Report

Current Biology

Megaherbivores Modify Trophic Cascades Triggered by Fear of Predation in an African Savanna Ecosystem

Highlights

- Megaherbivores modulate trophic cascades triggered by prey's response to predators
- Megaherbivores redistribute nutrients across the landscape of fear

Authors

Elizabeth le Roux, Graham I.H. Kerley, Joris P.G.M. Cromsigt

Correspondence

elizabeth.liza.le.roux@gmail.com

In Brief

le Roux et al. experimentally show how megaherbivores can modify predator-triggered trophic cascades. Where aggregations of fearful prey can lead to fecal nutrient accumulation, megaherbivores redistribute these nutrients away from such predator-maintained biogeochemical hotspots by feeding in areas frequented by prey species but defecating widely.

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Megaherbivores Modify Trophic Cascades Triggered by Fear of Predation in an African Savanna Ecosystem

Elizabeth le Roux,[1,3,*] Graham I.H. Kerley,[1] and Joris P.G.M. Cromsigt[1,2]
[1]Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela University, P.O. Box 77000, Port Elizabeth 6031, South Africa
[2]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå 901 83, Sweden
[3]Lead Contact
*Correspondence: elizabeth.liza.le.roux@gmail.com
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SUMMARY

The loss of apex consumers (large mammals at the top of their food chain) is a major driver of global change [1]. Yet, research on the two main apex consumer guilds, large carnivores [2] and megaherbivores [3], has developed independently, overlooking any potential interactions. Large carnivores provoke behavioral responses in prey [1, 4], driving prey to distribute themselves within a "landscape of fear" [5] and intensify their impacts on lower trophic levels in low-risk areas [6], where they may concentrate nutrients through localized dung deposition [7, 8]. We suggest, however, that megaherbivores modify carnivore-induced trophic cascades. Megaherbivores (>1,000 kg [9]) are largely invulnerable to predation and should respond less to the landscape of fear, thereby counteracting the effects of fear-triggered trophic cascades. By experimentally clearing plots to increase visibility and reduce predation risk, we tested the collective role of both apex consumer guilds in influencing nutrient dynamics in African savanna. We evaluated whether megaherbivores could counteract a behaviorally mediated trophic cascade by redistributing nutrients that accumulate through fear-driven prey aggregations. Our experiment showed that mesoherbivores concentrated fecal nutrients in more open habitat, but that megaherbivores moved nutrients against this fear-driven nutrient accumulation by feeding within the open habitat, yet defecating more evenly across the risk gradient. This work adds to the growing recognition of functional losses that are likely to have accompanied megafaunal extinctions by contributing empirical evidence from one of the last systems with a functionally complete megaherbivore assemblage. Our results suggest that carnivore-induced trophic cascades work differently in a world of giants.

RESULTS

Collectively, mesograzers deposited nearly three times as much dung in cleared plots than in un-cleared plots (Figures 1A and 1B; $\bar{x}_{dung\ in\ cleared}$ = 24.5 kg, SE = 6.8 kg; $\bar{x}_{dung\ in\ un\text{-}cleared}$ = 8.3 kg, SE = 1.9 kg). The dung of blue wildebeests (*Connochaetes taurinus*), impalas (*Aepyceros melampus*), and warthogs (*Phacochoerus africanus*) accumulated significantly more in cleared plots than in un-cleared plots (Figure S1). Dung of mesobrowsers (kudu, *Tragelaphus strepsiceros*; nyala, *Tragelaphus angasii*; and gray duiker, *Sylvicapra grimmia*) and megaherbivores (elephant, *Loxodonta africana*; white rhino, *Ceratotherium simum*; and giraffe, *Giraffa camelopardalis*) was deposited evenly across experimental treatments but in amounts that were negligible compared to that of mesograzers (Figures 1A and 1B).

For the two species for which behavior had been quantified (white rhinos and impalas), visitation correlated positively with feeding (rhino: r = 0.88, p = 0.0004; impala: r = 0.95, p = 0.0001), and hence we considered herbivore visitation as a proxy for potential herbivore pressure (PHP). We quantified PHP per plot by calculating a unit-less value by multiplying the number of 30 s trap-camera video clips by the number of individuals appearing on each clip multiplied by three-quarters of the average female metabolic biomass (see STAR Methods). We included the metabolic correction because we wanted the visitation measure to reflect herbivore pressure exerted on the plot as closely as possible. Mesograzer PHP increased significantly with visibility as covariate (Table 1), and, collectively, mesograzer PHP was on average 56% higher in cleared than in un-cleared plots (Figures 1C and 1D; $\bar{x}_{PHP\ in\ cleared} = 100$, SE = 12; $\bar{x}_{PHP\ in\ un\text{-}cleared} = 64$, SE = 8). That the relationship between herbivore PHP and cleared or un-cleared as a factor was not significant was most likely because this factorial treatment ignores variation in baseline visibility across our un-cleared plots (see Figure S2 for visibility differences across plots). With the exception of the warthog, all mesograzers (buffalo, *Syncerus caffer*; zebra, *Equus quagga*; blue wildebeest; and impala) demonstrated higher PHP on cleared plots (Figure S1). Crucially, however, megaherbivore PHP dwarfed that of mesoherbivores and did not vary significantly with visibility (Figures 1C and 1D). Mesobrowser PHP was comparable across experimental treatments (Table 1), but their contribution to overall PHP was negligible (Figures 1C and 1D).

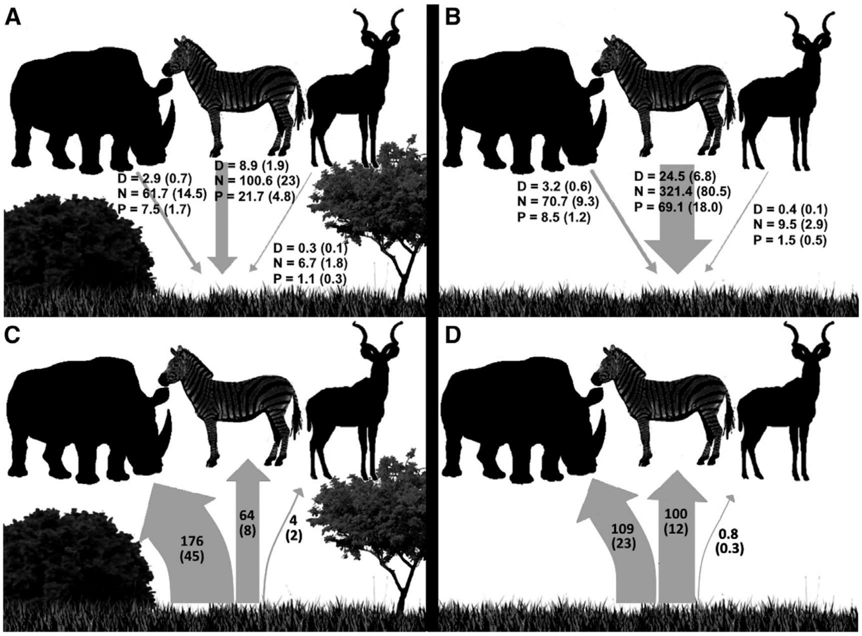

Figure 1. The Comparison of Dung Accumulation and Potential Herbivore Pressure of Different Herbivore Functional Groups across Risk Treatments

Dung accumulation (A and B) and potential herbivore pressure (PHP) (C and D) by megaherbivores, mesograzers, and mesobrowsers in un-cleared (more risky area; A and C) and cleared (less risky area; B and D) plots. Downward arrows in (A) and (B) indicate nutrient return, where the size of the arrow and the associated values represent the average input of dung in kilograms/plot (100 m^2) and the estimated input of nitrogen and phosphorus in grams/plot (100 m^2). Nutrient values were calculated by converting dung weights to nitrogen and phosphorus content obtained from literature-based estimates per species (see STAR Methods). Upward arrows in (C) and (D) indicate potential nutrient removal, where arrow size and the associated values represent average PHP exerted. PHP is a unit-less value combining the number of 30 s trap-camera video clips multiplied by the number of individuals per clip multiplied by three-quarters of the average female metabolic biomass (see STAR Methods). SEs are reported in parentheses.

Summarizing, mesoherbivores (grazers and browsers combined) deposited on average 2.9 times more dung on cleared plots compared to un-cleared plots (Figure 2A), and the addition of megaherbivore dung did not change this pattern (Figure 2B). However, although mesoherbivore PHP increased with visibility (Figure 2C; Table 1), PHP from megaherbivores counteracted this. The megaherbivore contribution led to even PHP between cleared and un-cleared plots (Figure 2D).

On a landscape scale, zebra and wildebeest dung accumulated significantly more in open woodland than in dense thicket vegetation (Figure 3A). In contrast, elephant dung accumulated more in thicket than in open woodland. Overall, mesoherbivore dung accumulated more in open woodland relative to thicket, whereas megaherbivore dung accumulated more in thicket relative to open woodland. When the dung of all herbivore species is considered together, it is distributed equally between open woodland and thicket habitats.

DISCUSSION

The creation of open patches, that contrast with the surrounding matrix of closed habitat caused mesograzers to congregate and their fecal nutrients to accumulate within the clearings. This pattern of mesoherbivore dung accumulation in less risky, more visible areas was also evident on a landscape scale, with greater dung accumulation in open woodland. Conversely, megaherbivores' apparent disregard of the artificially created fear landscape, coupled with their greater consumptive demand, overrode the feeding impact of mesoherbivores. In the presence of megaherbivores, plots were subjected to similar intensities of potential herbivore pressure and thus potential nutrient removal, regardless of risk. Yet despite playing a prominent role in removing nutrients, megaherbivores' contribution to fecal nutrient replenishment was minor. On a landscape scale, the dung of megaherbivores accumulated more in dense thicket vegetation than in open woodland. This suggests that megaherbivores serve as net exporters of nutrients from open, less risky habitat, i.e., moving nutrients against the fear-driven gradient of mesoherbivore nutrient accumulation. In this way, megaherbivores modulate this fear-driven spatial discrepancy in mesoherbivores' foraging impact and partly counteract the ''landscape of fear'' effect, specifically on fecal nutrient accumulation.

Variation in tree density is a key feature of savanna landscapes, resulting in a gradient both in food availability (for browsers and grazers) and in the risk of predation. However, previous experimental studies, with a similar design as ours, have shown that herbivore dung accumulation in areas of lower tree cover were in response to enhanced visibility (predation risk) rather than to the changes in food availability associated with low tree cover [8, 10]. What sets our study aside from these studies is that we performed an experiment in one of the very few remaining areas with a functionally complete megaherbivore assemblage. Megaherbivore communities throughout Africa have been severely impoverished, and contemporary systems are often dominated by elephants. Yet, historically, rhinos formed a major component of the megaherbivore assemblages. Accounts from early-19th-century explorers often highlight the abundance of rhinos; e.g., during his travel in 1836, C. Harris saw 22 white rhinos within a half a mile distance near the Limpopo river [11]. Indeed, in our study, the megaherbivore contribution was largely driven by white rhinos. Megaherbivores are considered particularly important agents of lateral nutrient transfer ([3, 12, 13]), yet the impact of white rhinos on the landscape is likely to differ considerably from that of other megaherbivores. While megaherbivores such as elephants and giraffes have expansive ranging behavior and may distribute nutrients broadly, white rhinos have relatively small home ranges [14, 15], comparable to that of mesoherbivores the size of the kudu [16]. Moreover, rhino species mainly defecate in communal latrines (typically located on territorial boundaries), behavior that spatially decouples their nutrient removal from their

Table 1. Model-Averaged Parameter Estimates of the Effect of Clearing Treatment and Plot Visibility on PHP and Dung Accumulation for Different Groupings of Herbivores

Herbivore Grouping	Analysis	Estimate	SE	p value
Potential Herbivore Pressure				
Mesograzer	Clearing treatment (factorial)	0.5	0.41	0.299
Mesograzer	Visibility (covariate)	0.11	0.05	0.029*
Mesobrowser	Clearing treatment (factorial)	−0.75	0.27	0.018*
Mesobrowser	Visibility (covariate)	−0.41	0.03	0.099•
Megaherbivores	Clearing treatment (factorial)	−0.26	0.3	0.476
Megaherbivores	Visibility (covariate)	−0.02	0.04	0.656
All Mesoherbivores	Clearing treatment (factorial)	0.44	0.39	0.341
All Mesoherbivores	Visibility (covariate)	0.1	0.05	0.045*
All Herbivores	Clearing treatment (factorial)	0.12	0.28	0.729
All Herbivores	Visibility (covariate)	0.04	0.04	0.269
Dung Accumulation				
Mesograzer	Clearing treatment (factorial)	1.03	0.26	0.004**
Mesograzer	Visibility (covariate)	0.11	0.03	0.009**
Mesobrowser	Clearing treatment (factorial)	[a]	[a]	[a]
Mesobrowser	Visibility (covariate)	[b]	[b]	[b]
Megaherbivores	Clearing treatment (factorial)	[a]	[a]	[a]
Megaherbivores	Visibility (covariate)	[b]	[b]	[b]
All Mesoherbivores	Clearing treatment (factorial)	1.01	0.26	0.004**
All Mesoherbivores	Visibility (covariate)	0.11	0.03	0.004**
All Herbivores	Clearing treatment (factorial)	0.8	0.22	0.006**
All Herbivores	Visibility (covariate)	0.08	0.03	0.020*

Significance codes: •$p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Results were obtained from linear mixed effects models to account for the nested experimental design (four plots in each of three sites) and the repeated-measures (six seasonal measurements). See also Figure S2.

[a] Risk treatment not retained in ΔAICc < 4.

[b] Visibility not retained in ΔAICc < 4.

nutrient replenishment. This is likely to be the reason that, in our experimental plots, rhinos were the leading contributors to PHP, yet they contributed the least to nutrient replenishment. Thus, in contrast to other megaherbivores that may be distributing nutrients widely across the landscape, white rhinos' use of latrines concentrates nutrients locally. Yet their even use of our experimentally created risk gradient, and their relatively even distribution of dung between thicket and open woodland highlights that their fecal nutrient distribution is unrelated to the landscape of fear, as well as that they are perhaps creating an alternative nutrient patchwork to the one created by mesograzers' fear response. Current perspectives on megaherbivore impacts are based on studies that rarely incorporate such functional differences among megaherbivore species. Considering these distinctive characteristics of white rhino behavior introduces an additional dimension to the role of megaherbivores in translocating nutrients across the landscape and the functional losses associated with the multitude of rhino species that went extinct during the Pleistocene.

Mesograzers' more intense use of open patches and the greater accumulation of fecal material may suggest a local recycling of nutrients [17], i.e., the higher amounts of nutrients returned to less risky patches merely originates from these patches. However, the scale of our experiment (10 × 10 m plots) would in addition suggest a net import of nutrients from beyond the plot borders. The home range of most mesoherbivores are large (at least a few square kilometers e.g., 0.8–1.8 km^2 for impalas [9]), and they are thus likely to have moved well beyond the experiment. Moreover, studies in other savanna systems have shown how vulnerable herbivores are compelled to forage away from the relative safety of open areas, yet return to the relative safety of these patches for resting and/or ruminating [6, 18], leading to a net import of nutrients into refuge areas [18].

Some species-specific attributes such as feeding type and predator avoidance strategy make it more difficult to generalize responses to landscapes of fear. For example, most browsing species in our study system did not respond to the clearing of vegetation, and nyalas even selected for high woody cover. Although these browsers are still likely to be highly susceptible to predation, forage requirements perhaps compel them to follow a cryptic predator-avoidance strategy [19] (although nyalas are a mixed feeders, they include considerable amounts of browse in their diet). Warthogs' use of burrows provides refuge from predation during the riskiest times (at night), perhaps allowing some use of denser, more risky area. This may explain why warthogs responded differently to the other mesograzers, this has also been shown in studies elsewhere [20].

Although less vulnerable to predation, megaherbivores do not escape predation entirely. Calves remain vulnerable, and megaherbivores such as giraffes, at the smaller end of the

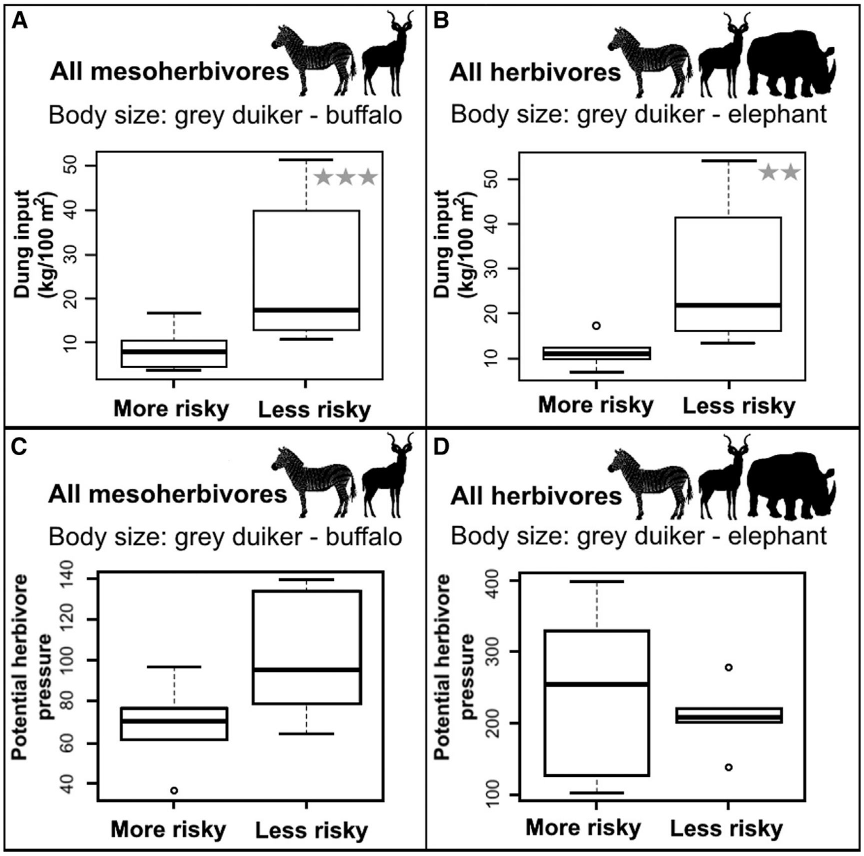

Figure 2. Herbivores' Collective Influence on Dung Accumulation and Potential Herbivore Pressure across Risk Treatments

Dung accumulation in kilograms/plot (100 m^2) (A and B) and PHP (C and D) by mesoherbivores only (A and C) and by all herbivores combined (B and D) in un-cleared (more risky) and cleared (less risky) plots. The box-and-whisker plots display the median, the lower and upper quartiles (25% and 75%), the minimum and maximum values, and outlying points. PHP is a unit-less value combining the number of 30 s trap-camera video clips multiplied by the number of individuals per clip multiplied by three-quarters of the average female metabolic biomass (see STAR Methods). See also Figure S1.

megaherbivore size spectrum, are still targeted by large predators. Indeed, previous studies have shown giraffes to also select for clearings [8]. Regardless, in our system, giraffes used the experimentally created risk gradient evenly, and their dung was distributed equally between the relatively risky thicket vegetation and the less risky open woodland vegetation. Thus, despite some degree of vulnerability, avoiding risky habitat may not be a viable anti-predatory strategy for megaherbivores that need to consume large volumes of forage [19, 21]. On the other hand, buffalo, which are at the larger end of the mesoherbivore size spectrum, although showing an affiliation with open woodland, did not respond significantly to the experimentally created risk gradient. This suggests that buffalo may also be contributing to this counter-current of fear-driven nutrient movement. Thus, species' differential contribution to nutrient distribution is most likely linked to a continuous gradient of size-based vulnerability to predation rather than a distinction between mega- and mesoherbivores.

Our study is the first to examine the joint involvement of large carnivores and megaherbivores in altering the potential for trophic cascades. Others before us have convincingly demonstrated mesoherbivores' selection of open habitat to be a response driven from the top down [6, 8, 10], leading to spatial variation in nutrient deposition with cascading impacts on vegetation. We build on their work by additionally showing how the foraging action of species less vulnerable to predation can counteract this nutrient accumulation, thereby masking some of the effects of predator-triggered trophic cascades and attenuating top-down trophic controls. We also demonstrate the decisive influence of white rhinos, which contribute substantially to PHP. Despite having once occurred widely throughout Africa [22], the white rhino now occurs below functional densities across all but a few localities, with the northern subspecies now extinct in the wild [23]. Thus, although their influence may be deemed trivial in many of today's savanna systems, their historical role is likely to have been considerable. Hence, our work contributes much needed information to recent attempts at estimating ecosystem functional losses associated with Pleistocene and more recent megafaunal extinctions. Scientists are looking to African systems to provide the empirical basis of megafaunal function [24], and our study system (Hluhluwe-iMfolozi Park) is one of the last where white rhinos' ecological impact can still be tested empirically.

In summary, we highlight the following important concepts:

Having megaherbivores in the system could modulate certain trophic cascades triggered by mesoherbivores' responses to the presence of predators (such as was the case here with PHP). A masking role of megaherbivores could help explain the paucity of clear predator-induced trophic cascades in Africa.

Through their apparent disregard for the landscape of fear, megaherbivores play an important role in lateral nutrient transport by distributing nutrients across the risk gradient. Our experimental design did not allow us to conclude that megaherbivores entirely negate the accumulation effect of mesoherbivores, but our results certainly show a counteracting effect of megaherbivores, suggesting a much more heterogeneous nutrient accumulation in their absence.

And finally, functional differences within the megaherbivore guild with regard to characteristics such as ranging patterns and defecation behavior may introduce considerable variation in how they distribute nutrients across the landscape. Latrine use of rhino species spatially decouples nutrient removal and return, thereby ensuring nutrient movement

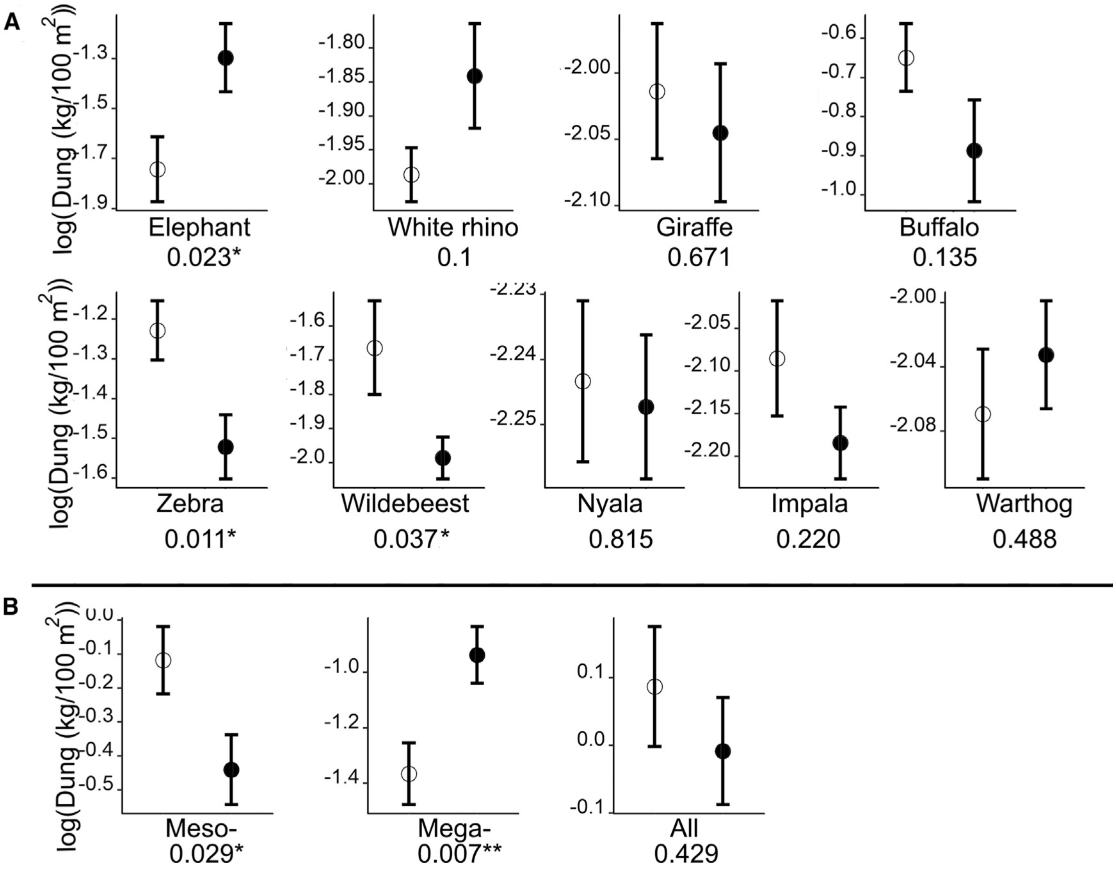

Figure 3. Landscape-Scale Dung Accumulation in Vegetation Types that Contrast in Predation Risk

Log-transformed average dung accumulation (kg/100 m^2) in thicket (black) and open woodland (white) vegetation types for the different herbivore species (A) and the combined dung accumulation of meso-, mega- and all herbivore species (B). Error bars represent SEs. p values are shown beneath each panel and were obtained from species-specific linear models. Significance codes: •$p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

against the gradient of fear-driven accumulation. The current poaching onslaught stresses the urgency to quantify megaherbivores' role in nutrient movement and the implications for nutrient distribution patterns, if we are to anticipate the ecosystem-level consequences of Anthropocene megaherbivore declines.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- QUANTIFICATION AND STATISTICAL ANALYSIS
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SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and can be found with this article online at https://doi.org/10.1016/j.cub.2018.05.088.

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AUTHOR CONTRIBUTIONS

All authors contributed to study design. E.I.R. performed the fieldwork and analyzed the data. G.K. and J.C. supervised the work. All authors contributed to writing the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Data and analysis script	This paper	https://doi.org/10.17632/3trxpngmdt.1
Software and Algorithms		
R software environment for statistical computing and graphics	CRAN	RRID:SCR_003005

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Elizabeth le Roux (elizabeth.liza.le.roux@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study Area

The study was conducted in Hluhluwe-iMfolozi Park (hereafter HiP), a 900 km^2 mesic savanna protected area in South Africa. The vegetation is structurally variable, ranging from open grassland to closed Acacia and broad-leaved woodland [25]. The experimental site was situated in the northern section of the park that receives approximately 950 mm rain annually (EKZNW unpublished rainfall records recorded at Research station between 2000 and 2014), falling mainly between October and March. Substantive woody encroachment has occurred in the park, particularly in the northern parts, over the past century, with species such as *Dichrostachys cinerea*, *Acacia karroo*, and *Euclea racemosa* increasing in density [26, 27]. Historical hunting and persecution drove some megaherbivore species and some predator species to local extinction. Recently, faunal restoration programs in HiP have successfully restored the predator and megaherbivore guilds. Lion (*Panthera leo*) numbers doubled in the past two decades (from approximately 60 to 120 animals) and wild dog (*Lycaon pictus*) numbers increased approximately three fold since 2002 (from approximately 20 to 70 individuals) [28]. Elephant and giraffe were (re)introduced in the early 1980s and mid-1950s, respectively and their populations have grown dramatically to a current density of 0.7 elephants/km^2 [29] and approximately 0.5 giraffes/km^2 [30]. Active protection of white rhino has seen populations recover from near extinction to an estimated 2.6 individuals/km^2 [31]. In contrast, populations of small to medium-sized mammalian herbivore species have generally declined across HiP, and particularly from the northern parts of the park [30].

Experimental Design

We set up a long term experiment in March 2013, where we manipulated risk and resources in a full-factorial layout. We delineated four 40 × 40 m plots in three separate sites (i.e., 12 plots). Plot size was informed by a study on hunting success of female lion [32], wherein the probability of escape with a flight distance of 20 m was calculated at 75% for blue wildebeest and zebra and 100% for Thomson’s gazelle (*Eudorcas thomsonii*). Plots were spaced between 60 m to 350 m apart, and the distances among sites were between 1.5 km and 6 km. The sites were similar in slope and contained a woody component composed of *D. cinerea* and *Acacia* species in relatively homogeneous density. In the center of each 40 × 40 m plot we delineated a further 10 × 10 m subplot, which served as our focal sampling plot throughout the study. We manipulated the perception of risk by removing the entire woody component from two randomly selected plots of the four 40 × 40 m plots in each of the three sites with the purpose of enhancing visibility. To enable comparable measurements in all plots we cleared the woody component from the center 10 × 10 m subplot of the remaining two plots, such that the only risk-related differences between the plots were in the visibility surrounding the central subplot. All further manipulations and measurements were taken from these central subplots (see Figure S3).

To attract herbivores to the experiment and standardize grass height (and thereby the attractiveness to grazers) across all plots, we mowed all central subplots in April 2013 and in November 2013. Because we were initially interested in trade-offs between risk and resources, we fertilized the central subplot of one cleared and one un-cleared plot in each site. We used standard slow release NPK fertilizer (Wonder 3-2-1 SR from EFEKTO) on three separate occasions (April 2013, November 2013 and April 2014). The first two applications equated to 1.5 g nitrogen, 1 g phosphorus and 1 g potassium per m^2 and we doubled the amounts in the third application. These amounts are comparable to previous such studies that successfully elicited a response from herbivores [33]. None of the species responded to the nutrient treatment and the fertilization treatment had no detectable effect on any of the measured variables.

Large parts of HiP burn each year at the end of the dry season. To avoid the risk of hot fires destroying the woody cover gradients, we (with the help of park staff) burnt all 12 plots with cool fires in the early dry season of 2013 and 2014. This ensured that the fire was of low enough intensity to not influence the structural differences among plots.

METHOD DETAILS

Experiment measurements and data preparation

Potential herbivore pressure (PHP)

Using movement triggered camera traps, set to record 30 s video clips, we measured ungulate visitation to the central subplots over 20 months (April 2013 to November 2014). We were interested in the pressure exerted on the treatment plot (regardless of whether it was from the same individual). In order to link herbivore visitation to potential herbivore pressure, we quantified the behavior of impala and white rhino during three periods (11 – 23 April 2013, 20 June – 10 July 2013, and 11 – 27 Sept 2013). For each species we performed Pearson correlations, comparing the number of videos per plot with the number of videos in which the individual was recorded feeding.

Potential herbivore pressure was calculated separately per species and expressed as the number of 30 s video clips multiplied by the number of individuals recorded in each clip multiplied with three quarters the average female metabolic biomass (metabolic biomass = weight $^{0.75}$; ref. [9]). The three quarters weight adjustment corrects for the likelihood that some individuals were sub-adults or young and the conversion to metabolic biomass reflects the relative differences in consumptive demand that species of different body size present. Body weight estimates were obtained from [9]. We discarded all the last clips in a sequence (where the animal did not necessarily remain on the plot for the full 30 s duration). We also excluded all the single clips where species only passed through the plot. Potential herbivore pressure was calculated per season (early dry season, late dry season and wet season), the seasonal delineation being based on average rainfall received. Thus the two years yielded six data points per plot, totalling 72 data points.

Camera failure and animal interference frequently disrupted recording, resulting in variable sampling duration among plots. We accounted for this variation by dividing the estimate of PHP with the number of days recorded to obtain a seasonal estimate of "potential herbivore pressure/day." We excluded estimates where the camera recorded for less than 20 days per season (a loss of just one datum). Potential herbivore pressure was log transformed to reduce skewness.

Dung accumulation

We measured species-specific faecal biomass accumulation within each central subplot on average every 20 days (10 – 33) over approximately 30 months (890 days). Counted dung piles were crushed *in situ* to avoid recounting. Total dung return (kg) per species was approximated by multiplying counts of dung piles with average dung pile weight (N = 5 per species). We log transformed the dung weight values to reduce skewness.

Using published estimates of faecal nutrient content for each species (ref. [34]; supplemented by ref. [35]), we approximated the total input of nitrogen and phosphorus (g) to each of the 12 plots. Faecal nutrient estimates for some species were missing from these publications so we used estimates from impala dung for nyala, estimates from warthog for bushpig (*Potamochoerus larvatus*) and estimates from elephant for white and black rhino (*Diceros bicornis*). Although the difference in size and feeding habits between elephant and the two rhino species and between warthog and bushpig suggest the values are not interchangeable, this error should be minimal as white rhino dung was only recorded on three occasions, while black rhino and bushpig dung were each only recorded once.

Perceived predation risk

Apart from the risk treatment (cleared versus un-cleared), we also considered visibility as a measure of perceived predation risk. Using a 1.6 m Nudds' density board [36] divided into 0.2 m sections, we estimated visibility in the 8 cardinal and inter-cardinal directions. The measurement involved estimating for each of the 8 directions, the distance at which approximately half of each 0.2 m section of the board is no longer visible. Visibility may differ between species depending on species height and this has been shown to influence habitat selection [37]. Hence we quantified visibility at three height levels, corresponding to the eye level of blue wildebeest (~140 cm), impala (~90 cm) and warthog (~60 cm). We made the measurements from the center of each plot and averaged per animal height level per plot. We used visibility measured at blue wildebeest height for all analysis involving blue wildebeest and taller species, visibility measured at impala height for impala and nyala analyses, and visibility measured at warthog height for analyses involving warthog and gray duiker. For analyses where herbivore species were combined we used visibility measurements made at impala height.

We repeated the measurement in the dry and the wet season of 2013 and again during the dry season of 2014 to incorporate seasonal changes in visibility. In seasonal comparisons we used the corresponding visibility measurement and in analyses where seasons were amalgamated we used an average value per plot.

While the experiment was set up as a 2 × 2 full factorial design with a clearing treatment and a fertilization treatment, visibility varied due to variation in initial area visibility and seasonal changes. As such we analyzed both the two-level factorial risk treatment (cleared/un-cleared) and visibility as a covariate.

Landscape-scale dung distribution

We mapped dung distribution along a network of 24 line transects (varying between 4 – 11 km and totalling 190 km) during March 2004. We identified and quantified dung of all mammalian herbivore species at 5 m intervals and recorded the dominant vegetation type every 100 m. Vegetation type was categorised as grassland, open woodland, closed woodland, thicket and forest (see [38] for more details). For the purpose of the study presented here, we selected two vegetation types that were abundant and contrasting in terms of lateral visibility (open woodland and thicket). Thicket was defined as near-impenetrable woody vegetation (> 75% of surface area covered with shrubs and/or trees) and open woodland was defined as a woodland with separated tree canopies [38]. We calculated the dung density per species (kg/100 m^2) to compare dung accumulation between these two vegetation types.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data Analyses

Statistical analyses were performed in R [39]. Species-specific analyses were performed on a subset of herbivore species for which we had sufficient data, including elephant, white rhino, giraffe, buffalo, zebra, blue wildebeest, kudu, nyala, impala, warthog and gray duiker. We subsequently categorized species according to their vulnerability to predation (see ref. [40]). We grouped buffalo and smaller species (<1000 kg) into mesoherbivores (species considered to be vulnerable to predation) and further subdivided mesoherbivores into grazers and browsers. Although impala and nyala are both mixed feeders we classified impala as a grazer and nyala as a browser based on the bulk component of their diets. Giraffe, white rhino and elephant were classified as megaherbivores (species considered to be generally invulnerable to predation [9]).

We used separate models per species and per group (megaherbivores, mesograzers and mesobrowsers; Table 1 and Figure 2) to model the degree to which PHP and dung accumulation were determined by risk treatment (or visibility as a covariate) and fertilization treatments. To account for the nested experimental design and the repeated-measurements, we used linear mixed effects models using the package "nlme" [41]. Potential herbivore pressure was modeled with risk treatment as a factor, fertilization treatment and the interaction as fixed components. In addition, we reran all models replacing the factorial "risk treatment" with visibility (as covariate). We nested plot ID in site ID as random terms and incorporated a continuous first order autoregressive correlation structure to account for the temporal correlation. Dung accumulation was modeled using the same fixed effect structure. We modeled total accumulation i.e., disregarding season and analyzing a single value per plot and specified site as a random factor.

We checked for homogeneity of variance both visually and statistically, using a variance test for continuous variables and the Bartlett test for categorical variables [42]. Where appropriate we corrected heteroscedasticity by specifying the "weights" argument from the nlme package. We selected reasonably supported models using AICc, retaining all models with a delta AICc value of <4. Using the retained model set, we averaged parameter values using a conditional average (R package "MuMIn" [43]).

For the analysis of the landscape scale dung distributions, we log-transformed dung density due to a highly skewed distribution and tested for significant differences in dung density between habitats using species-specific linear models.

DATA AND SOFTWARE AVAILABILITY

The analysis script and all data files have been deposited in the Mendeley Data repository and can be accessed here: https://doi.org/10.17632/3trxpngmdt.1.