hartebeest switched from negative to positive following experimental exclusion of lions (Ng'weno et al. 2017). Hartebeest within a lion-proof sanctuary exhibited negative density dependence, while those exposed to lions exhibited an Allee effect (positive density dependence, supporting trophic control; Ng'weno et al. 2017).

Non-reciprocal Apparent Competition (NRAC)

The three focal savannas share key similarities regarding how prey populations are controlled. In each case, ungulate biomass is dominated by one or a few a species (wildebeest, buffalo, or zebra; Packer et al. 2005, Funston and Mills 2006, Maruping-Mzileni et al. 2017, Frank 2023) that, despite comprising the primary prey of predators, are donor controlled. The same predators also consume subordinate (i.e., less common) prey species, some of which are trophic controlled (Figure 3). As described above, this coupling of donor and trophic control by predation qualifies as non-reciprocal apparent competition (NRAC).

That NRAC was operating in Laikipia was affirmed by a combination of field experiments and monitoring of primary prey (zebra), a focal species of secondary prey (hartebeest), and predator (lion) populations (Ng'weno et al. 2017, Ng'weno et al. 2019a, Ng'weno et al 2019b). In addition to the Allee effect described above, lions killed hartebeest selectively (but infrequently, given their scarcity), especially in proximity to their primary prey, zebras, such that areas >0.5 km from zebra herds functioned as spatial refugia for hartebeest (Ng'weno et al. 2019b). The same indirect effects, involving many of the same species, also operate in Kruger and Serengeti (Georgiadis et al. 2007a). Sinclair et al. 2010 described this process as "the bottom-up [food] chain intensif[ying] the top-down [food] chain".

Serengeti, Kruger, and Laikipia also differ in ways that are instructive about how NRAC operates. First, different populations of a given prey species are not controlled uniformly by the same mode of control. Zebras are strongly donor controlled in Laikipia, are mostly donor controlled in Kruger, and appear to be trophic controlled in Serengeti. Second, the focal savannas also differ in the evenness of their ungulate biomass distributions. In Serengeti, a single donor-controlled population (migratory wildebeest) comprises ~79% of the prey biomass (Figure 3), whereas in Kruger, four species are trophic controlled, comprising ~73% of total biomass (buffalo, zebra, giraffe, and wildebeest). Migratory wildebeest in Serengeti are strongly donor controlled; in Kruger, donor and trophic control vary subtly among and even within ungulate species over time. Therefore, despite profound differences in climate and landscape attributes, histories of human-caused perturbations, and the identity of prey species that are donor vs. trophic controlled, NRAC is a persistent feature of trophic dynamics in all three focal savannas.

Is NRAC widespread among African savannas?

Assuming the three focal savannas comprise a random (albeit small) sample, such consistency suggests that NRAC is a prevalent feature of predator-prey dynamics among African savannas. Support for the NRAC hypothesis is threefold.

1. The potential for indirect effects is high

As observed by Wollrab et al. (2012), linear food chains within food webs become 'looped' if two or more are linked by a generalist predator. A food web with 2 species of apex predator sharing 3 species of prey has a maximum of 6 looped pathways (Figure 1). With 5 predators sharing 10 prey species – typical of an intact savanna large-mammal system – the maximum number of looped pathways increases nonlinearly to 225 (Estes et al. 2013). Not all looped food chains necessarily manifest as apparent competition, but the potential for indirect effects in savannas is high.

2. Outside savannas, large carnivore-ungulate systems exhibit similar structure and dynamics

Across the globe, large carnivore-ungulate systems exhibit similar dynamics to African savanna systems. At temperate and boreal latitudes, biomass density of wild ungulates collectively increases with resource availability (Figure 1 in Fløjgaard et al. 2021), yet trophic control of ungulates also is prevalent (e.g., Estes et al. 2011, Kauffman et al. 2007, Christianson and Creel 2014, Donadio and Buskirk 2016, MacNulty et al. 2016, Smith et al. 2019). Some ecologists have even proposed that strong trophic control should be the null expectation of large mammal predator-prey systems (Terborgh and Estes 2010, Estes et al. 2011, Ripple et al. 2014). Repeatedly, and in temperate and boreal systems, trophic control via apparent competition has been documented following disturbance by humans (e.g. Latham et al. 2011, Serrouya et al. 2021, but see Tjaden-McClement et al. 2025). In a review of declining species for which apparent competition had been implicated, DeCesare et al. (2010) observed that "common to most systems linking apparent competition and species endangerment is a predator population supported by an abundant primary prey species" (see also Wittmer et al. 2013, Holt 2023).

3. Traits that affect predation risk shape biomass distributions of savanna ungulates

A feature of Serengeti, Kruger, and Laikipia is that the same species—wildebeest, buffalo, and zebra—tend to dominate ungulate biomass (Figure 3). This feature is widespread across African savannas. Among 56 other savannas (Table SI 2), biomass distributions were dominated by the same three species (in addition to giraffe; Figure 4). Despite being among the preferred prey of lions (Hayward and Kerley 2005), populations of these ungulates are likely to escape trophic control for several reasons. First, they are medium- to large-bodied, and therefore preyed upon only by the largest of carnivores (Sinclair et al. 2003, Hopcraft et al. 2010). They also tend to be gregarious, tend to graze in open habitats with less cover for predators, and tend to flee from – or, in the case of buffalo, can fight off – predators. By contrast, numerically subordinate species tend to be smaller-bodied and are thus preyed upon by more species of predators (Sinclair et al. 2003, Radloff and Du Toit 2004). They tend to be solitary or live in small groups, relying on crypsis and camouflage to avoid predators (Ford and Goheen 2015b, Atkins et al. 2019), rather than the enhanced predator detection and risk dilution afforded by larger groups (Hamilton 1971, Schmitt et al. 2014, Ford and Goheen 2015a).

Collectively, these traits – body size, group size, and feeding style – have long been accepted to affect vulnerability to predation (Jarman 1974, Brashares et al. 2000, Creel et al. 2014, Le Roux et al. 2019, Owen-Smith 2019). To test if differences among species in vulnerability to predation were correlated with prey abundance, we used a linear mixed model to correlate species biomass density (see http://datadryad.org/share/vTtYm0p8erwl8RozWe4I7L04lGfTZ0SyALojeQhI660) with estimates of mean body size, group size, and feeding preference (measured as percent graminoids in the diet) from the literature (Table SI 3). Prey biomass density was positively correlated with all three traits, particularly body size (Table 2; Figure SI 3), suggesting that predation is a potent factor shaping ungulate biomass distributions within African savannas.

Structural congruence (i.e., similarity in species identity and rank) between the 56 ungulate assemblages and the three systems where NRAC has been confirmed provides inferential basis that biomass distributions of savanna ungulates are shaped by the same interplay of donor and trophic control. Although they support an abundant and diverse suite of predators, prey species that are less vulnerable to predation account for most of the biomass, consistent with those from

Serengeti, Kruger, and Laikipia that are donor controlled. In contrast, species with traits that make them more vulnerable to predation are numerically subordinate, consistent with those from Serengeti, Kruger, and Laikipia that are trophic controlled.

When isn’t it NRAC?

Although the evidence from 56 African ungulate assemblages is consistent with NRAC, it is based on correlation and congruence of patterns among prey biomass distributions. Holt et al. (2008, also Holt and Lawton 1994) cautioned that mechanisms underlying indirect effects are challenging to predict. For example, if the migratory wildebeest population in Serengeti crashed, trophic control might actually intensify for numerically subordinate ungulates, at least until predator numbers declined. In this regard, prey switching—a behavioral response of predators involving changes in prey consumption rates—would precede declines in predator populations, which is the ultimate expectation under NRAC. For the three focal savannas, NRAC was inferred to operate because numerically dominant ungulates were shown to be donor controlled. But donor control of numerically dominant ungulates cannot be assumed. For example, in Etosha National Park (Namibia) and Liuwa National Park (Zambia), numerically dominant wildebeest and zebra declined steeply following human-caused perturbations (perimeter fencing in Etosha, and poaching in Liuwa). In the 1990s migratory wildebeest and zebra dominated ungulate biomass in Etosha, yet all ungulates were trophic controlled, by a combination of disease (anthrax) and predation (Gasaway et al. 1996, Trinkel 2013). In Liuwa, a migratory wildebeest population dominated prey biomass, but was limited mostly by hyenas (lions had been almost eradicated; Watson et al. 2022, Martens et al. 2025). This does not mean that NRAC cannot operate in a food web featuring only trophic control, just that it cannot be assumed that NRAC is operating solely from a prey biomass distribution, even when it resembles the 'mean' distribution (Figure 4). Because these were severely perturbed systems that likely were not in equilibrium, we posit that NRAC is likely to operate in systems that are at or close to equilibrium.

Conservation Implications

Of the 57 species of terrestrial wild ungulates (artiodactyls and perissodactyls) inhabiting African savannas, 14 (25%) are categorized as "Threatened" by the IUCN, and 34 (60%) are reported to exhibit "decreasing" population trends (International Union for the Conservation of Nature, 2025). By definition, rare species of conservation concern are likely to occupy a low rank within ungulate biomass distributions, and thus be susceptible to trophic control via NRAC (Figure 3, Figure 4). Apparent competition has been demonstrated through focal studies on roan (Harrington et al. 1999), hartebeest (Georgiadis et al 2007a, Ng'weno et al 2019b), and perhaps sable (Chirima et al. 2012), but not Grevy's zebra (*Equus grevyi*; O'Brien et al. 2018). The world's rarest antelope—hirola (*Beatragus hunteri*)—exhibits characteristics consistent with population suppression by apparent competition: loss of preferred habitat (open grasslands), within a geographic range where abundant large carnivores reduce its annual population growth, but subsist on more abundant wild ungulates (Ali et al. 2017; Ali et al. 2018).

When NRAC presents challenges for conservation, it usually is the proximate cause for population declines. Instances where apparent competition jeopardizes populations or entire species tend to be driven ultimately by environmental disturbances, like species introductions, habitat fragmentation, or habitat alteration (DeCesare et al. 2010, Wittmer et al. 2013, Berger et al. 2020). Additionally, NRAC can result from the reintroduction of (native) predators following a period of extirpation, as shown in Laikipia. NRAC is likely to arise following predator reintroduction, especially when predators have been absent for lengthy periods, during which environmental conditions may have changed to make prey more vulnerable to predation than they were historically (DeCesare et al 2010, Alston et al. 2019). Against the backdrop of shifting environmental conditions, effects of predator reintroductions often are stronger than expected, presenting an insidious threat to species of numerically subordinate prey that already were rare prior to predator reintroduction (DeCesare et al 2010).

Under NRAC, declines of already-rare species sometimes reflect a transient dynamic, through which a wild ungulate assemblage transitions toward a new equilibrium. Strong potential exists for NRAC to extirpate rare species if predation is depensatory (i.e., mortality due to predation is proportionally higher at lower population sizes; Holling 1959, DeCesare et al. 2010). Depensatory predation often coincides with both a Type II predator functional response and an Allee effect of prey, thereby decoupling predator population size from that of rare prey. Alternatively, if predation is regulatory (i.e., mortality due to predation abates at lower population sizes), predators exhibit a Type III functional response, such that prey populations have the potential to increase when rare (Holling 1959, DeCesare et al. 2010). In the absence of lethal control of predators (see, e.g., Lamb et al. 2024), Sinclair et al. (1998) described one of the few strategies with empirical support available to offset undesired effects of depensatory predation: spatial separation between primary and rare prey. Spatial separation between numerically dominant prey and numerically subordinate prey can result in ‘gradients of consumption’, in which risk of consumption varies directionally (Orrock et al 2008) thereby creating refuges and reduce encounter rates between predators and secondary prey (see also

Forrester and Steele 2004). In giving numerically subordinate prey a potential foothold for positive population growth, refuges are one of the few ways empirically demonstrated to negate Allee effects in nature, resulting in a shift by predators from a Type II to a Type III functional response (Sinclair et al. 1998). Although they have been limited in number and scope, attempts to create spatial separation between numerically dominant and numerically subordinate prey species within assemblages of savanna ungulates are promising, and have focused on habitat manipulations (e.g., increased fire return intervals [Pacifici et al. 2015], rotational grazing [Ng'weno et al. 2019b]).

Conclusions

For ungulate assemblages across African savannas, published evidence for donor control exceeded that for trophic control until the last 20 years. Our analysis affirms that such assemblages are dominated by prey species with a suite of traits associated with lower vulnerability to predation, suggesting that apex predators shape ungulate prey composition and relative abundance. Given structural congruence with three well-studied savannas (Serengeti, Kruger, Laikipia) in which donor and trophic control of prey are coupled by shared predators, it is parsimonious to assume that such widespread conformity arises by non-reciprocal apparent competition, at least for systems that are at or close to dynamic equilibrium.

Under NRAC, total ungulate biomass declines because populations of trophic-controlled prey are suppressed by predators. In turn, plant biomass persists that would otherwise have been consumed (as has been shown at many savanna locations by herbivore exclusion experiments).

Thus, NRAC can cause the cascading pattern that Borer et al. (2005) revealed to be pervasive among experimentally perturbed ecosystems.

Also under NRAC, total ungulate biomass is dominated by species that escape trophic control to become donor controlled (comprising 72-79% of total biomass in Serengeti, Kruger and Laikipia). By definition, this biomass varies with resource availability, both within and among systems. For example, donor control permits allometric patterns to arise along a rainfall gradient (Hatton et al. 2015). Species that fail to escape predator control contribute little to these correlations, but play an often-hidden role in ecosystem dynamics. Only trophic-controlled species conform with expectations of the Exploitation Ecosystem Hypothesis (Oksanan et al. 1981), because their total biomass does not increase much with net primary productivity (as in Letnic and Ripple 2017). Donor-controlled species do not conform because their total biomass does increase with net primary productivity. Under NRAC, therefore, both donor- (Hatton et al. 2015) and trophic-controlled mechanisms (Borer et al. 2005) operate simultaneously.

There is nothing about the patterns, processes, and mechanisms described in this synthesis that is unique to savanna large-mammal assemblages. Few food webs lack generalist predators, are entirely donor controlled, or are entirely trophic controlled, at least not at equilibrium. Collectively, these observations create the potential for NRAC to operate wherever there are generalist predators, providing a candidate mechanism contributing to the prevalence of allometric power laws and trophic cascades in nature.

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Conflict of Interest Statement

The authors declare no conflicts of interest.

References

Ali, A. H., A. T. Ford, J. S. Evans, D. Mallon, M. M. Hayes, J. King, R. Amin, and J. R. Goheen. 2017. Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. Journal of Applied Ecology **54:**1720-1729.

Ali, A. H., M. J. Kauffman, R. Amin, A. Kibara, J. King, D. Mallon, C. Musyoki, and J. R. Goheen. 2018. Demographic drivers of a refugee species: large-scale experiments guide strategies for reintroductions of hirola. Ecological Applications **28:**275-283.

Allen, B. L. L. R. Allen, H. Andrén, G. Ballard, L. Boitani, R. M. Engeman, P. J. S. Fleming, A. T. Ford, P. M. Haswell, R. Kowalczyk, J. D. C. Linnell, L. D. Mech, and D. M. Parker. 2019. Can we save large carnivores without losing large carnivore science? Food Webs **12:**64-75.

Alston, J. M., B. M. Maitland, B. T. Brito, S. Esmaeili, A. T. Ford, B. Hays, B. R. Jesmer, F. J. Molina, and J. R. Goheen. 2019. Reciprocity in restoration ecology: when might large carnivore reintroduction restore ecosystems? Biological Conservation **234:**82-89.

Archibald, K. M., H. M. Sosik, H. V. Moeller, and M. G. Neubert. 2023. Predator switching strength controls stability in diamond-shaped food web models. Journal of Theoretical Biology **570:**111536.

Atkins, J. L., R. A. Long, J. Pansu, J. H. Daskin, A. B. Potter, M. E. Stalmans, C. E. Tarnita, and R. M. Pringle. 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. Science **364:**173-177.

Barbier, M. and M. Loreau. 2019. Pyramids and cascades: a synthesis of food chain functioning and stability. Ecology Letters **22:**405-419.

Bascompte, J. and C. J. Melián. 2005. Simple trophic modules for complex food webs. Ecology **86:**2868-2873.

Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. T. B. Hunter, D. W. MacDonald, and C. Packer. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa except in intensively managed areas. Proceedings of the National Academy of Sciences **112:**14894-14899.

Berger, J., T. Wangchuk, C. Briceño, A. Vila, and J. E. Lambert. 2020. Disassembled food webs and messy projections: modern ungulate communities in the face of unabating human population growth. Frontiers in Ecology & Evolution **8:**128.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. Blanchette, B. R. Broitman, S. Cooper, B. J. Halpern. 2005. What determines the strength of a trophic cascade? Ecology **86:**528-537.

Brashares, J. S., T. Garland Jr., and P. Arcese. 2000. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behavioral Ecology **11:**452-463.

Carbone, C. and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science **295:**2273-2276.

Chaneton, E. J. and M. B. Bonsall. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. Oikos **88:**380-394.

Chirima, G. J., N. Owen-Smith, B. F. N. Erasmus, and F. Parrini. 2012. Distributional niche of relatively rare sable antelope in a South African savanna: habitat versus biotic relationships. Ecography **35:**68-79.

Christianson, D. and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: a before-after-control-impact approach. PLoS One **9:**e102330

Closs, G. P., S. R. Balcombe, and M. J. Shirley. 1999. Generalist predators, interaction strength, and food-web stability. Advances in Ecological Research **28:**93-126.

Coe, M. J., D. H. Cumming, and J. Phillipson. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. Oecologia **22:**341-354.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology **25:**773-784.

Daskin, J. H. and R. M. Pringle. 2018. Warfare and wildlife declines in Africa's protected areas. Nature **553:**328-332.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apprently: the role of apparent competition in endangered species conservation. Animal Conservation **13**:353-362.

Deshmukh, I. K. 1984. A common relationship between precipitation and grassland peak biomass for East and southern Africa. African Journal of Ecology **22:**181-186.

Donadio, E. and S. W. Buskirk. 2016. Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. Journal of Mammalogy 97:966-977.

Du Toit, J., K. Rogers, and H. Biggs. 2003. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press.

East, R. 1984. Rainfall, soil nutrient status, and biomass of large African savanna mammals. African Journal of Ecology **22:**245-270.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science **333:**301-306.

Estes, J.A., Brashares, J.S. and Power, M.E. 2013. Predicting and detecting reciprocity between indirect ecological interactions and evolution. The American Naturalist **181**:S76-S99.

Estes, R. D. and R. K. Estes. 1979. The birth and survival of wildebeest calves. Zeitschrift für Tierpsychologie **50:**45-95.

Fløjgaard, C., P. B. M. Pedersen, C. J. Sandom, J-C Svenning, and R. Ejrnæs. 2021. Exploring a natural baseline for large-herbivore biomass in ecological restoration. Journal of Applied Ecology **59:**18-24.

Ford, A. T. and J. R. Goheen. 2015a. Trophic cascades by large carnivores: a case for strong inference and mechanism. Trends in Ecology & Evolution **30:**725-735.

Ford, A. T. and J. R. Goheen. 2015b. An experimental study on risk effects in a dwarf antelope, *Madoqua guentheri*. Journal of Mammalogy **96:**918-926.

Ford, A. T., J. R. Goheen, D. J. Augustine, M. F. Kinnaird, T. G. O'Brien, T. M. Palmer, R. M. Pringle, and R. Woodroffe. 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. Ecology **96:**2705-2714.

Forrester, G. E. and M. A. Steele. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology **85:**1332-1342.

Frank, L. G. 2011. Living With Lions: Lessons from Laikipia. In Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem. Georgiadis, N. J., ed. Smithsonian Contributions to Zoology, Number 632.

Frank, L. G. 2023. Twenty years of lion conservation in a commercial rangeland. Frontiers in Ecology & Evolution **11:**1141195.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos **50:**291-301.

Fritz, H. and P. Duncan. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. Proceedings of the Royal Society B **256:**77-82.

Funston, P. J. and M. G. L. Mills. 2006. The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. South African Journal of Wildlife Research **36:**9-22.

Gasaway, W. C., K. T. Gasaway, and H. H. Berry. 1996. Persistent low densities of plains ungulates in Etosha National Park, Namibia: testing the food-regulating hypothesis. Canadian Journal of Zoology **74:**1556-1572.

Georgiadis, N. J. 2011. Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem. Smithsonian Contributions to Zoology, Number 632.

Georgiadis, N. J., M. Hack, and K. Turpin. 2003. The influence of rainfall of zebra population dynamics: implications for management. Journal of Applied Ecology **40:**125-136.

Georgiadis, N. J., F. Ihwagi, J. G. N. Olwero, and S. S. Romañach. 2007a. Savanna herbivore dynamics in a livestock-dominated landscape: II. Ecological, conservation, and management implications of predator restoration. Biological Conservation **137:**473-483.

Georgiadis, N. J., J. G. N. Olwero, G. Ojwang, and S. S. Romañach. 2007b. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. Biological Conservation **137:**461-472.

Gertenbach, W. P. D. 1980. Rainfall patterns in the Kruger National Park. Koedoe **23:**35-43.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94:**421-425.

Hamilton, W. D. Geometry for the selfish herd. Journal of Theoretical Biology **31:**295-311.

Harrington, R., N. Owen-Smith, P. C. Viljoen, H. C. Biggs, D. R. Mason, and P. Funston. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. Biological Conservation **90:**69-78.

Hatton, I. A., K. S. McCann, J. M. Fryxell, T. J. Davies, M. Smerlak, A. R. E. Sinclair, and M. Loreau. 2015. The predator-prey power law: biomass scaling across terrestrial and aquatic biomes. Science **349:**aac6284.

Hayward, M. W. and G. I. H. Kerley. 2006. Prey preferences of the lion (*Panthera leo*). Journal of Zoology **267:**309-322.

Hayward, M. W., J. O'Brien, and G. I. H. Kerley. 2007. Carrying capacity of large African predators: predictions and tests. Biological Conservation **139:**219-229.

Holdo, R. M., A. R. E. Sinclair, A. P. Dobson, K. L. Metzger, B. M. Bolker, M. E. Ritchie, and R. D. Holt. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. PLoS Biology **7:**e1000210.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist **91:**293-320.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities.

Theoretical Population Biology **12:**197-229.

Holt, R. D. 2023. Apparent competition: reflections on humans as mediators, agents, and victims of a pervasive ecological (and sociological) interaction. Evolutionary Ecology Research **2023:**103-117.

Holt, R. D. and M. B. Bonsall. 2017. Apparent competition. Annual Review of Ecology, Evolution, and Systematics **48:**447-471.

Holt, R. D. and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology, Evolution, and Systematics **25:**495-520.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74:**559-566.

Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources, and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution 25:119-128.

Hopcraft, J. G. C., R. M. Holdo, E. Mwangomo, S. A. R. Mduma, S. J. Thirgood, M. Borner, J. M. Fryxell, H. Olff, and A. R. E. Sinclair. 2015. Why are wildebeest the most abundant herbivore in the Serengeti ecosystem? Pages 125-175 *in* A. R. E. Sinclair, K. L. Metzger, S. A. R. Mduma, and J. M. Fryxell, editors. Serengeti IV: Sustaining Biodiversity in a Coupled Human-Natural System. University of Chicago Press.

Huang, Y-H, K. Kausrud, A. Hassim, S. O. Ochai, O. L. van Schalkwyk, E. H. Dekker, A. Buyantuev, C. C. Cloete, J. W. Kilian, J. K. E. Mfune, P. L. Kamath, H. v Heerden, and W. C. Turner. 2022. Environmental drivers of biseasonal anthrax outbreak dynamics in two multihost savanna systems. Ecological Monographs **92:**e1526.

IUCN. 2025. The IUCN Red List of Threatened Species. Version 2025-1.

https://www.iucnredlist.org. Accessed on 1 July 2025.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour **48:**215-267.

Kamaru, D. N., T. M. Palmer, C. Riginos, A. T. Ford, J. Belnap, R. M. Chira, J. M. Githaiga, B. C. Gituku, B. R. Hays, C. M. Kavwele, A. K. Kibungei, C. T. Lamb, N. J. Maiyo, P. D. Milligan, S. Mutisya, C. C. Ng'weno, M. Ogutu, A. G. Pietrek, B. T. Wildt, and J. R. Goheen. 2024. Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. Science **383:**433-438.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters **10:**690-700

Kruuk, H. 1972. The Spotted Hyena: A Study of Predation and Social Behavior. University of Chicago Press.

Lamb, C. T., S. Williams, S. Boutin, M. Bridger, D. Cichowski, K. Cornhill, C. DeMars, M. Dickie, B. Ernst, A. Ford, M. P. Gillingham, L. Greene, D. C. Heard, M. Hebblewhite, D. Hervieux, M. Klaczek, B. N., McLellan, R. S. McNay, L. Neufeld, B. Nobert, J. J. Nowak, A. Pelletier, A. Reid, A-M Roberts, M. Russell, D. Seip, C. Seip, C. Shores, R. Steenweg, S. White, H. U. Wittmer, M. Wong, K. L. Zimmerman, and R. Serrouya. 2024. Effectiveness of population-based recovery actions for threatened southern mountain caribou. Ecological Applications **34:**e2965.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. Journal of Wildlife Management **75:**204-212.

Letnic, M. and W. J. Ripple. 2017. Large-scale responses of herbivore prey to canid predators and primary productivity. Global Ecology and Biogeography **26:**860-866.

Le Roux, E., D. G. Marneweck, G. Clinning, D. J. Druce, G. I. H. Kerley, and J. P. G. M. Cromsigt. 2019. Top-down limits on prey populations may be more severe in larger prey species, despite having fewer predators. Ecography **42:**1115-1123.

MacNulty, D. R., D. R. Stahler, C. T. Wyman, J. Ruprecht, and D. W. Smith. 2016. The challenge of understanding northern Yellowstone elk dynamics after wolf reintroduction. Yellowstone Science **24:**25-33.

Martens, S., S. Creel, M. S. Becker, G. Spong, D. Smit, E. Droge, J. M'soka, B. Mayani-Nkhoma, T. Mukula, S. Mwaba, and H. Ndakala. 2025. Long-term demography of spotted hyena (Crocuta Crocuta) in a lion-depleted but prey-rich ecosystem. Ecology and Evolution **15:**e71025.

Maruping-Mzileni, N. T., P. J. Funston, and S. M. Ferreira. 2017. State-shifts of lion prey selection in the Kruger National Park. Wildlife Research **44:**28-39.

Mazzarisi, O., M. Barbier, and M. Smerlak. 2025. General mechanisms for a top-down origin of the predator-prey power law. Oikos e11232.

McNaughton, S. J. and N. J. Georgiadis. 1986. Ecology of African grazing and browsing mammals. Annual Review of Ecology and Systematics **17:**39-65.

McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature **341:**142-144.

Mduma, S. A. R., A. R. E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology **68:**1101-1122.

Mills, M. G. L., H. C. Biggs, and I. J. Whyte. 1995. The relationship between rainfall, lion predation, and population trends in African herbivores. Wildlife Research **22:**75-87.

Montgomery, R. A., R. J. Moll, E. Say-Sallaz, M. Valeix, and L. R. Prugh. 2019. A tendency to simplify complex systems. Biological Conservation **233:**1-11.

Ndibalema, V. G. 2009. A comparison of sex ratio, birth periods, and calf survival among Serengeti wildebeest sub-populations, Tanzania. African Journal of Ecology **47:**574-582.

Ng'weno, C. C., N. J. Maiyo, A. H. Ali, A. K. Kibungei, and J. R. Goheen. 2017. Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. Journal of Mammalogy 98:1078-1087.

Ng'weno, C. C., A. T. Ford, A. K. Kibungei, and J. R. Goheen. 2019. Interspecific prey neighborhoods shape risk of predation in a savanna ecosystem. Ecology **100:**e02968.

Ng'weno, C. C., S. W. Buskirk, N. J. Georgiadis, B. C. Gituku, A. K. Kibungei, L. M. Porensky, D. I. Rubenstein, and J. R. Goheen. Apparent competition, lion predation, and managed livestock: can conservation value be enhanced? Frontiers in Ecology & Evolution **7:**123.

O'Brien, T. G., M. F. Kinnaird, S. Ekwanga, C. Wilmers, T. Williams, A. Oriol-Cotterill, D. Rubenstein, and L. G. Frank. 2018. Resolving a conservation dilemma: vulnerable lions eating endangered zebras. PLoS One **13:**e0201983

Ogutu, J.O. and Owen-Smith, N. 2005. Oscillations in large mammal populations: are they related to predation or rainfall? African Journal of Ecology, **43:**332-339.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118:**240-261.

Orrock, J. L., M. S. Witter, and O. J. Reichman. 2008. Apparent competition with an exotic plant reduces native plant establishment. Ecology **89:**1168-1174.

Owen-Smith, N. 2019. Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. Biological Conservation **232:**51-58.

Owen-Smith, N. and M. G. L. Mills 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. Ecological Monographs **76:**73-92.

Owen-Smith, N. and M. G. L. Mills. 2008. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. Ecology **89:**1120-113.

Owen-Smith, N., G. J. Chirima, V. Macandza, and E. Le Roux. 2011. Shriking sable antelope numbers in Kruger National Park: what is suppressing population recovery? Animal Conservation **15:**195-204.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurt, S. Mduma, and A. R. E. Sinclair. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science **307:**390-393.

Pacifici, M., P. Visconti, E. Scepi, A. Hausmann, F. Attorre, R. Grant, and C. Rondinini. 2015. Fire policy optimization to maximize suitable habitat for locally rare species under different climatic conditions: a case study of antelopes in the Kruger National Park. Biological Conservation **191:**313-321.

Perkins, D. M., I. A. Hatton, B. Gauzens, A. D. Barnes, D. Ott, B. Rosenbaum, C. Vinagre, and U. Brose. 2022. Consistent predator-prey biomass scaling in complex food webs. Nature Communications **13:**4990.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology **73:**733-746.

Prokopenko, C. M., T. Avgar, A. T. Ford, and E. Vander Wal. 2022. Optimal prey switching: predator foraging costs provide a mechanism for functional responses in multi-prey systems. Ecology **104:**e3928.

Radloff, F. G. T. and J. T. Du Toit. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. Journal of Animal Ecology **73:**410-423.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. D. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science **343:**DOI:10.1126/science.1241484

Saha, S. and G. Samanta. 2021. Modelling of a two prey and one predator systems with switching effect. Computational Mathematics and Biophysics **9:**90-113.

Salashour, M. 2023. Predator-prey power laws: trophic interactions give rise to scale-invariant ecosystems. New Journal of Physics **25:**123012.

Schaller, G. 1972. The Serengeti Lion: A Study of Predator-Prey Relations. University of Chicago Press.

Schmitt, M. H., K. Stears, C. Wilmers, and A. M. Shrader. 2014. Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. Animal Behavior **96:**151-158.

Seno, H. 2025. Persistent prey species in the Lotka-Volterra apparent competition system with a single shared predator. Journal of Mathematical Biology **90:**19.

Serrouya, R., M. Dickie, C. Lamb, H. van Oort, A. P. Kelly, C. DeMars, P. D. McLoughlin, N. C. Larter, D. Hervieux, A. T. Ford, and S. Boutin. 2021. Trophic consequences of terrestrial eutrophication for a threatened ungulate. Proceedings of the Royal Society of London B **288:**20202811

Sinclair, A. R. E. 1977. The African Buffalo: A Study of Resource Limitation of Populations. University of Chicago Press.

Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? Journal of Animal Ecology **54:**899-918.

Sinclair, A. R. E. 2003. Patterns of predation in a diverse predator-prey system. Nature **425:**288-290.

Sinclair, A. R. E. and P. Arcese. 1995a. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology **76:**882-891.

Sinclair, A. R. E. and P. Arcese. 1995b. Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press.

Sinclair, A. R. E. and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society of London B Biological Sciences **357:**1221-1231.

Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology **12:**564-575.

Sinclair, A. R. E., K. Metzger, J. S. Brashares, A. Nkwabi, G. Sharam, and J. M. Fryxell. 2010. Trophic Cascades in African Savanna: Serengeti as a Case Study. In Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Terborgh, J. and J. A. Estes, eds. Island Press.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, O. R. Bidder, and A. D. Middleton. 2019. Habitat complexity mediates the predator-prey space race. Ecology **100:**e02724.

Tjaden-McClement, K., T. Gharajehdaghipour, C. Shores, S. White, R. Steenweg, M. Bourbonnais, Z. Konanz, and A.C. Burton. 2025. Mixed evidence for disturbance-mediated apparent competition for declining caribou in western British Columbia, Canada. Journal of Wildlife Management e70040.

Trinkel, M. 2013. Climate variability, human wildlife conflict and population dynamics of lions *Panthera leo*. Naturwissenschaften **100:**345-353.

Van Baalen, M., V. Krivan, P. C. van Rijn, and M. W. Sabelis. 2001. Alternative food, switching predators, and the persistence of predator-prey systems. American Naturalist **157:**512-524.

Watson, F., M. S. Becker, D. Smit, E. Droge, T. Mukula, S. Martens, S. Mwaba, D. Christianson, S. Creel, A. Brenna, J. M'soka, A. Gaylard, C. Simukonda, M. Nyirenda, and B. Mayani. 2022. Predation strongly limits demography of a keystone migratory herbivore in a recovering transfrontier ecosystem. Ecology and Evolution **12:**e9414.

Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation strategies for species affected by apparent competition. Conservation Biology **27:**254-260.

Woodroffe, R. 2011. Demography of a recovering African wild dog (*Lycaon pictus*) population. Journal of Mammalogy **92:**305-315.

Wollrab, S., S. Diehl, and A. M. De Roos. 2012. Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways. Ecology Letters **15**:935-936.

Tables

Table 1. Details of the linear model simulating the transition from donor to trophic control among ungulate species that declined in Laikipia over the period of predator recovery (depicted as the red line in Figure 2). The model relates total *Biomass Density* ($kg.km^{-2}$) of declining species to *Cumulative Monthly Rainfall* between surveys, *Predation Pressure*, and their interaction. All data were $\log_{10}$ transformed. Data are provided in Supplementary Information Table SI 1.

Summary of Fit				
r	0.7305	-	-	-
Adjusted r	0.6294	-	-	-
Root Mean Square Error	0.1928	-	-	-
Mean of Response	0.8411	-	-	-
Observations	12	-	-	-
Analysis of Variance				
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**
Model	3	0.8060	0.2687	7.2277
Error	8	0.2974	0.0372	**Prob > F**
Total	11	1.1034	-	0.0115*
Parameter Estimates				
Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
Intercept	0.8675	0.2451	3.54	0.0076*
Cumulative Rainfall	0.6520	0.2580	2.53	0.0354*
Predation Pressure	-0.8526	0.1961	-4.35	0.0025*
Cumulative Rainfall * Predation Pressure	-2.8286	0.9832	-2.88	0.0206*

Table 2. Details of the mixed effects linear model showing that ungulates that ungulate species dominating the biomass density of savanna systems across Africa tend to have larger body sizes, gather in larger groups, and graze more than browse. The model relates ungulate *Biomass Density* (kg.km^{-2}) to *Body Weight* (kg), mean *Group Size*, and *Percent Monocotyledons* in the diet. Because body size and mean group size were correlated (*r* = 0.69; Figure SI 2), residuals of mean group size were used to reduce collinearity. *Protected Area* was the random independent variable. Data available from: http://datadryad.org/share/vTtYm0p8erwl8RozWe4I7L04lGfTZ0SyALojeQhI660). All data were log$_{10}$ transformed, and independent variables were centered.

Random Effects Covariance Parameter Estimates

Variance Component	Var Ratio	Estimate	Std Error	Wald p-Value	Pct of Total
Protected Area	0.9893	0.3781	0.0805	<.0001*	49.732
Residual		0.3822	0.0265	-	50.268
Total		0.7603	0.0835	-	100

Fixed Effects Parameter Estimates

Term	Estimate	Std Error	DFDen	t Ratio	Prob>|t|
Intercept	-0.7020	0.1705	399.5	-4.12	<.0001*
Body Weight	1.0659	0.0678	429.9	15.71	<.0001*
% Monocots in Diet	0.1934	0.0499	424.7	3.88	0.0001*
Residual of Mean Group Size	0.2666	0.0971	427.5	2.75	0.0063*

Figures

Figure 1. A hypothetical African savanna food web, simplified to illustrate the pathways and processes in our study. Two apex predators, hyenas (H) and lions (L), share three prey species that do not compete with each other for resources: wildebeest (W), a grazer, impala (I), a mixed feeder, and greater kudu (K), a browser. This structure yields six 'looped' trophic pathways, linking WHI, WLI, WHK, WLK, IHK, and ILK. Arrow color represents mode of control. Wildebeest and impala are donor controlled (blue) by rainfall and density, but kudu are trophic controlled by predators (red). Apparent competition is non-reciprocal because wildebeest and impala are not affected by predation. Within trophic layers, biomass density of each species is proportional to its silhouette area, with dotted black lines depicting biomass density in the absence of trophic control (kudu), or of intraguild competition and predation (double-ended red arrow).

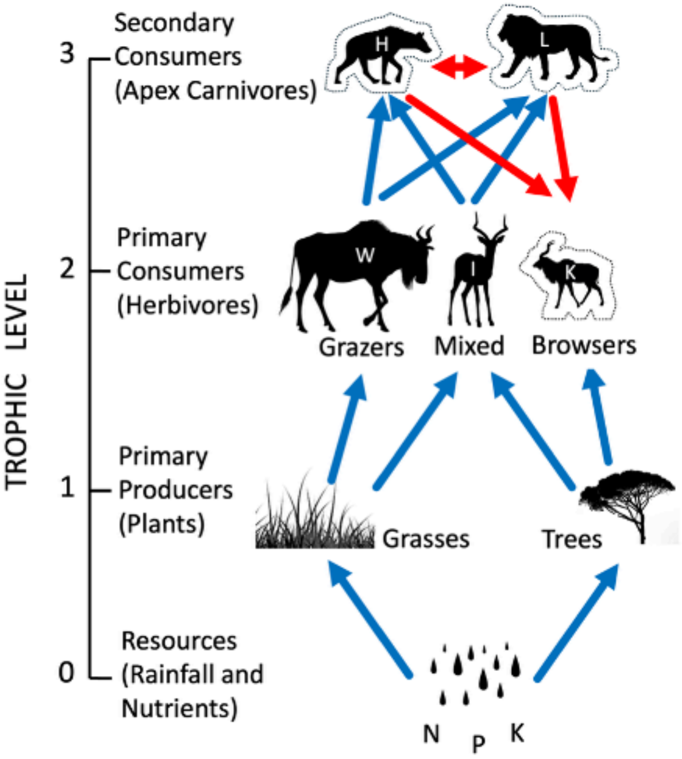

TROPHIC LEVEL
3
Secondary Consumers (Apex Carnivores)
H
L
2
Primary Consumers (Herbivores)
W
I
K
Grazers
Mixed
Browsers
1
Primary Producers (Plants)
Grasses
Trees
0
Resources (Rainfall and Nutrients)
N
P
K

Figure 2. The impact of predators on a savanna ungulate community in Laikipia, Kenya. Prior to 1990, predators were suppressed, and wild ungulate populations were donor controlled (Georgiadis et al. 2007b). Predator recovery between ~1987-2005 was the most likely cause of declines in a subset of ungulate species (buffalo, eland, giraffe, Thomson's gazelle, waterbuck and especially hartebeest; Georgiadis et al. 2007a). The combined biomass density of declining species (red dots) initially varied with rainfall (dashed blue line), but the mode of population control transitioned from donor to trophic with increasing predation pressure (dashed red line). This transition was modeled (red line) by $B = 0.87 + 0.65.R - 0.85.P - 2.83.R.P$, where B is Biomass Density, R is Cumulative Monthly Rainfall between surveys (dashed blue line), and P is Predation Pressure (dashed red line; details in Table 1). Cumulative monthly rainfall between surveys was normalized, such that wetter (drier) than average intervals had values greater (less) than 1 (methods and data in Georgiadis et al. 2007b, also given in Table SI 1). The shape of the predation pressure curve (dashed red line), which reflected the recovery of all predator species, was optimized as described in Supporting Information Figure SI 4.

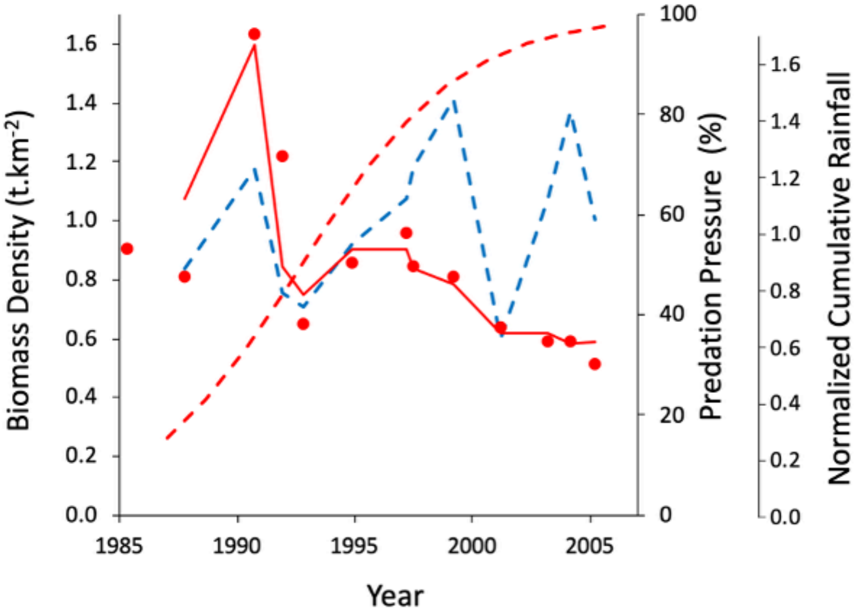


Figure 3. Ranked biomass distributions of ungulates in three well-studied savannas: (a) Greater Serengeti Ecosystem, after rinderpest was eradicated (Mduma and Hopcraft 2008); (b) Kruger National Park (Table 1 in Owen-Smith and Mills 2006); Laikipia before (c) and after (d) predator recovery (Georgiadis et al. 2007b). Columns are colored blue if a species is donor controlled, red if trophic controlled (some are both, alternating over time; buffalo were also reduced by disease and culling in Kruger, and by illegal hunting in Serengeti). In Laikipia, predation reduced prey evenness by reducing the biomass density of trophic-controlled prey (Figure SI 1).

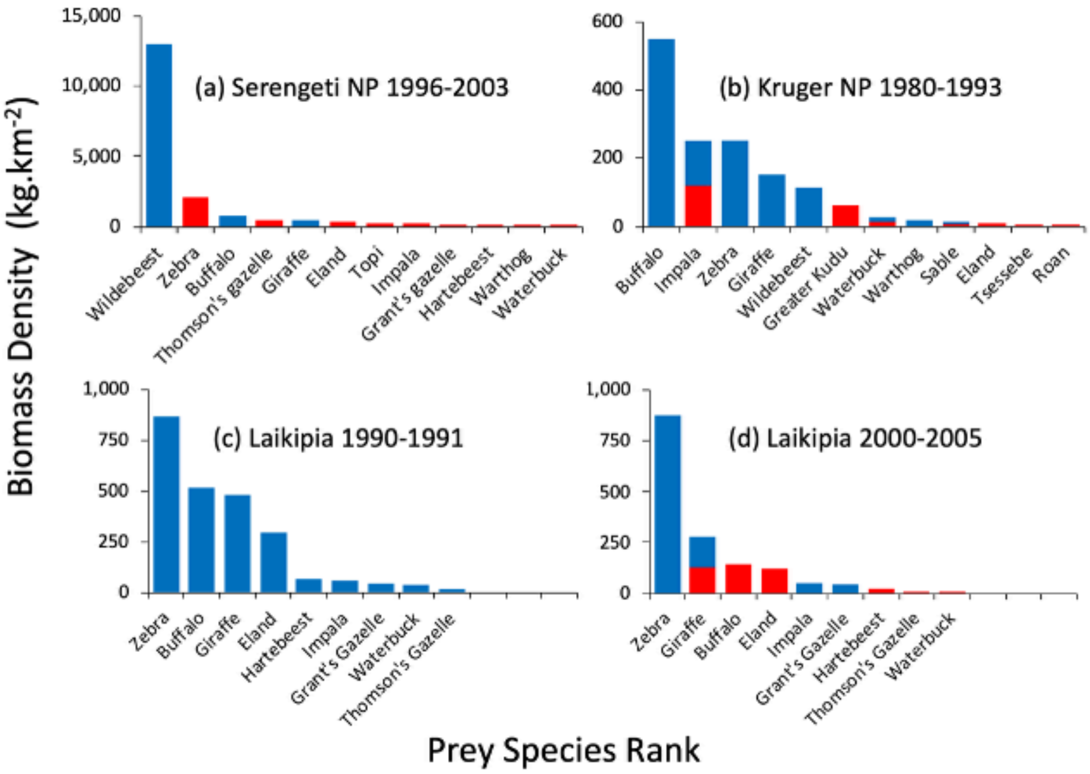
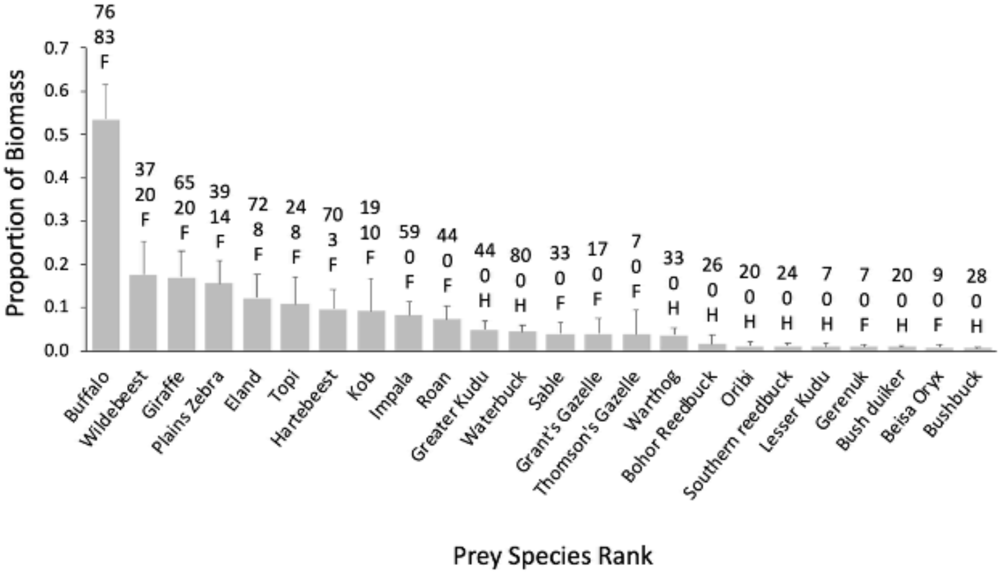


Figure 4. Mean proportions of biomass contributed by each of 27 species at 56 savanna ungulate assemblages in sub-Saharan Africa (data from Daskin and Pringle 2018; Serengeti, Kruger and Laikipia data were omitted from this analysis, as were species that occurred at fewer than 4 locations). Error bars are 95% confidence intervals. Numbers above the error bars are the percent of locations at which a species was found (upper), and the percent of those in which a species had the highest biomass (lower). To illustrate, buffalo occurred at 76% of the 56 savannas, and of those, dominated the biomass in 83%. ‘F’ and ’H’ denote species that flee or hide from predators.



Georgiadis et al. 2025: Supporting Information

Table SI 1. Data used to derive the linear model described in Table 1.

Survey Date	Biomass Density of Declining Species [a]	Rainfall Deficit [b]
1987.8	0.8099	0.8400
1990.8	1.6351	1.1765
1991.9	1.2158	0.7526
1992.8	0.6475	0.7068
1994.9	0.8529	0.9199
1997.2	0.9576	1.0727
1997.5	0.8424	1.1842
1999.2	0.8103	1.4157
2001.2	0.6346	0.6002
2003.2	0.5902	1.0761
2004.2	0.5858	1.3697
2005.2	0.5113	1.0050
a	Total biomass of herbivore species that declined during the period of predator recovery ($kg.km^{-2}$).	
b	Cumulative rainfall deficit (<1) or surplus (>1) over months that elapsed between surveys, normalized by mean monthly rainfall.	

Table SI 2. Names, countries, and latitude/longitude coordinates of savanna locations featured in this paper.

Number	Country	Protected Area Name	Latitude	Longitude
1	Kenya	Amboseli NP	-2.65	37.26
2	CAR	Bamingui-Bangoran	8.16	19.76
3	Tanzania	Biharamulo & Burigi GR	-2.63	31.31
4	Uganda	Bokora Corridor Wildlife Reserve	2.43	34.00
5	Nigeria	Borgu Forest Reserve	9.42	3.67
6	Cameroon	Bouba Ndijida	8.72	14.71
7	Namibia	Caprivi Reserve/Nkasa Rupara NP/Mudumu NP	-18.35	23.67
8	Zimbabwe	Chizarira NP	-17.75	28.17
9	Namibia	Etosha NP	-18.95	15.90
10	DRC	Garamba NP	4.18	29.51
11	Zimbabwe	Gonarezhou NP	-21.67	31.67
12	Mozambique	Gorongosa NP	-18.69	34.07
13	South_Africa	Hluhluwe Nature Reserve; Umfolozi GR	-28.04	32.06
14	South_Africa	Ithala NR	-27.52	31.33
15	Tanzania	Katavi NP	-6.83	31.25
16	Uganda	Kidepo Valley NP	3.88	33.87
17	South_Africa	Kruger NP	-25.36	31.89
18	Tanzania	Lake Manyara NP	-3.50	35.83
19	Kenya	Lake Nakuru NP	-0.36	36.08
20	Zambia	Liuwa NP	-14.50	22.48
21	Zambia	Lower Zambezi NP	-15.95	28.92
22	Zambia	Luambe NP	-12.50	32.33
23	Angola	Luengue-Luaiana NP	-16.58	21.83
24	Zambia	Lukusuzi NP	-13.00	32.50
25	Zambia	Lupande GMA	-12.00	31.00
26	Kenya	Maasai Mara NR	-1.49	35.14
27	Zimbabwe	Mana Pools NP	-15.94	29.46
28	CAR	Manovo-Gounda St Floris	8.46	21.77
29	Mozambique	Marromeu Game Reserve	-18.29	35.95
30	Zimbabwe	Matetsi Safari Area	-18.52	25.66
31	Zimbabwe	Matusadona NP	-16.83	28.58
32	Kenya	Meru Cons Area	0.09	38.19
33	Tanzania	Mikumi NP	-7.41	37.06
34	Tanzania	Mkomazi GR	-4.29	38.39
35	South_Africa	Mkuzi GR	-27.64	32.21
36	Tanzania	Moyowosi & Kigosi GRs	-4.01	30.91
37	Kenya	Mpala Ranch	0.33	36.88
38	Uganda	Murchison Falls NP	2.15	31.81
39	Kenya	Nairobi NP	-1.36	36.84
40	Tanzania	Ngorongoro Conservation Area Authority	-2.98	35.45
41	Mozambique	Niassa GR	-11.83	36.88
42	Malawi	Nkhota-Kota Wildlife Reserve	-12.00	34.02
43	Zambia	North Luangwa NP	-12.00	32.00
44	Benin	Pendjari NP	11.23	1.49
45	Uganda	Pian Upe Wildlife Reserve	2.06	34.21
46	South_Africa	Pilanesberg NP	-25.33	27.15
47	Uganda	Queen Elizabeth NP	-0.16	30.02
48	Kenya	Rahole NR	-0.17	38.42
49	Tanzania	Ruaha NP	-7.61	34.90
50	Kenya	Ruma NP	-0.65	36.91
51	Kenya	Segera Private Nature Reserve	0.18	36.80
52	Tanzania	Selous GR	-7.82	38.35
53	Tanzania	Serengeti NP	-2.33	34.83
54	Zambia	South Luangwa National Park	-13.17	31.50
55	Kenya	Taita Hills Wildlife Sanctuary	-3.51	38.25
56	Tanzania	Tarangire NP	-3.83	36.00
57	Kenya	Tsavo NP ecosystem	-2.96	37.91
58	Kenya	Tsavo West NP	-3.40	37.96
59	Malawi	Vwaza March Game Reserve	-11.04	33.78
60	Burkina_Faso	W du Burkina Faso NP	11.93	2.18
61	Chad	Zakouma NP	10.84	19.64

Table SI 3. Names and scientific names of species mentioned in the text, with their body sizes, mean group sizes, and mean percent monocots in their diets.

Species Name	Scientific Name	Mean Group Size	Pct. Monocot in Diet (9)	Body Weight (kg) (10)
Beisa Oryx	*Oryx beisa*	23 (1)	75	169
Bohor Reedbuck	*Redunca redunca*	4 (1)	95	44
Bontebuck	*Damaliscus pygargus*	5 (2)	90	102
Buffalo	*Syncerus caffer*	35 (1)	77.5	580
Bush Duiker	*Sylvicapra grimmia*	2 (1)	12	20
Bush pig	*Potamochoerus larvatus*	3.2 (3)	35.5	98
Bushbuck	*Tragelaphus scriptus*	2 (1)	10	30
Dikdik	*Madoqua spp.*	2 (1)	10	8
Eland	*Taurotragus oryx*	45 (1)	50	569
Fringe-eared Oryx	*Oryx beisa callotis*	35 (4)	75	169
Gemsbok	*Oryx gazella*	14 (1)	75	169
Gerenuk	*Litocranius walleri*	3 (1)	0	38
Giant Eland	*Taurotragus derbianus*	20 (1)	5	680
Giraffe	*Giraffa camelopardalis*	5.4 (5)	0.5	899
Grant's Gazelle	*Nanger granti*	10 (1)	65	55
Greater Kudu	*Tragelaphus strepsiceros*	16 (1)	15	214
Grevy's Zebra	*Equus grevyi*	4.6 (6)	98	408
Guenther's Dik-dik	*Madoqua guentheri*	2 (1)	10	12
Hartebeest	*Alcelaphus buselaphus*	10 (1)	75	171
Harvey's Duiker	*Cephalophus harveyi*	1 (1)	1	15
Impala	*Aepyceros melampus*	20 (1)	45	53
Kirk's Dik-dik	*Madoqua kirkii*	2 (1)	17	5
Klipspringer	*Oreotragus oreotragus*	2 (1)	20	13
Kob	*Kobus kob*	25 (1)	95	79
Lechwe	*Kobus leche*	12 (1)	95	111
Lesser Kudu	*Tragelaphus imberbis*	5 (1)	33.5	82
Mountain Reedbuck	*Redunca fulvorufula*	4 (1)	95	30
Nyala	*Tragelaphus angasii*	4 (1)	20	87
Oribi	*Ourebia ourebi*	3 (1)	90	17
Red forest duiker	*Cephalophus natalensis*	2 (1)	1	12
Red-flanked Duiker	*Cephalophus rufilatus*	1 (1)	1	12
Roan	*Hippotragus equinus*	13 (1)	85	270
Sable	*Hippotragus niger*	20 (1)	85	227
Sharpe's Grysbok	*Raphicerus sharpei*	1 (1)	30	10
Sitatunga	*Tragelaphus spekii*	2 (1)	67.5	78
Southern Reedbuck	*Redunca arundinum*	3 (1)	95	58
Springbok	*Antidorcas marsupialis*	24 (1)	32.5	39
Steenbuck	*Raphicerus campestris*	1.5 (1)	34	11
Thomson's Gazelle	*Eudorcas thomsonii*	28 (1)	75	21
Topi	*Damaliscus lunatus*	6 (1)	95	136
Warthog	*Phacochoerus africanus*	2 (7)	70	82
Waterbuck	*Kobus ellipsiprymnus*	8 (1)	84	210
Wildebeest	*Connochaetes spp.*	15 (1)	87.5	180
Zebra	*Equus quagga*	4 (8)	91	276

1. Brashares, J. S., Garland Jr, T., & Arcese, P. (2000). Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behavioral Ecology, 11(4), 452-463.
2. David, J. 1970. The behaviour of the bontebok Damaliscus Dorcas Dorcas, with special reference to territorial behaviour. MSc. Thesis. University of Cape Town.
3. Ghiglieri, M. P., Butynski, T. M., Struhsaker, T. T., Leland, L., Wallis, S. J., & Waser, P. (1982). Bush pig (Potamochoerus porcus) polychromatism and ecology in Kibale Forest, Uganda. African Journal of ecology, 20(4), 231-236.
4. Lee, D. N., Dolman, R. W., & Leslie Jr, D. M. (2013). Oryx callotis (Artiodactyla: Bovidae). Mammalian Species, 45(897), 1-11.

5. Bond, M. L., Lee, D. E., Ozgul, A., & König, B. (2019). Fission–fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. Oecologia, 191(2), 335-347.
6. Zero, V. H., Sundaresan, S. R., O'Brien, T. G., & Kinnaird, M. F. (2013). Monitoring an endangered savannah ungulate, Grevy's zebra Equus grevyi: choosing a method for estimating population densities. Oryx, 47(3), 410-419.
7. White, A. M. (2010). A pigheaded compromise: do competition and predation explain variation in warthog group size? Behavioral Ecology, 21(3), 485-492.
8. Smuts, G. L. (1976). Population characteristics of Burchell's zebra (Equus burchelli antiquorum. H. Smith, 1841) in the Kruger National Park. South African Journal of Wildlife Research-24-month delayed open access, 6(2), 99-112.
9. Gagnon, M. and Chew, A.E., 2000. Dietary preferences in extant African Bovidae. Journal of Mammalogy, 81(2), pp.490-511.
10. Smith, F.A., Lyons, S.K., Ernest, S.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. and Haskell, J.P., 2003. Body mass of Late Quaternary mammals: ecological archives E084-094. Ecology, 84(12), pp.3403-3403.

Supporting Information Figures

Figure SI 1. Frequency histogram of evenness values (Pielou's J') of the 56 ungulate biomass distributions featured in this study. Vertical lines show evenness of the Laikipia ungulate community before (Laikipia 1) and after (Laikipia 2) predators recovered.

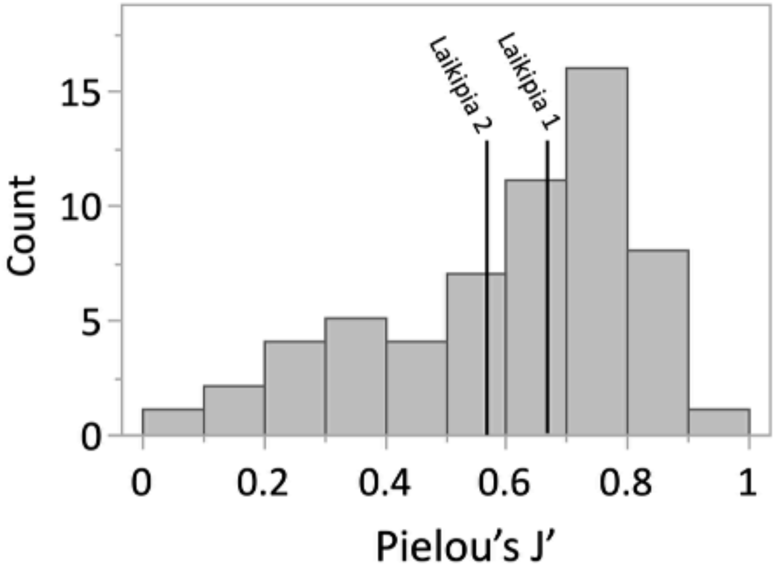


Figure SI 2. Bivariate plots of variables listed in Table SI 3.

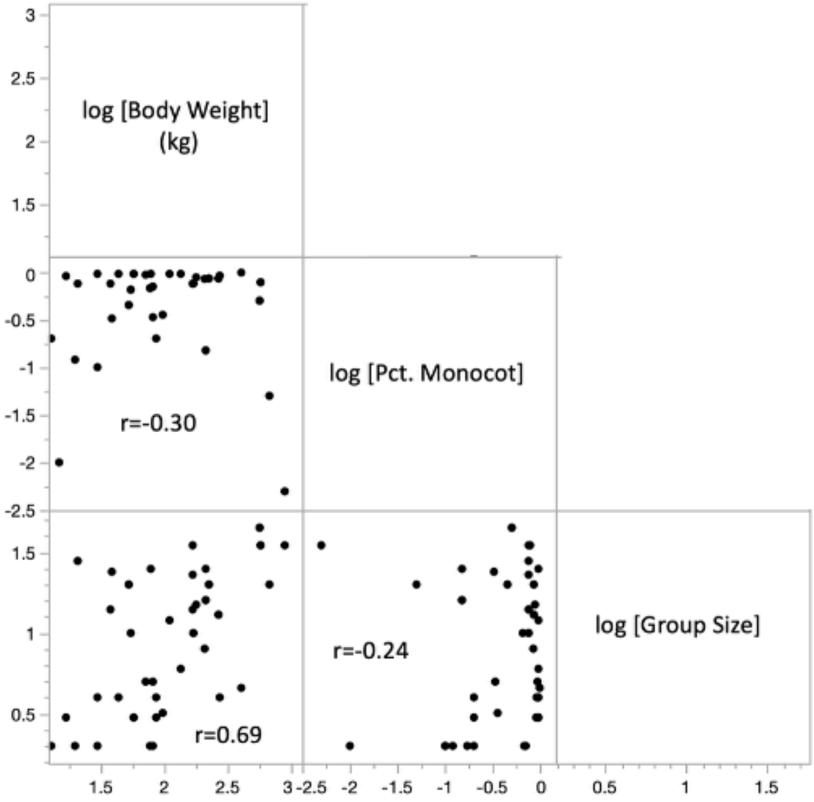


Figure SI 3. Plot of observed values vs. values predicted by the mixed effects model in Table 2. The diagonal line is y=x.

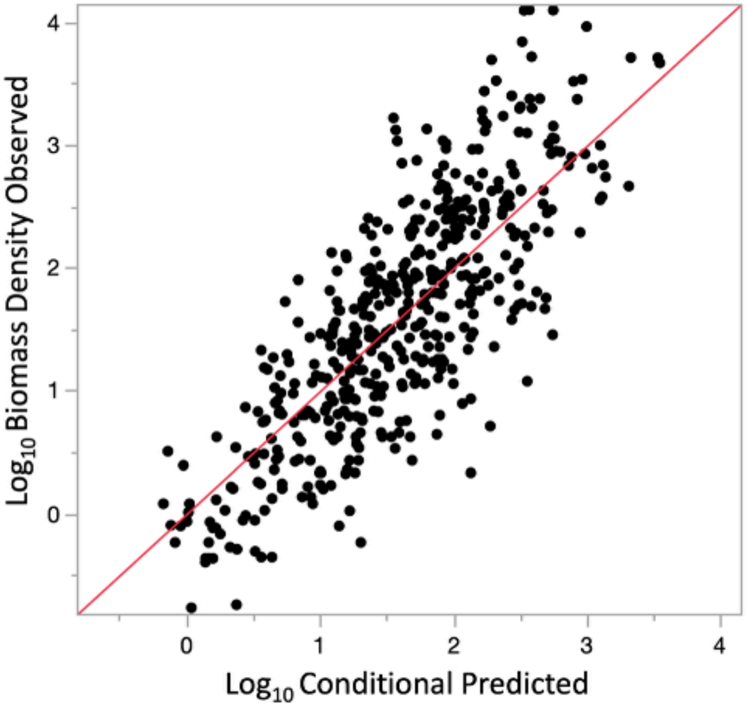


Figure SI 4. In Laikipia, predators were suppressed or eliminated on most properties until ~1990 and then recovered over the next decade (Frank 2023). Wild dogs were absent until the early 2000s. Initial numbers of lions were not known but their density was low (Frank 2011, Frank 2023). Lions recovered during the 1990s, stabilizing at around 113 individuals in ~2003 (Frank 2023). Numbers of hyenas, leopards, and cheetahs were also initially low, but not known. We assumed that recovery of all large predators was identical to that of lions, expressing combined predator recovery as 'Predation Pressure'. The model fit to declining ungulate biomass (Table 1, and solid red line in Figure 2), was sensitive to the shape of the Predation Pressure curve (*P*), expressed as a percentage of the asymptote ($K = 100$) from a logistic equation, with initial value $P_0 = 15\%$, and growth rate $r = 0.5$ (red dotted line) or 0.7 (blue dotted line). The yellow dotted line is a straight line. A logistic curve with rate of increase of 0.5 (shown here as the red dashed line, also shown in Figure 2) gave the best model fit.