

RESEARCH ARTICLE SUMMARY

NETWORK ECOLOGY

Importance of elephants for dung beetle biodiversity and ecosystem functions

Finote Gijsman*, Ciara M. Nutter, Fathiya M. Khamis, Fidelis L. O. Ombura, Matthew C. Hutchinson, Todd M. Palmer, Jacob R. Goheen, Scott E. Miller, Robert M. Pringle*



Full article and list of author affiliations:
<https://doi.org/10.1126/science.aeb7062>

INTRODUCTION: Large mammals are disproportionately affected by human activities such as overhunting and land conversion. All species of megaherbivores—ecologically influential mammals 1000 kg or larger, such as elephants and rhinoceroses—are considered at risk of extinction, and local population declines and extirpations of these species have already profoundly altered many ecosystems. Insects are also declining in abundance and diversity, raising concerns that important ecosystem services such as pollination and waste recycling will diminish. Moreover, because co-occurring species are interlinked through complex networks of interactions, the extinction of one species can trigger declines and losses of others that depend on it (“coextinction”), leading to a snowballing collapse of biodiversity and ecosystem functions. Thousands of dung beetle species (Coleoptera: Scarabaeinae, Aphodiinae) feed on the feces of large mammals and may therefore be prone to coextinction, along with their multibillion dollar services.

RATIONALE: Countless theoretical studies have investigated coextinction by computationally simulating the loss of species from ecological networks, showing that coextinction cascades stem from the removal of critical nodes—typically, species that are linked to many others as predators or food sources. However, there is little concrete evidence of coextinction in nature. There is similarly little in situ support for other predictions of ecological network analysis, such as that the most highly connected species are “keystones” that sustain biodiversity and functionality, or that generalists with broad dietary niches are less susceptible to coextinction than specialists. Following calls to confront these predictions with data from experiments that mimic extinction, we tested how a community of 179 dung beetle species responded to the simulated, experimental, and real-world removal of elephants and other large herbivores in East Africa.

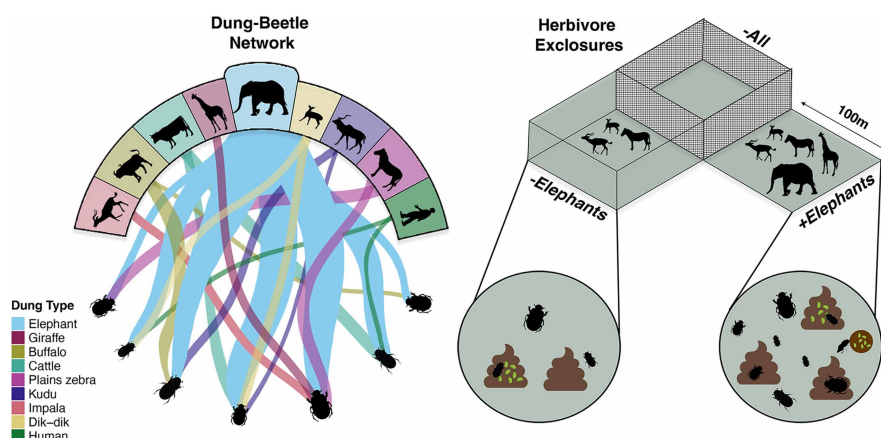
RESULTS: We measured dung beetles’ preferences for the dung of different herbivore species and constructed a network of beetle–mammal interactions. Dung beetles had an inordinate fondness for elephant dung, which was the most connected node in the network. Simulated elephant removal predicted the secondary extinction of 28% of dung beetle species. A 15-year experiment supported that prediction, with 23% fewer species, 51% less biomass, and 67% fewer individual dung beetles in plots where elephants were selectively excluded. Dung beetles with stronger preference for elephant dung were more likely to be absent in elephant exclosures. None of the smaller ungulate species had comparable effects. Landscape-scale surveys of areas where elephants had been displaced by high livestock densities revealed similar and even starker depletions of dung beetle abundance and biomass (66 to 93%). A final experiment showed that the depletion of dung beetles in elephant exclosures impaired two ecosystem services: dung decomposition and seed dispersal.

CONCLUSION: Elephants act as a true keystone species by sustaining the abundance, diversity, and functioning of dung beetle communities with their prodigious defecations. Our findings uphold predictions of ecological network theory that have seldom been tested in nature and suggest a strategy for building a mechanistic, predictive understanding of coextinction. Although our work is consistent with prior speculation that coextinction contributes significantly to global biodiversity loss, we highlight the potential of species reintroductions and range expansions to combat these losses while deepening our understanding of how they occur. □

*Corresponding author. Email: fgijzman@princeton.edu (F.G.); rpringle@princeton.edu (R.M.P.) Cite this article as: F. Gijsman et al., *Science* 392, eaeb7062 (2026). DOI: 10.1126/science.aeb7062

Elephants sustain diverse, abundant, and high-functioning dung beetle communities.

Elephant (*Loxodonta africana*) dung is disproportionately used by dung beetles, making elephants a central node in the mammal–dung beetle network. Experimental plots selectively excluded herbivore species by size, showing that elephants’ centrality predicts the outsized impact of their loss, including steep declines of dung beetle abundance, diversity, and ecosystem services. [Credit to Phylopic for the herbivore and beetle silhouettes]



NETWORK ECOLOGY

Importance of elephants for dung beetle biodiversity and ecosystem functions

Finote Gijsman^{1*}, Ciara M. Nutter¹, Fathiya M. Khamis^{2,3}, Fidelis L. O. Ombura², Matthew C. Hutchinson⁴, Todd M. Palmer⁵, Jacob R. Goheen⁶, Scott E. Miller⁷, Robert M. Pringle^{1,8*}

Ecologists theorize that removing highly connected species from ecological networks will trigger waves of coextinction, but empirical evidence is scant. We show that elephants are central to a generalized network of interactions between dung beetles and large herbivores in East Africa. Computer simulations based on this network predicted disproportionate dung beetle losses if elephants go extinct, and a 15-year experiment supported this prediction: Excluding elephants diminished dung beetle abundance, diversity, and ecosystem functions, whereas excluding smaller ungulates had little added effect. Dung beetle abundance was depressed in nearby landscapes where livestock had displaced elephants, corroborating the experimental results. Our findings affirm the long-standing idea that large animals—which are inordinately extinction-prone—act as keystone species by provisioning many linked consumers with essential resources, thereby sustaining biodiversity and ecosystem services.

The world's largest mammals are acutely vulnerable to population decline and extinction from overhunting and environmental change, a trend that dates back to the Pleistocene (1, 2). All extant megaherbivores (>1000 kg) are at imminent risk, and their declines have already transformed many ecosystems (3). Smaller mammalian herbivores fare slightly better, but most species >100 kg are threatened (4). At the other end of the body size spectrum, insect abundance and diversity are also declining as a result of pollution, habitat loss, and warming (5), raising concerns that an “insect apocalypse” (6) will impair nutrient cycling, pollination, and other ecosystem services. Insects that depend on large herbivores for food—blood suckers, carcass consumers, and dung decomposers—may therefore be in double jeopardy.

Species are linked through networks of interactions, meaning that the loss of one species can cause secondary extinction (“coextinction”) of others that depend on it. Many interactions appear to be highly specialized, which implies that dependencies between species are strong, and that coextinction could be a leading cause of biodiversity loss (7, 8). In the past 25 years, hundreds of studies have simulated the removal of species from ecological networks to predict the risk of coextinction and snowballing community collapse (9–13; reviewed in 14, 15). Risk factors include a given species' degree of specialization and connectedness to other species, along with the functional redundancy of their interactions (15). One of the earliest predictions was that the most highly connected species are potential “keystones” on which many others depend, and that removing such species would trigger avalanches

of coextinction. A quarter-century later, however, this prediction remains essentially untested. Investigators struggle to pinpoint a single conclusive historical example of coextinction (16, 17), making it impossible to confront theory with data. The orders-of-magnitude disparity between predicted and observed coextinction frequencies reflects the difficulty of documenting the effects of real-world extinctions and reveals gaps in our understanding of ecological specialization and network structure (18, 19). Experiments that mimic species loss can offer valuable mechanistic insight into coextinction, but such experiments are rare. A recent review collated 16 predictions based on *in silico* simulations, of which only three had any *in situ* experimental support (15).

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae and Aphodiinae) feed and nest in feces (hereafter, “beetles” refers to dung beetles unless otherwise specified). Most species belong to one of three functional groups: “Dwellers” feed and nest inside dung piles; “tunnelers” bury dung beneath piles; and “rollers” move dung away from piles and then bury it (20). By breaking up, distributing, and burying dung, beetles contribute to vital ecosystem services such as soil aeration, nutrient cycling, and seed dispersal, which enhance plant growth and carbon storage (21, 22). They also suppress gut parasites, lungworms, flies, and other pests (22). The value of these services to the USA and UK cattle industries alone was estimated at more than \$1 billion USD in the mid-2000s (equivalent to roughly \$1.6 billion USD in 2026) (23, 24).

Several studies predict that the decline of wild populations of large herbivores will erode dung beetle abundance, diversity, and functions (25–27). Other lines of evidence, however, suggest competing interpretations. On the one hand, coextinction risk is thought to be highest for specialists, but dung beetles tend to be generalists (28). Such dietary flexibility could buffer dung beetles against coextinction if they can compensate for the loss of one food source by switching to a functionally redundant alternative (29)—especially because wild ungulates are often replaced by livestock and small mammals that might produce at least as much dung (30). On the other hand, generalism is not universal: Dung beetles exhibit varying degrees of specialization (31, 32), partial preferences (33, 34), and resource partitioning (20, 35), which might create dependencies on particular mammal species. Moreover, if morphologically cryptic resource specialists are common in dung beetles, as they are in other insects (36), then dung beetles may be far more specialized and coextinction-prone than current knowledge indicates. Finally, even if dung beetles were universally generalized, food scarcity could still promote coextinction. The “more individuals hypothesis” posits that species richness is a function of abundance, which in turn depends on usable energy (37); mammal declines that reduce the energy available in dung might thus deplete the diversity of dung beetles regardless of how generalized they are.

We documented the interactions of a diverse community of dung beetles and large herbivores in an African savanna, cross-validating morphological identifications with DNA barcodes to ensure accurate species delineation. We analyzed the effects of removing mammal species from this network using both computer simulations and a field experiment in which (i) only megaherbivores (elephants and giraffes) and (ii) all herbivores ≥ 5 kg were excluded from 1-ha plots for 15 years (38). In a second manipulation, nested within the first, we tested whether experimentally induced shifts in dung beetle communities affected two ecosystem services, dung decomposition rate (which is crucial for nutrient cycling) and secondary seed dispersal (which is crucial for plant regeneration) (21). To probe the scalability of our experimental results, we surveyed dung beetle abundance across a landscape-scale gradient in wildlife abundance. Using these data, we evaluated a series of general questions and predictions of network theory that have seldom, if ever, been tested in nature (15). Do *in silico* simulations predict *in situ* outcomes? Do the most connected species really function as keystones? Are food webs more robust to the loss of large species than small ones? And to what extent do generalism and functional redundancy limit coextinction, stabilize network structure, and preserve ecosystem functions?

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA.

²International Centre of Insect Physiology and Ecology, Nairobi, Kenya. ³Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa. ⁴Department of Life and Environmental Sciences, University of California Merced, Merced, CA, USA. ⁵Department of Biology, University of Florida, Gainesville, FL, USA. ⁶Department of Natural Resource Ecology and Management and Department of Global Resource Systems, Iowa State University, Ames, IA, USA. ⁷National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. ⁸Collegium Helveticum, the joint Institute of Advanced Study of ETH Zurich, University of Zurich, and Zurich University of the Arts, Zurich, Switzerland. *Corresponding author. Email: fgijsman@princeton.edu (F.G.); rpringle@princeton.edu (R.M.P.)

Results

Dung beetle–mammal interaction network

We conducted field experiments and surveys from 2021 to 2025 at Mpala Research Centre in Laikipia, Kenya (hereafter, “Mpala”; 0.29°N, 36.89°E). To catalog the dung beetle community, we created an extensive local reference database by archiving representative specimens at the National Museums of Kenya for taxonomic identification and sequencing the mitochondrial COI (cytochrome *c* oxidase subunit I) DNA barcode region (36) for 4383 specimens. We detected 179 putative species, ranging from 2 mm to 50 mm in body length (figs. S1 and S2), some of which were not distinguished morphologically yet nonetheless formed distinct COI haplotypes.

To evaluate the relative attractiveness of different dung types and the preferences of different dung beetle species, we conducted cafeteria experiments during the wet and dry seasons of 2021 and 2022. At seven sites, we baited standardized pitfall traps ($n = 504$; fig. S1) with fresh dung from eight herbivore species (elephant, zebra, giraffe, buffalo, cattle, kudu, impala, and dik-dik) and a vegetarian human. These species account for >95% of all mammal dung at Mpala and are representative of the phylogenetic and functional diversity of large herbivores in African savannas more broadly, encompassing four mammalian orders, five families, and variation in evolutionary history (wild, domesticated), body size (5 to 5000 kg), digestive system (ruminant, monogastric), diet (C_4

grazer, C_3 browser, mixed), and extinction risk (least concern, near threatened, vulnerable, endangered) (table S1). Baits were identical in size (20 g), duration (12 hours), and proximity (50 m). Capture rates therefore signify beetle preference—i.e., selection from a set of equally available options—which should in turn reflect the relative appeal of each dung type as a nutritional and/or reproductive resource for a given dung beetle species (26).

This experiment captured 4231 dung beetles of 132 species (74% of the 179 total) and showed that generalism was the norm. We detected 413 (35%) of the 1188 possible network links (Fig. 1). Among the beetle species sampled ≥ 3 times, 92% were attracted to the dung of ≥ 2 herbivore species. The number of links per species (“degree”) saturated rapidly with sample size (fig. S4), and all dung types attracted a similar set of beetle species (Fig. 1E). Despite these signatures of generalism, however, the network as a whole was more specialized than expected at random (Fig. 1D). In particular, beetles had an inordinate fondness for elephant dung, which attracted 1.5 to 24 times more individuals and 2 to 6 times more species per trap than any other dung type (Fig. 1, B and C; figs. S5 to S7; table S1). Elephant thus had the highest degree and was the most connected node in the network, accounting for nearly half (44%) of all individual beetles sampled and having links to two-thirds (67%) of all beetle species in the network. Zebra, the only other hindgut-fermenting herbivore species besides elephant, was the

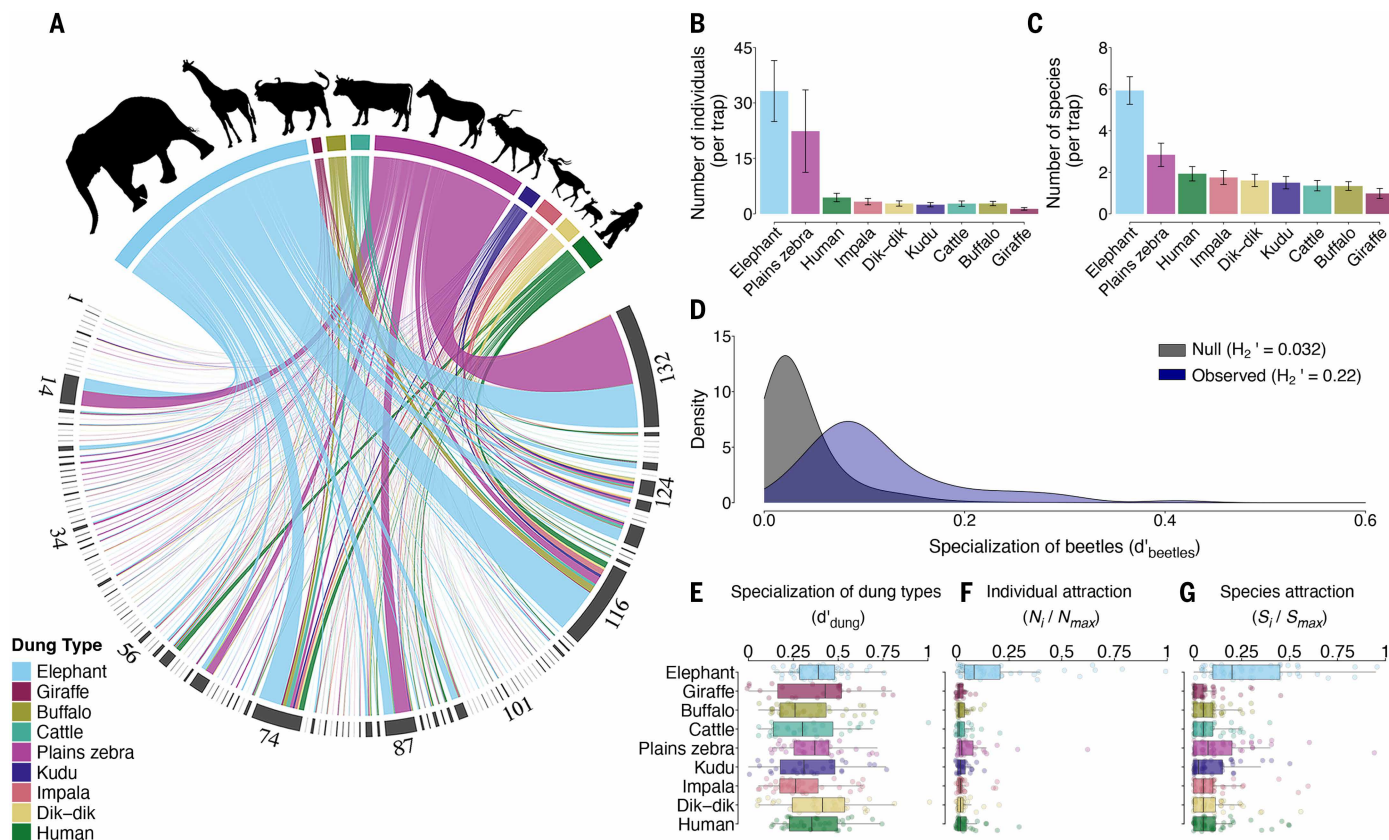


Fig. 1. Dung beetles are generalists but prefer elephant dung. (A) Network of interactions between herbivore (colors) and beetle species (numbered 1 to 132; table S3). Bar width shows number of interactions per species; line width shows interaction frequency (beetle preference). (B and C) Number of beetle individuals (B) and species (C) per trap (mean $\pm$ SE). (D) Observed species-level specialization (d'_{beetle}) for beetle species with at least three sampled individuals (blue; mean = 0.11 $\pm$ 0.009, median = 0.09) exceeded that of 1000 Patefield null models (gray; mean = 0.04 $\pm$ 0.0001, median = 0.03), as did observed network-level specialization ($H'_2_{obs} = 0.22$, mean $H'_2_{null} = 0.032$; $P < 0.001$; tables S1 and S3). Results were unaffected by varying the minimum sample size threshold from 3 to 10. (E to G) Elephant dung attracted the most individuals and species. (E) Baits differed little in the composition of dung beetle species attracted (d'_{dung} ; table S2), but elephant dung attracted more individual beetles (F; N_i / N_{max} , number of individuals per bait divided by the maximum observed on any bait) and beetle species (G; S_i / S_{max}) than other dung types (all $P < 0.001$; table S2). Boxes show median and interquartile range (IQR); whiskers show $1.5 \times$ IQR; and points show value for each trap ($n = 504$, 56 per species). Three traps (1 elephant, 2 zebra) captured extreme beetle numbers (≥ 416 versus ≤ 154) and are omitted in (F) to facilitate visualization, but they were included in statistical analyses and did not affect the results (table S2).

next most connected node, accounting for 30% of sampled individuals and having links to 48% of all species. By contrast, the six ruminant species—and especially giraffe—attracted far fewer dung beetles (<6% of individuals) and had the fewest links (<4% of species) in the network (tables S1 and S2).

Similarly, although all beetle guilds and size classes were found on all dung types, they exhibited strong and overlapping preferences (figs. S5 to S7 and table S4), with herbivore gut type and dung abundance predicting the subtle niche differences between groups. Small beetles (<5 mm) and dwellers strongly preferred hindgut fermenters, with gut type explaining $\geq 97\%$ of the variance in capture rate. Larger beetles and rollers were equally responsive to gut type and dung abundance. Tunneler preference was best predicted by dung abundance alone ($R^2 = 0.95$). We found no direct link between beetle and mammal body sizes (20, 35). We conclude instead that beetle preference depends on dung composition and availability, which helps to explain why elephants—hindgut fermenters that deposit more dung than any other species (fig. S3)—are so central to the network.

Simulated herbivore removals predict keystone role of elephants

We used this empirical network to simulate the impacts of sequential herbivore removal. We first removed species in random order, tallying coextinctions at each step, under four thresholds (the fraction of links that a species can lose before going extinct, assuming no new links can form: 100, 70, 40, or 10%) (39). We tested the sensitivity of these results by repeating the process on reduced networks that omitted beetle species sampled fewer than 3 or 5 times, and by simulating scenarios that allowed beetles to establish new links (“rewire”) after each removal step. Last, we simulated plausible selective extinction scenarios by removing herbivore species in ascending and descending order of body size, and in descending order of global extinction risk until only cattle and humans (and then only humans) remained (4).

In random removal sequences, the mean number of coextinctions per herbivore species was a linear function of herbivore degree at all thresholds ($R^2 > 0.93$). Under the most conservative threshold (100%), random-order removal of elephants caused 2 to 8 times more coextinctions (40.3 ± 0.6) than any other species (11.5 ± 0.14 ; Fig. 2, A and B). More liberal thresholds only intensified the impact of elephant removal. These results were qualitatively consistent across sample size criteria and rewiring scenarios (figs. S8 and S9). Non-random sequences that selectively eliminated larger-bodied and more threatened species (mimicking two common real-world scenarios, both of which remove elephants first) predicted 25 to 50% higher-than-random levels of coextinction; by contrast, the less common small-to-large removal scenario was more robust than random (Fig. 2C).

Such topological simulations are useful for theoretical and heuristic insight but entail simplifying assumptions (14, 15). For one, our network is based on beetle

preference rather than on realized feeding or breeding interactions. Our simulations therefore implicitly assume that adult preference is related to some form of demographic constraint, such as obligate dietary specialization, energy limitation, competition, or reproductive requirements. Our data reject the first of these possibilities (fig. S4), but the rest are plausible. We surmise that preference tracks adult consumption rates and integrates the relative fitness benefits of a given resource, thereby proxying demographic value. For example, that elephant dung is the most preferred and most abundant resource implies that it is the most frequently consumed, and independent data from Mpala confirm this (40). Furthermore, feeding and breeding resources often overlap, albeit to varying degrees. Recent work in Brazil found high overlap between dung types used for feeding and breeding (26), consistent with the idea that adult nutrition and reproductive output depend on the same preferred resources. In other cases, adult foraging is more opportunistic, whereas larval provisioning and brood-ball formation are more constrained by dung volume and texture. Examples include several large African dung beetle taxa, in which elephant dung is considered even more essential for breeding than feeding (20, 40, 41); in these taxa, adult preferences might stem largely from specialized larval needs and hence closely reflect demographic reliance on elephant dung. A related caveat is that our static simulations (Fig. 2) ignore potential compensatory shifts in resource use.

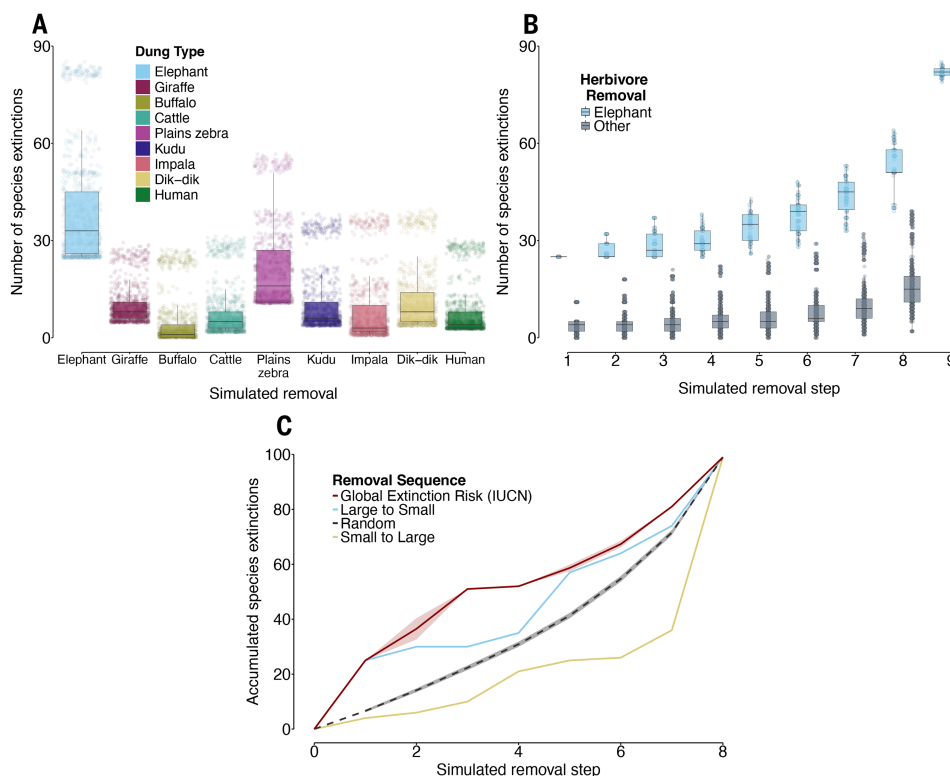


Fig. 2. Simulations predict dependency of dung beetle communities on elephants. (A and B) Simulated random removal sequences predict that elephant extirpation causes dozens of beetle coextinctions. Plots show number of coextinctions across 1000 simulations (points), in which coextinction occurs only if all links are lost (100% threshold). Boxes are as in Fig. 1. Elephant loss caused the greatest number of coextinctions (A) regardless of sequence order (B). Horizontal rows of points in (A) are simulations in which that herbivore species was eliminated last (above boxes) or first (below boxes). (C) Coextinction accumulation curves for random (dashed) and selective (solid) herbivore removal sequences. Humans were not removed in these scenarios. Line color denotes order of herbivore removals. Black: mean $\pm$ 95% confidence intervals (CI) of 1000 random-order simulations. Red: highest to lowest extinction risk based on IUCN (International Union for the Conservation of Nature) global risk status (Endangered, Vulnerable, Near Threatened, Least Concern, and cattle); for species in the same risk category, we tested all unique sequence permutations and averaged across them (shading: 95% CI). Blue: largest to smallest herbivore. Gold: smallest to largest herbivore.

Although we simulated dynamic scenarios that allowed probabilistic rewiring and found that they reproduced the same core conclusions (figs. S8 and S9), these models, too, rest on plausible but unverified assumptions about the substitutability of different dung types. Ultimately, we cannot rule out the possibility that a preference-based network creates only the illusion of demographic dependency. In that case, however, we would not expect field experiments to support our simulation predictions.

Experimental evidence that elephants sustain dung beetle abundance and diversity

Exclosure experiments enable causal inference about effects of species loss. Although controlled manipulations cannot mimic all facets of real extirpation and are inherently limited in scale, they are essential for developing a mechanistic and predictive understanding of coextinction (15). Most such experiments comprise just one fenced treatment and an unfenced control and therefore cannot test predictions about selective or sequential extinction scenarios (15). In 2008, we

established a set of 10,000-m² plots that exclude large herbivores in a nested, largest-to-smallest design (fig. S1). In April 2023, 15 years into the experiment, we assayed dung beetle community structure in three treatments: unfenced plots (“Open”), which are accessible to all animals; megaherbivore exclosures (“Mega”), which exclude only elephants and giraffes; and total exclosures (“Total”), which exclude all herbivores >5 kg. Treatments were replicated in three blocks at two sites 20 km apart ($n = 18$ plots), spanning a moderate rainfall gradient. As expected, exclosures altered the abundance of large-herbivore dung (fig. S3 and table S5); we did not record other types of dung, but we note that small vertebrates, which supply food for many dung beetles (32, 41, 42), occur at higher densities inside exclosures (38). To survey dung beetles, we placed three traps, baited with elephant, zebra, and cattle dung, in the center of each plot and collected contents after 24 hours.

In line with our simulations, dung beetle abundance, biomass, and species richness were greater in plots accessible to elephants (Open) than in either exclusion treatment (Fig. 3). Megaherbivore exclusion

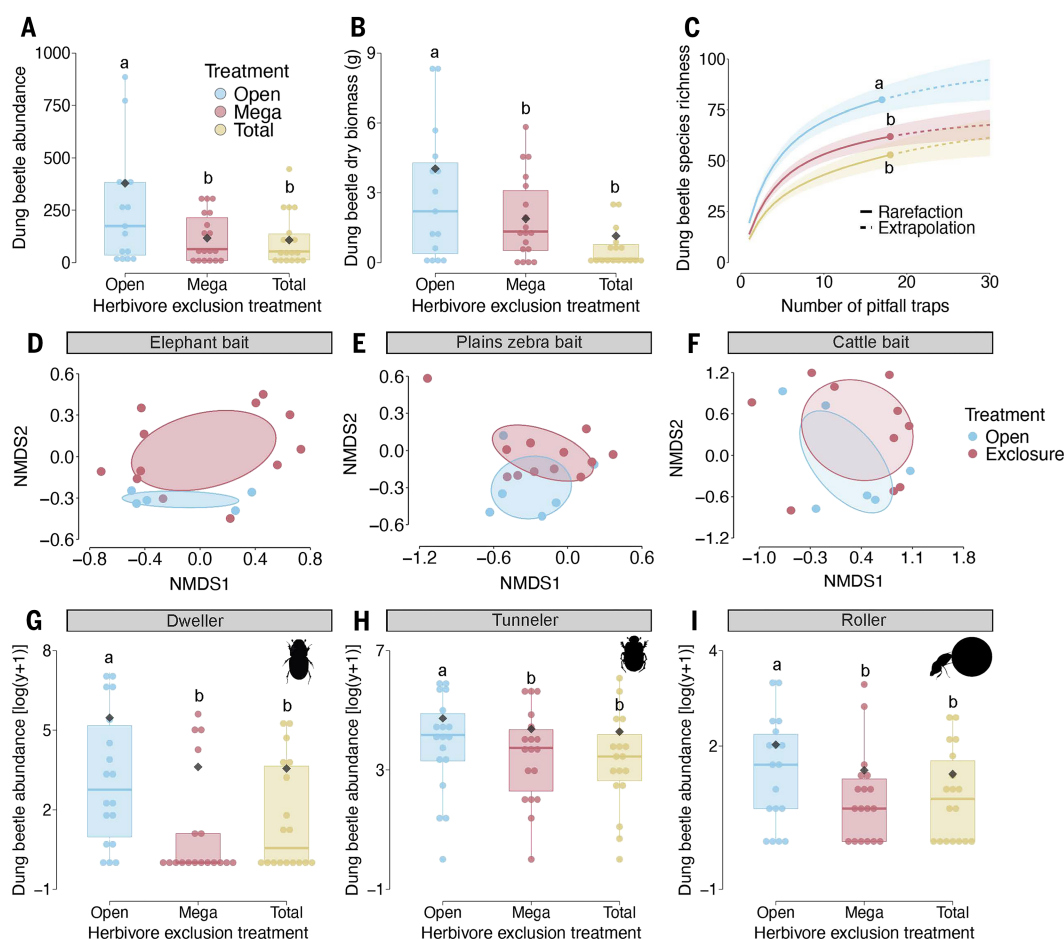


Fig. 3. Depletion of dung beetle communities in plots without elephants. (A to C) Beetle abundance, biomass, and species richness were all lower in plots without elephants (Mega, Total), based on generalized linear mixed models (GLMMs) with main effects of treatment (joint tests: $\chi^2_2 = 33.3$, $F_{2,45} = 6.9$, and $\chi^2_2 = 19.6$, respectively; all $P \leq 0.003$) and bait type ($\chi^2_2 = 63.5$, $F_{2,45} = 9.7$, $\chi^2_2 = 89.1$, $P \leq 0.001$) and random intercepts for site and block-within-site. Boxes are as in Fig. 1. Points show each trap ($n = 3$ per plot, 18 per treatment), diamonds show the mean, and letters denote differences inferred from planned pairwise contrasts (Holm-Bonferroni $P_{\text{adj}} \leq 0.02$) (table S7). Two high outliers in Open plots are omitted from graphs but were included in analyses and did not affect the results (table S7). (C) Rarefaction and extrapolation of species richness per treatment (points: observed richness; shading: 95% CI). (D to F) Nonmetric multidimensional scaling (NMDS) ordinations of Jaccard dissimilarity in species composition per trap (points) by bait type in Open plots versus exclosure treatments, both in red for visualization [permutational analysis of variance (PERMANOVA) pseudo- $F_{2,48} = 3.29$, $P < 0.001$; all pairwise $P < 0.01$; all stress < 0.2] (table S8). (G to I) Treatment effects on abundance by functional guild (joint tests: all $\chi^2_2 \geq 7.23$, all $P \leq 0.03$). Letters denote pairwise differences ($P_{\text{adj}} = 0.07$ for Open versus Total in (I); all other $P_{\text{adj}} \leq 0.04$; table S10). Equivalent results for beetle size classes are in fig. S10 and table S12. Small differences in sample size per treatment reflect the destruction of one trap by wildlife and, in (D) to (F), two cattle-baited traps that attracted no beetles.

alone (Mega) reduced abundance by 67%, biomass by 51%, and richness by 23%, on average (tables S6 to S8). This effect on richness is comparable to that predicted when elephants were removed first in static simulations (28%). Exclusion of other large herbivores (Total) had little added effect, indicating that megaherbivores alone regulate dung beetle communities. These results do not rule out a contributing effect of giraffes. However, given the trifling attractiveness of giraffe dung (which accounted for a mere 76 of 4231 beetles in the cafeteria experiment, 96% fewer than elephants; Fig. 1 and table S1) and elephants' overriding contribution to dung mass (61 kg/ha, 12 times more than that of giraffes; fig. S3), we attribute the “megaherbivore effect” to elephants.

Elephant exclusion also altered dung beetle species composition (Fig. 3, D to I). All guilds and size classes were most abundant in Open plots. Dwellers, tunnelers, rollers, and small dung beetles were 40 to 86% less abundant in enclosures, with no differences between Mega and Total (tables S9 to S12). Larger beetles declined in steps from Open to Mega to Total, perhaps due to their stronger links with two abundant ungulates, dik-dik and impala (figs. S5 and S10 and table S12).

The strength and consistency of these results are notable given the limits of experimental scale. Although the extent of our experiment is unusual, with 200-fold larger plots and fivefold longer duration than the median enclosure study (43), each plot is still a 1-ha defaunated island in a sea of megafauna. Mark-recapture studies show that a typical dung beetle travels just a few meters per day [e.g., interquartile range (IQR) 1 to 11 m/day; (44–46)], suggesting that our 24-hour trapping bouts were not swamped by long-distance immigration. However, dung beetles occasionally fly much farther than their routine daily movements indicate (20). We therefore interpret our results cautiously as reflecting functional responses to experimentally induced variation in dung availability; to what extent they also reflect local numerical responses remains to be verified. We hypothesize that in enclosures, lack of elephant dung and resultant lower total dung mass and energy concentration limit the number of adult beetles that can meet their food and reproductive needs. This in turn limits plot occupancy (space use tracks dung availability) and recruitment (fewer occupants make fewer offspring), especially in species that strongly prefer elephant dung for trophic, reproductive, or competitive reasons. Traps in these plots would thus mainly capture occupants that subsist on ungulate and small vertebrate dung, along with some transients that fly in from nearby areas, either coincidentally or in response to olfactory cues from baited traps. Because local immigration should only dampen the effects of 1-ha enclosure plots relative to those of large-scale extirpation, our results may underestimate true coextinction risk. If so, then we expect that dung beetle abundance should be at least three times greater (the Mega:Open effect size on abundance) in landscapes with elephants than in those where elephants have been displaced by livestock.

Landscape-scale corroboration that elephants sustain dung beetle abundance

In November 2025, we surveyed dung beetle abundance at Mpala and at two communal “group ranches” located 1 km and 10 km away from Mpala (fig. S11), using traps identical to those in the enclosures. The group ranches have high densities of sheep and goats, lower densities of donkeys, camels, and cattle, and sporadic wild ungulates. However, elephants avoid them. Both group ranches had higher dung density than Mpala (driven by sheep and goats, $R^2 = 0.80$) but lower total dung mass (driven by elephants, $R^2 = 0.92$) (fig. S11). Dung beetle abundance and biomass were 3 to 14 times greater at Mpala than at either group ranch and were positively correlated with elephant dung density (fig. S11 and table S13). These results are consistent with our hypotheses that the enclosure results are qualitatively predictive of real extirpation events at large scales but represent a lower-bound proxy for the actual magnitude of coextinction risk. They also suggest that even high livestock densities cannot sustain the native dung beetle fauna

without elephants. Anecdotes and comparative data bolster these inferences: Elephant extirpations in West and South Africa are thought to have reduced dung beetle species richness (20), and surveys across land-use gradients have reported higher dung beetle abundance and diversity in areas with viable elephant populations (47–49).

Correspondence between network simulations and experimental results

We next assessed whether the responses of individual beetle species to enclosure treatments were predicted by their degree (number of links to different herbivore species) and relative preference for elephant dung (which we treated both as a continuous proportion and as a binary categorical factor denoting species captured exclusively with elephant baits, i.e., preference = 1). Proportional preference was uncorrelated with degree ($r = -0.21$). We regressed these predictors against each of three responses: the proportion of individuals found in Open plots (null expectation: $\frac{1}{3}$); the difference in frequency of occurrence between Open and Mega plots (null expectation: 0); and the number of “pseudoextinctions”, where a species was found in an Open plot but not in the Mega plot of the same experimental block (null expectation: unrelated to degree or preference).

Both degree and dung preference predicted species' responses to elephant exclusion, indicating unexpectedly granular alignment between our simple simulations and experimental results. Relative occurrence in Open plots was negatively related to dung beetle degree and positively related to both metrics of elephant preference (Fig. 4, A to C). Similarly, species with lower degree and higher elephant preference occurred less frequently in Mega than in Open plots (Fig. 4, D to F, and fig. S12). Thus, network topology predicted effects of elephant exclusion not just on dung beetle species richness (Fig. 3C), but also on species occurrence and hence community composition.

Cascading effects on ecosystem functions

In a final experiment, we crossed herbivore and dung beetle exclusion to test (i) whether the effect of herbivore exclusion on beetle communities reduced rates of dung and seed removal and (ii) whether these functions were dependent on beetle body size. In March 2023, we deployed 200-g pats of elephant dung in each plot and assigned them to four treatments (with three replicates per treatment per plot; $n = 216$ replicates; fig. S1). Two treatments were enclosed: Coarse mesh (C) excluded dung beetles >5 cm, whereas fine mesh (F) excluded all dung beetles. The other two treatments were open to all decomposers: An unmeshed, unmanipulated control (U) and an unmeshed set of pats mixed with 25 small (1 mm) and 25 large (10 mm) artificial seeds (U+S). We measured removal of dung dry mass and seeds after 10 days. We were unable to exclude termites, the other major group of dung decomposers, so we used termite presence as a covariate in our statistical models.

Dung-removal rate was higher in Open plots than in Mega or Total (which did not differ from each other, indicating that the effect is driven by exclusion of elephants, not ungulates) and greater in unmeshed pats (U, U+S) than meshed ones (with a statistically marginal difference between C and F, indicating weak effects of beetle body size; Fig. 5 and table S14). Excluding elephants slowed dung decomposition almost as much as excluding beetles: Decomposition rates were highest when elephants and all beetles were present (3.56 ± 0.36 g/day) and were only slightly higher with all beetles present and elephants absent (2.30 ± 0.23 g/day) than with all beetles absent and elephants present (1.98 ± 0.34 g/day; $n = 216$). The decay rate of unmeshed pats increased with the mean dung beetle biomass sampled in a given plot (Fig. 5D), further highlighting that elephants indirectly support ecosystem services by sustaining dung beetles. Termites had strong effects on the 56 pats that they colonized (table S14), which lost $\sim 70\%$ of dry mass. However, analyzing just the 160 termite-free replicates reproduced the original result: Elephants indirectly accelerated dung removal (1.28 ± 0.13 versus

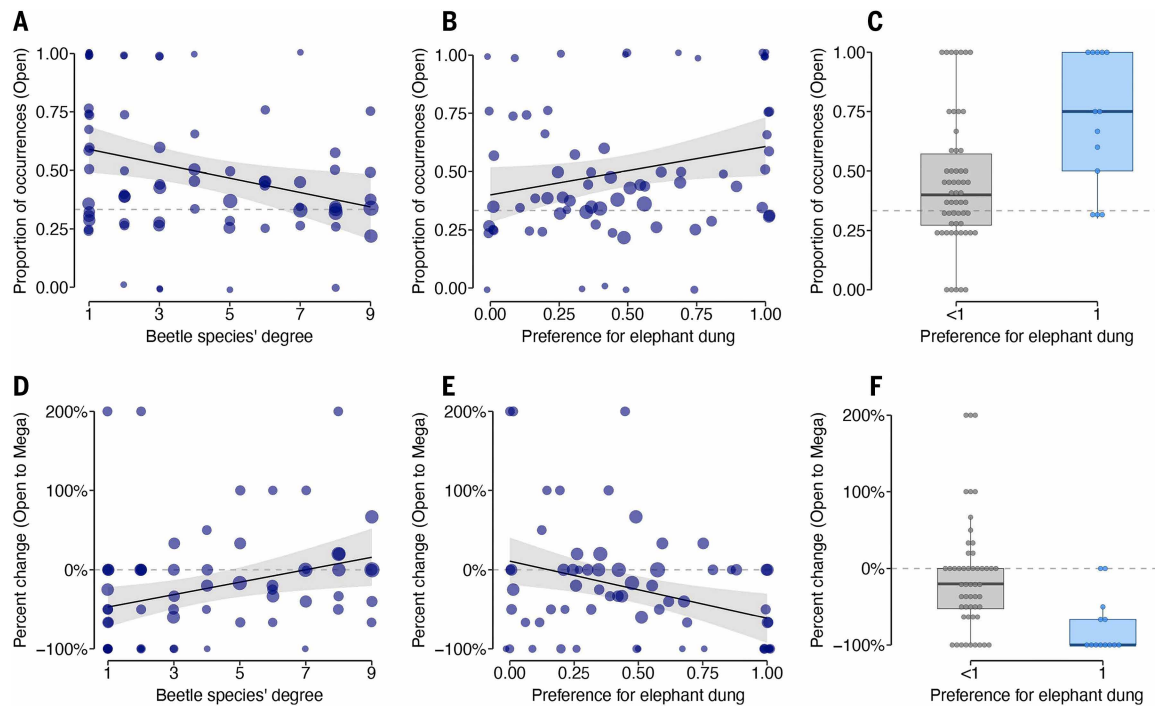


Fig. 4. Network structure predicts species-level responses to megaherbivore exclusion. Beetle responses to megaherbivore exclusion were predicted by their observed network degree and affinity for elephant dung. Points (species) are scaled by relative number of detections in experimental plots. Dashed lines show the null expectation. (A to C) Proportional occurrence in Open plots with elephants was inversely related to observed degree (A) (least squares $F_{1,68} = 6.30$, $P = 0.01$), positively related to relative preference for elephant dung (B) ($F_{1,68} = 4.20$, $P = 0.04$), and higher in species detected only on elephant baits (C) ($F_{1,68} = 9.20$, $P = 0.004$); $n = 70$ species detected in both the network and the experimental plots. (D to F) Percent difference in occurrence in Open versus Mega [$(N_{i, Mega} - N_{i, Open}) / N_{i, Open} \times 100$ (values $< 0\%$ indicate fewer occurrences in Mega)]; $n = 65$ species, omitting five never detected in Open plots. Species with degree ≤ 4 occurred less often in Mega (D) ($F_{1,63} = 6.29$, $P = 0.01$), as did those with elephant affinity ≥ 0.4 (E) ($F_{1,63} = 8.23$, $P = 0.006$); (F) ($F_{1,63} = 9.15$, $P = 0.004$). Similar results for “pseudoextinction” are in fig. S12.

0.93 ± 0.08 g/day), largely reproducing the effect that beetles exerted directly (1.58 ± 0.11 versus 0.53 ± 0.05 g/day).

Mean removal rates of both large and small seeds were two times greater in Open (0.8 and 1.0/day) than in either exclosure treatment (0.4 and 0.5/day) and were highly correlated with overall dung removal ($R^2 \geq 0.64$). When accounting for the strong positive effects of termites, the main effect of exclosure treatment remained statistically significant for large seeds only (Fig. 5C and table S15).

Discussion

Elephants as a keystone species

Elephants have been described as keystone species—and as agents of disturbance or even destruction (50)—because they transform and deplete vegetation (51, 52), which generally reduces the density and diversity of other species in “green” food webs fueled by live plant biomass (53). Such impacts match one definition of keystones—those that exert disproportionate influence relative to their abundance (52)—but they contrast with the original use of the term for animals that overwhelmingly enhance and stabilize community diversity (54). For dung beetles, elephants are a keystone by both definitions, with positive effects on the densities of individuals, biomass, and species that are measurably disproportionate to their abundance and biomass (table S16).

That these effects were so well predicted by network topology is noteworthy, because it highlights the prospect of a unified framework for one of ecology’s most prominent yet elusive ideas. Ecologists have never converged on a uniform operational definition of “keystoneness” (55). The textbook criterion, disproportionate community importance (52), is quantifiable but rarely quantified, as it entails removing candidate species in turn to gauge their effects, along with data on their

relative abundance. Studies of ecological networks have long embraced proxy measures, postulating that species with high degree or centrality are keystones (9–11), while conceding that “the ability of network structure measures to identify keystone species is highly dubious” without “careful experimental or observational validation” (56). Despite the rapid growth of research on both ecological networks and keystone species, there has been no such validation. Our study bridges this gap, showing that network-based identification of keystones might not be so dubious after all.

Mechanisms of coextinction and community robustness

Our study answers calls to merge network analysis and field experiments to test predictions about coextinction and community robustness (15). We reject one such prediction, that networks are more robust to the loss of large species than small ones, an idea inspired by marine ecosystems in which tiny plankton provision many larger consumers (57). In our network, the biggest species was also the primary, most connected food source. We hypothesize that this scenario is generalizable to many “brown” (detritus-based) food webs: Because population biomass scales with body size (53, 58), bigger species represent larger pools of dung and carrion for generalist scavengers.

We affirm the classic prediction that communities are sensitive to the loss of the most connected species (9, 10). This outcome is trivial in sequential simulations that hold link structure constant, but it is hardly inevitable in nature because the loss of one species tends to rewire the links between those that remain. Rewiring often exposes unforeseen generalism: Ostensibly specialized, dependent species turn out to be more flexible than assumed, which can rescue communities from the loss of even highly connected species (59, 60). Rewiring is

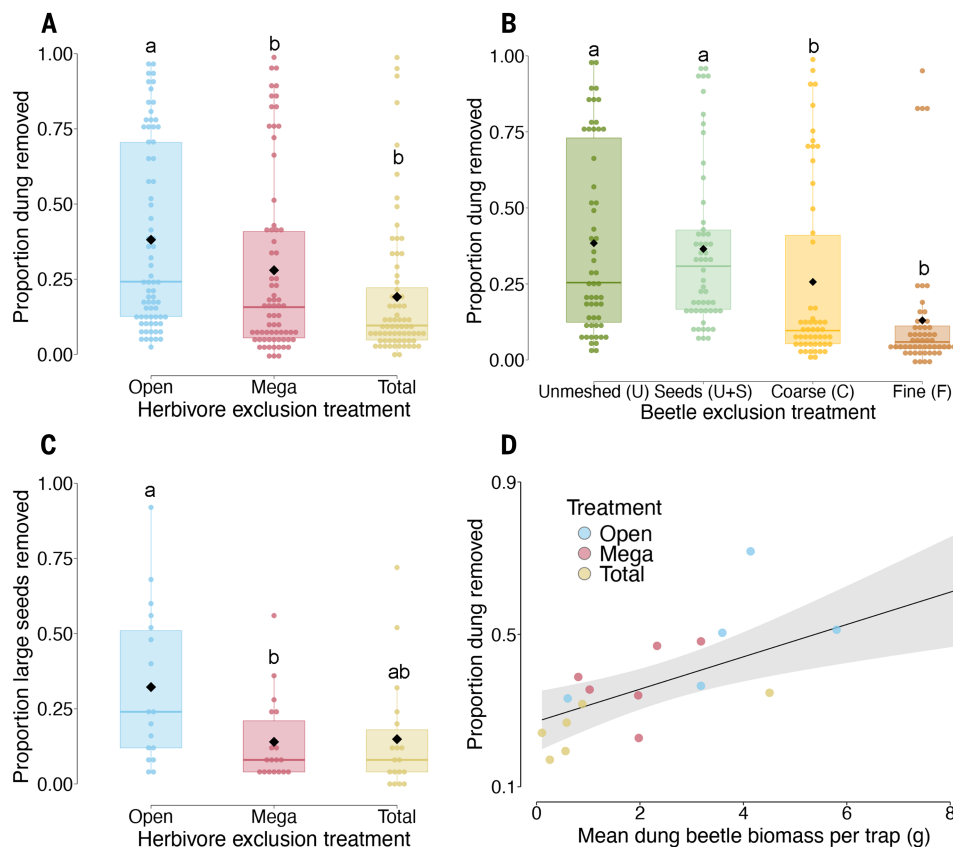


Fig. 5. Elephant exclusion impairs dung beetle ecosystem services. (A) Large-herbivore exclusion ($\chi^2_2 = 9.7$, $P = 0.008$) and (B) beetle exclusion ($\chi^2_2 = 72.1$, $P < 0.0001$) independently reduced dung removal (interaction term: $\chi^2_2 = 4.0$, $P = 0.67$). Termites had a strong additional effect ($\chi^2_1 = 351$, $P < 0.0001$; table S14). (C) Herbivore exclusion reduced the dispersal of large artificial seeds ($\chi^2_2 = 6.2$, $P = 0.05$; termite effect: $\chi^2_1 = 35.2$, $P < 0.0001$; table S15). Boxes are as in Fig. 1; points show each replicate dung pat ($n = 216$); letters denote pairwise differences. Due to the directional prior expectation implied by Fig. 3 [Open > (Mega $\approx$ Total)] and hypothesized for the beetle-exclusion design [(U $\approx$ U+S) > C > F], we consulted both one- and two-tailed Holm-adjusted contrasts (tables S14 and S15). (D) Dung beetle biomass predicted dung removal from unmeshed pats (U, U+S) across plots (least-squares regression, $R^2 = 0.46$, $F_{1,16} = 13.8$, $P = 0.002$). Points show mean removal for the six pats per plot with no mesh barrier (U, U+S).

thus a major source of model-data disconnect and an obstacle to predicting coextinction (15, 16). We did not measure rewiring in response to elephant exclusion, and enclosures are too small to host fully self-contained communities of flying insects. It is thus possible that our enclosure results partly reflect beetles' behavioral avoidance of resource-poor patches and their selection of elephant-dung-rich habitat outside the plots—we did not strictly test the ability of the community to adaptively rewire around other dung sources, and the extent to which resource switching and rewiring buffers coextinction risk remains a crucial question. Several of our results, however, make it seem unlikely that rewiring could wholly salvage the community from elephant extinction. First, if rewiring is costless, dispersal unconstrained, and resources limiting, then rewiring should have neutralized treatment effects regardless of plot size. For example, removal of the most connected seed-dispersing ant from 100-m² plots in Portugal caused rewiring of the network, an influx of other ant species, and consequent maintenance of dispersal function (60). Second, we found that effects of elephant exclusion conservatively mimicked the effects of genuine elephant depopulation on dung beetle abundance (and, by deduction, on beetle diversity too, given the well known positive relationship between the numbers of individuals sampled and species detected). Third, assorted descriptive evidence, referenced above, indicates that elephant declines and extirpations elsewhere have also

depleted dung beetle populations and communities.

We also found support for the predictions that generalism and functional redundancy confer robustness to coextinction (15). Species with higher degree and weaker preference for elephant dung (proxies for generalism and redundancy, reflecting resource breadth and substitutability) were less affected by elephant exclusion, whereas species with lower degree and stronger elephant preference declined. These trends suggest a mechanistic basis for the agreement of our simulation and experimental results, implying that networks can be used not just to predict the extent of coextinction but also to identify species at risk. Superficially, however, these trends also seem to be in tension with the extreme polyphagy of dung beetles in this community. Many species shared a preference for elephant dung, but we have no evidence that any of them is a strict dietary specialist. We posit three compatible mechanisms to reconcile these findings: First, adult beetles are similarly generalized but differentially competitive; species prefer resources for which they compete effectively and are first to be outcompeted when those resources disappear. Second, larval requirements for dung quantity and/or quality are stricter than adult requirements, and preference is dictated by species-specific breeding constraints (20, 61–63). These mechanisms would create interspecific variation in adult preference and demographic dependency on elephant dung while still being consistent with polyphagous adult foraging. Third, elephants sustain the community through energy subsidy: More energy supports more individuals and hence more viable popula-

tions of more species (37). This last model does not predict interspecific variation in elephant preference but it can explain the results for beetle degree: Low observed degree was a function of rarity, and rare species would be the first to drop out when energetic carrying capacity declines. Several additional factors highlight a plausible role of energetic constraint. Dung beetles are energy-limited (62), and elephants produce the largest quantity of dung-bound energy. Elephant dung also has traits thought to enhance energy availability for dung beetles, including high C content and C:N ratios (which relax stoichiometric constraints on energy intake; 64) along with coarse texture and high moisture content (which increase accessibility and prolong usability).

There is indirect evidence that all three mechanisms are causing coextinctions of African dung beetles. Elephant numbers have declined by an order of magnitude since 1800, with ~500,000 surviving (65). Many local extinctions are documented. At Mpala, one elephant feeds up to 2.1 million dung beetles per day, and the whole elephant population could sustain up to 260,000 individuals per square km (66). Most of these are dwellers (Aphodiinae), which are competitively inferior to other guilds (20). Dwellers in our study had the narrowest preferences (88% elephant and zebra) and the steepest declines when elephants were excluded. Plausibly, then, the “hyper-abundance of Aphodiinae in African savannas” (66) depends on elephant dung, as large fiber fragments impede removal by competitively dominant rollers and tunnelers

(mechanism 1, competition). Larval demands have been invoked to explain the loss of large tunnelers and rollers such as *Helicopriss* and *Circellium* spp. in areas where pachyderms are extinct (mechanism 2, picky larvae; 20, 41, 67). These species “use various kinds of dung for their own nutrition” but bury huge amounts of dung for larvae (up to 2.6 kg) and thus plausibly depend on elephants (20). Some “occasionally use a substitute when elephants have disappeared” but attain smaller sizes as a result (20), as expected if energy limits the ability of resource switching to maintain viable populations (mechanism 3, more individuals). In general, megaherbivore loss is only partly offset by increases in smaller species (53); thus, even if other dung types are substitutable, they cannot fully compensate energetically for elephant extinction. Exceptions to this rule of biomass undercompensation occur mainly when wild megafauna are replaced by high densities of livestock (30), as in the two group ranches that we surveyed. Those survey results, together with our results for cattle on Mpala and the handful of systematic surveys across anthropogenic land-use gradients (47, 48, 68), indicate that livestock alone cannot sustain intact African dung beetle communities.

Dependency of dung beetle biodiversity on megaherbivores through time

Our results buttress the idea that the diversity of dung beetles past, present, and future is tied to the fate of the world's largest herbivores. Phylogenetic and fossil data are compatible with the theory that dung beetles first radiated in the Cretaceous, associated with dinosaur herbivores, and that diversity was lost with the dinosaurs, 66 million years ago (69). Another period of rapid dung beetle diversification in the early Cenozoic, coinciding with the rise of mammalian megaherbivores (including more than 100 genera of proboscidean and rhinoceros), and the subsequent slowing of that rate with the rise of smaller ruminants in the Miocene (69), is also consistent with a singular importance of hindgut-fermenting megaherbivores. Fossil data from several continents suggest that large dung beetles were coextinguished with monogastric megaherbivores in the Pleistocene (27, 70, 71). Finally, many studies from modern ecosystems have found correlations between defaunation and dung beetle abundance, species composition, and/or diversity (25, 26, 48, 68, 71–73). All of these interpretations are the focus of research and debate, yet none explains why “dietary plasticity appears to have had limited effect on dampening coextinctions” (71).

By providing experimental evidence that dung beetles are vulnerable to the loss of a globally endangered megaherbivore—despite the flexibility of beetle diets—we contribute new evidence to this investigation. Our approach provides a blueprint for a mechanistic and predictive understanding of coextinction. Replicating this approach in other systems, coupled with systematic macro-scale surveys of beetle diversity and resource use across defaunation gradients, will test the generality and scalability of our finding that network structure identifies keystones and predicts coextinction dynamics. Experimental work is also needed to explain why dung beetles prefer and ultimately rely on elephant dung, which requires disentangling feeding and breeding constraints. We identified three plausible, testable mechanisms and expect that each will earn some support.

Our findings underscore the value of conserving elephants, not just for their own sake, but also for the biogeochemical integrity of savannas, the prosperity of pastoral and agro-ecosystems, and the cosurvival of charismatic minifauna. The collapse of megaherbivore populations over the past 2 centuries is being counteracted by programs to recover lost elephant and rhino populations. Such reintroductions have the potential to fend off dung beetle coextinction (41, 67) while also offering opportunities to test the ideas in our study at huge spatial scales (53). For 60 million years, dung beetles have shadowed Earth's megaherbivores. Restoration and rewilding can shine new light on both groups of fascinating creatures and help prevent the sun from setting on either one.

Materials and methods are available in the supplementary materials (76).

REFERENCES AND NOTES

1. F. A. Smith, R. E. Elliott Smith, S. K. Lyons, J. L. Payne, Body size downgrading of mammals over the late Quaternary. *Science* **360**, 310–313 (2018). doi: [10.1126/science.aao5987](https://doi.org/10.1126/science.aao5987); pmid: 29674591
2. T. B. Atwood *et al.*, Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Sci. Adv.* **6**, eabb8458 (2020). doi: [10.1126/sciadv.abb8458](https://doi.org/10.1126/sciadv.abb8458); pmid: 32923612
3. E. J. Lundgren *et al.*, Functional traits—not nativeness—shape the effects of large mammalian herbivores on plant communities. *Science* **383**, 531–537 (2024). doi: [10.1126/science.adh2616](https://doi.org/10.1126/science.adh2616); pmid: 38301018
4. IUCN, “The IUCN List of Threatened Species” (Version 2025-1, 2025): <https://www.iucnredlist.org>. Accessed on July 21, 2025.
5. D. L. Wagner, Insect Declines in the Anthropocene. *Annu. Rev. Entomol.* **65**, 457–480 (2020). doi: [10.1146/annurev-ento-011019-025151](https://doi.org/10.1146/annurev-ento-011019-025151); pmid: 31610138
6. D. Goulson, The insect apocalypse, and why it matters. *Curr. Biol.* **29**, R967–R971 (2019). doi: [10.1016/j.cub.2019.06.069](https://doi.org/10.1016/j.cub.2019.06.069); pmid: 31593678
7. L. P. Koh *et al.*, Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634 (2004). doi: [10.1126/science.1101101](https://doi.org/10.1126/science.1101101); pmid: 15361627
8. G. Strona, C. J. A. Bradshaw, Coextinctions dominate future vertebrate losses from climate and land use change. *Sci. Adv.* **8**, eabn4345 (2022). doi: [10.1126/sciadv.abn4345](https://doi.org/10.1126/sciadv.abn4345); pmid: 36525487
9. R. V. Solé, J. M. Montoya, Complexity and fragility in ecological networks. *Proc. R. Soc. B* **268**, 2039–2045 (2001). doi: [10.1098/rspb.2001.1767](https://doi.org/10.1098/rspb.2001.1767); pmid: 11571051
10. J. A. Dunne, R. J. Williams, N. D. Martinez, Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecol. Lett.* **5**, 558–567 (2002). doi: [10.1046/j.1461-0248.2002.00354.x](https://doi.org/10.1046/j.1461-0248.2002.00354.x)
11. F. Jordán, Keystone species and food webs. *Philos. Trans. R. Soc. B.* **364**, 1733–1741 (2009). doi: [10.1098/rstb.2008.0335](https://doi.org/10.1098/rstb.2008.0335); pmid: 19451124
12. J. Memmott, N. M. Waser, M. V. Price, Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B* **271**, 2605–2611 (2004). doi: [10.1098/rspb.2004.2909](https://doi.org/10.1098/rspb.2004.2909); pmid: 15615687
13. E. L. Rezende, J. E. Lavabre, P. R. Guimarães, P. Jordano, J. Bascompte, Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925–928 (2007). doi: [10.1038/nature05956](https://doi.org/10.1038/nature05956); pmid: 17713534
14. J. Bascompte, D. B. Stouffer, The assembly and disassembly of ecological networks. *Philos. Trans. R. Soc. B.* **364**, 1781–1787 (2009). doi: [10.1098/rstb.2008.0226](https://doi.org/10.1098/rstb.2008.0226); pmid: 19451127
15. D. N. Morton, A. Keyes, A. K. Barner, L. E. Dee, Merging theory and experiments to predict and understand coextinctions. *Trends Ecol. Evol.* **37**, 886–898 (2022). doi: [10.1016/j.tree.2022.06.004](https://doi.org/10.1016/j.tree.2022.06.004); pmid: 35798612
16. R. R. Dunn, N. C. Harris, R. K. Colwell, L. P. Koh, N. S. Sodhi, The sixth mass coextinction: Are most endangered species parasites and mutualists? *Proc. R. Soc. B* **276**, 3037–3045 (2009). doi: [10.1098/rspb.2009.0413](https://doi.org/10.1098/rspb.2009.0413); pmid: 19474041
17. R. K. Colwell, R. R. Dunn, N. C. Harris, Coextinction and Persistence of Dependent Species in a Changing World. *Annu. Rev. Ecol. Evol. Syst.* **43**, 183–203 (2012). doi: [10.1146/annurev-ecolsys-110411-160304](https://doi.org/10.1146/annurev-ecolsys-110411-160304)
18. R. M. Pringle, M. C. Hutchinson, Resolving Food-Web Structure. *Annu. Rev. Ecol. Evol. Syst.* **51**, 55–80 (2020). doi: [10.1146/annurev-ecolsys-110218-024908](https://doi.org/10.1146/annurev-ecolsys-110218-024908)
19. N. Blüthgen, M. Staab, A Critical Evaluation of Network Approaches for Studying Species Interactions. *Annu. Rev. Ecol. Evol. Syst.* **55**, 65–88 (2024). doi: [10.1146/annurev-ecolsys-102722-021904](https://doi.org/10.1146/annurev-ecolsys-102722-021904)
20. I. Hanski, Y. Cambefort, *Dung Beetle Ecology* (Princeton Univ. Press, 1991). doi: [10.1515/9781400862092](https://doi.org/10.1515/9781400862092)
21. E. Nichols *et al.*, Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* **141**, 1461–1474 (2008). doi: [10.1016/j.biocon.2008.04.011](https://doi.org/10.1016/j.biocon.2008.04.011)
22. B. M. Doube, Ecosystem services provided by dung beetles in Australia. *Basic Appl. Ecol.* **26**, 35–49 (2018). doi: [10.1016/j.baee.2017.09.008](https://doi.org/10.1016/j.baee.2017.09.008)
23. J. E. Losey, M. Vaughan, The Economic Value of Ecological Services Provided by Insects. *Bioscience* **56**, 311 (2006). doi: [10.1641/0006-3568\(2006\)56\[311:TEVOES\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2)
24. S. A. Beynon, W. A. Wainwright, M. Christie, The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. *Ecol. Entomol.* **40**, 124–135 (2015). doi: [10.1111/een.12240](https://doi.org/10.1111/een.12240)
25. E. Nichols, T. A. Gardner, C. A. Peres, S. Spector, The Scarabaeinae Research Network, Co-declining mammals and dung beetles: An impending ecological cascade. *Oikos* **118**, 481–487 (2009).
26. E. H. Raine *et al.*, Extinctions of interactions: Quantifying a dung beetle–mammal network. *Ecosphere* **9**, e02491 (2018). doi: [10.1002/ecs2.2491](https://doi.org/10.1002/ecs2.2491)
27. A. H. Schweiger, J.-C. Svenning, Down-sizing of dung beetle assemblages over the last 53 000 years is consistent with a dominant effect of megafauna losses. *Oikos* **127**, 1243–1250 (2018). doi: [10.1111/oik.04995](https://doi.org/10.1111/oik.04995)

28. K. Frank *et al.*, Global dung webs: High trophic generalism of dung beetles along the latitudinal diversity gradient. *Ecol. Lett.* **21**, 1229–1236 (2018). doi: [10.1111/ele.13095](https://doi.org/10.1111/ele.13095); pmid: [29938888](https://pubmed.ncbi.nlm.nih.gov/29938888/)
29. D. Sanders, E. Thébault, R. Kehoe, F. J. Frank van Veen, Trophic redundancy reduces vulnerability to extinction cascades. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 2419–2424 (2018). doi: [10.1073/pnas.1716825115](https://doi.org/10.1073/pnas.1716825115); pmid: [29467292](https://pubmed.ncbi.nlm.nih.gov/29467292/)
30. L. Greenspoon *et al.*, The global biomass of wild mammals. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2204892120 (2023). doi: [10.1073/pnas.2204892120](https://doi.org/10.1073/pnas.2204892120); pmid: [36848563](https://pubmed.ncbi.nlm.nih.gov/36848563/)
31. T. H. Larsen, A. Lopera, A. Forsyth, Extreme Trophic and Habitat Specialization by Peruvian Dung Beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopt. Bull.* **60**, 315–324 (2006). doi: [10.1649/0010-065X\(2006\)60\[315:ETAHSB\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2006)60[315:ETAHSB]2.0.CO;2)
32. K. M. Pedersen, C. von Beeren, A. Oggioni, N. Blüthgen, Mammal dung-dung beetle trophic networks: An improved method based on gut-content DNA. *PeerJ* **12**, e16627 (2024). doi: [10.7717/peerj.16627](https://doi.org/10.7717/peerj.16627); pmid: [38500531](https://pubmed.ncbi.nlm.nih.gov/38500531/)
33. L. Dormont, G. Epinat, J.-P. Lumaret, Trophic Preferences Mediated by Olfactory Cues in Dung Beetles Colonizing Cattle and Horse Dung. *Environ. Entomol.* **33**, 370–377 (2004). doi: [10.1603/0046-225X-33.2.370](https://doi.org/10.1603/0046-225X-33.2.370)
34. N. Sathiandran, P. J. Vineesh, S. K. Thomas, Dung preference and trophic association of dung beetles (Coleoptera: Scarabaeidae) in the moist forests of the South-western Ghats of the Indian subcontinent. *J. Asia Pac. Entomol.* **24**, 739–748 (2021). doi: [10.1016/j.jaspen.2021.06.008](https://doi.org/10.1016/j.jaspen.2021.06.008)
35. S. B. Peck, H. F. Howden, Response of a Dung Beetle Guild to Different Sizes of Dung Bait in a Panamanian Rainforest. *Biotropica* **16**, 235 (1984). doi: [10.2307/2388057](https://doi.org/10.2307/2388057)
36. P. D. N. Hebert, E. H. Penton, J. M. Burns, D. H. Janzen, W. Hallwachs, Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astrates fulgerator*. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 14812–14817 (2004). doi: [10.1073/pnas.0406166101](https://doi.org/10.1073/pnas.0406166101); pmid: [15465915](https://pubmed.ncbi.nlm.nih.gov/15465915/)
37. K. J. Gaston, Global patterns in biodiversity. *Nature* **405**, 220–227 (2000). doi: [10.1038/35012228](https://doi.org/10.1038/35012228); pmid: [10821282](https://pubmed.ncbi.nlm.nih.gov/10821282/)
38. J. R. Goheen *et al.*, Conservation lessons from large-mammal manipulations in East African savannas: The KLEE, UHURU, and GLADE experiments. *Ann. N. Y. Acad. Sci.* **1429**, 31–49 (2018). doi: [10.1111/nyas.13848](https://doi.org/10.1111/nyas.13848); pmid: [29752729](https://pubmed.ncbi.nlm.nih.gov/29752729/)
39. M. I. E. Bassi, I. R. Stauda, Insects decline with host plants but coextinctions may be limited. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2417408121 (2024). doi: [10.1073/pnas.2417408121](https://doi.org/10.1073/pnas.2417408121); pmid: [39436666](https://pubmed.ncbi.nlm.nih.gov/39436666/)
40. F. Gijssman, “Coextinctions as a driver of biodiversity loss: the case of dung beetles in an African savanna,” thesis, Princeton University, Princeton, NJ (2025).
41. G. I. H. Kerley *et al.*, Diet shifts by adult flightless dung beetles *Circellium bacchus*, revealed using DNA metabarcoding, reflect complex life histories. *Oecologia* **188**, 107–115 (2018). doi: [10.1007/s00442-018-4203-6](https://doi.org/10.1007/s00442-018-4203-6); pmid: [29961180](https://pubmed.ncbi.nlm.nih.gov/29961180/)
42. F. Lopes *et al.*, Metagenomics reveals that dung beetles (Coleoptera: Scarabaeinae) broadly feed on reptile dung. Did they also feed on that of dinosaurs? *Front. Ecol. Evol.* **11**, 1132729 (2023). doi: [10.3389/fevo.2023.1132729](https://doi.org/10.3389/fevo.2023.1132729)
43. S. Jia *et al.*, Global signal of top-down control of terrestrial plant communities by herbivores. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 6237–6242 (2018). doi: [10.1073/pnas.1707984115](https://doi.org/10.1073/pnas.1707984115); pmid: [29848630](https://pubmed.ncbi.nlm.nih.gov/29848630/)
44. T. H. Larsen, A. Forsyth, Trap Spacing and Transect Design for Dung Beetle Biodiversity Studies I. *Biotropica* **37**, 322–325 (2005). doi: [10.1111/j.1744-7429.2005.00042.x](https://doi.org/10.1111/j.1744-7429.2005.00042.x)
45. P. G. da Silva, M. I. M. Hernández, Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PLOS ONE* **10**, e0126112 (2015). doi: [10.1371/journal.pone.0126112](https://doi.org/10.1371/journal.pone.0126112); pmid: [25938506](https://pubmed.ncbi.nlm.nih.gov/25938506/)
46. P. Ribeiro Anunciação *et al.*, Atlantic Dung Beetle Traits: A comprehensive dataset of functional traits for dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) in the Atlantic Forest. *Biodivers. Data J.* **13**, e170578 (2025). doi: [10.3897/BDJ.13.e170578](https://doi.org/10.3897/BDJ.13.e170578); pmid: [41262205](https://pubmed.ncbi.nlm.nih.gov/41262205/)
47. B. P. Tshikae, A. L. V. Davis, C. H. Scholtz, Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? *Ecol. Entomol.* **38**, 83–95 (2013). doi: [10.1111/j.1365-2311.2012.01409.x](https://doi.org/10.1111/j.1365-2311.2012.01409.x)
48. J. S. Pryke, F. Roets, M. J. Samways, Large African herbivore diversity is essential in transformed landscapes for conserving dung beetle diversity. *J. Appl. Ecol.* **59**, 1372–1382 (2022). doi: [10.1111/1365-2664.14152](https://doi.org/10.1111/1365-2664.14152)
49. R. Stanbrook-Buyer, M. Jones, C. P. Wheeler, Biotic and abiotic drivers of dung beetle assemblage structure in Kenyan Afromontane forest: Trees and elephants matter. *J. Trop. Ecol.* **41**, e11 (2025). doi: [10.1017/S0266467425000100](https://doi.org/10.1017/S0266467425000100)
50. D. H. M. Cumming *et al.*, Elephants, woodlands and biodiversity in southern Africa. *S. Afr. J. Sci.* **93**, 231–236 (1997).
51. N. Owen-Smith, Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* **13**, 351–362 (1987). doi: [10.1017/S0094837300008927](https://doi.org/10.1017/S0094837300008927)
52. M. E. Power *et al.*, Challenges in the Quest for Keystones. *Bioscience* **46**, 609–620 (1996). doi: [10.2307/1312990](https://doi.org/10.2307/1312990)
53. R. M. Pringle *et al.*, Impacts of large herbivores on terrestrial ecosystems. *Curr. Biol.* **33**, R584–R610 (2023). doi: [10.1016/j.cub.2023.04.024](https://doi.org/10.1016/j.cub.2023.04.024); pmid: [37279691](https://pubmed.ncbi.nlm.nih.gov/37279691/)
54. R. T. Paine, A Note on Trophic Complexity and Community Stability. *Am. Nat.* **103**, 91–93 (1969). doi: [10.1086/282586](https://doi.org/10.1086/282586)
55. I. Shukla, K. M. Gaynor, B. Worm, C. T. Darimont, The diversity of animals identified as keystone species. *Ecol. Evol.* **13**, e10561 (2023). doi: [10.1002/ece3.10561](https://doi.org/10.1002/ece3.10561); pmid: [37818247](https://pubmed.ncbi.nlm.nih.gov/37818247/)
56. E. Delmas *et al.*, Analysing ecological networks of species interactions. *Biol. Rev.* **94**, 16–36 (2019). doi: [10.1111/brev.12433](https://doi.org/10.1111/brev.12433); pmid: [29923657](https://pubmed.ncbi.nlm.nih.gov/29923657/)
57. U. Jacob *et al.*, “The Role of Body Size in Complex Food Webs” in *Advances in Ecological Research*. A. Belgrano, J. Reiss, eds. vol. 45 (Elsevier, 2011), pp. 181–223.
58. J. Damuth, Population density and body size in mammals. *Nature* **290**, 699–700 (1981). doi: [10.1038/290699a0](https://doi.org/10.1038/290699a0)
59. X. Lu *et al.*, Drought rewires the cores of food webs. *Nat. Clim. Chang.* **6**, 875–878 (2016). doi: [10.1038/nclimate3002](https://doi.org/10.1038/nclimate3002)
60. S. Timóteo, J. A. Ramos, I. P. Vaughan, J. Memmott, High Resilience of Seed Dispersal Webs Highlighted by the Experimental Removal of the Dominant Disperser. *Curr. Biol.* **26**, 910–915 (2016). doi: [10.1016/j.cub.2016.01.046](https://doi.org/10.1016/j.cub.2016.01.046); pmid: [26996503](https://pubmed.ncbi.nlm.nih.gov/26996503/)
61. U. Kryger, K. S. Coles, R. Tukker, C. H. Scholtz, Biology and ecology of *Circellium bacchus* (Fabricius 1781) (Coleoptera, Scarabaeidae), a South African dung beetle of conservation concern. *Trop. Zool.* **19**, 185–207 (2006).
62. P. Holter, C. H. Scholtz, Clarke. H. Scholtz, What do dung beetles eat? *Ecol. Entomol.* **32**, 690–697 (2007). doi: [10.1111/j.1365-2311.2007.00915.x](https://doi.org/10.1111/j.1365-2311.2007.00915.x)
63. S. P. Shukla, J. G. Sanders, M. J. Byrne, N. E. Pierce, Gut microbiota of dung beetles correspond to dietary specializations of adults and larvae. *Mol. Ecol.* **25**, 6092–6106 (2016). doi: [10.1111/mec.13901](https://doi.org/10.1111/mec.13901); pmid: [27801992](https://pubmed.ncbi.nlm.nih.gov/27801992/)
64. J. Sitters, M. Maechler, P. J. Edwards, W. Suter, H. Olde Venterink, Interactions between } C : N : P stoichiometry and soil macrofauna control dung decomposition of savanna herbivores. *Funct. Ecol.* **28**, 776–786 (2014). doi: [10.1111/1365-2435.12213](https://doi.org/10.1111/1365-2435.12213)
65. M. J. Chase *et al.*, Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* **4**, e2354 (2016). doi: [10.7717/peerj.2354](https://doi.org/10.7717/peerj.2354); pmid: [27635327](https://pubmed.ncbi.nlm.nih.gov/27635327/)
66. F.-T. Krell, S. Krell-Westerwalbesloh, One elephant may sustain 2 million dung beetles in East African savannas on any given day. *Naturwissenschaften* **111**, 5 (2024). doi: [10.1007/s00114-024-01894-9](https://doi.org/10.1007/s00114-024-01894-9); pmid: [38294560](https://pubmed.ncbi.nlm.nih.gov/38294560/)
67. S. L. Chown, C. H. Scholtz, C. J. Klok, F. J. Joubert, K. S. Coles, Ecophysiology, Range Contraction and Survival of a Geographically Restricted African Dung Beetle (Coleoptera: Scarabaeidae). *Funct. Ecol.* **9**, 30 (1995). doi: [10.2307/2390087](https://doi.org/10.2307/2390087)
68. H. U. J. Npenda, J. S. Pryke, F. Roets, Replacing native mammal assemblages with livestock in African savannas, impacts dung beetle diversity and reduces body size. *Biol. Conserv.* **260**, 109211 (2021). doi: [10.1016/j.biocon.2021.109211](https://doi.org/10.1016/j.biocon.2021.109211)
69. N. L. Gunter, T. A. Weir, A. Slipinski, L. Bocak, S. L. Cameron, If Dung Beetles (Scarabaeidae: Scarabaeinae) Arose in Association with Dinosaurs, Did They Also Suffer a Mass Co-Extinction at the K-Pg Boundary? *PLOS ONE* **11**, e0153570 (2016). doi: [10.1371/journal.pone.0153570](https://doi.org/10.1371/journal.pone.0153570); pmid: [27145126](https://pubmed.ncbi.nlm.nih.gov/27145126/)
70. S. E. Miller, Late Quaternary Insects of Rancho La Brea and McKittrick, California. *Quat. Res.* **20**, 90–104 (1983). doi: [10.1016/0033-5894\(83\)90067-4](https://doi.org/10.1016/0033-5894(83)90067-4)
71. M. Galetti *et al.*, Ecological and evolutionary legacy of megafauna extinctions. *Biol. Rev.* **93**, 845–862 (2018). doi: [10.1111/brev.12374](https://doi.org/10.1111/brev.12374); pmid: [28990321](https://pubmed.ncbi.nlm.nih.gov/28990321/)
72. L. Y. Chiew *et al.*, Tropical forest dung beetle-mammal dung interaction networks remain similar across an environmental disturbance gradient. *J. Anim. Ecol.* **91**, 604–617 (2022). pmid: [34954816](https://pubmed.ncbi.nlm.nih.gov/34954816/)
73. T. H. Larsen, N. M. Williams, C. Kremen, Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* **8**, 538–547 (2005). doi: [10.1111/j.1461-0248.2005.00749.x](https://doi.org/10.1111/j.1461-0248.2005.00749.x); pmid: [21352458](https://pubmed.ncbi.nlm.nih.gov/21352458/)
74. F. Gijssman, S. E. Miller, R. M. Pringle, A DNA reference library of dung beetles at the Mpala Research Centre, Barcode of Life Data Systems (BOLD SYSTEMS) (2024); <https://portal.boldsystems.org/recordset/DS-MRCDBREF>
75. F. Gijssman *et al.*, Importance of megaherbivores for dung beetle biodiversity and ecosystem functions, Dryad (2026); <https://doi.org/10.5061/dryad.9p8cz8wwn>.
76. Materials and methods are available in the supplementary materials.

ACKNOWLEDGMENTS

We thank Mpala Research Centre; the International Centre of Insect Physiology and Ecology; the Canadian Center for DNA Barcoding; and the Republic of Kenya and its National Museums, Wildlife Service, National Environment Management Authority, Wildlife Research Training Institute, and National Commission for Science, Technology and Innovation (permits NACOSTI P2325384; NEMA AGR1722023; WRTI 03500823). We thank the communities of Koija and Lekiji for allowing our surveys; F. Erii, J. Ekeno, S. Kurukura, and R. Kumar for assistance; M. Mutua, L. Njoroge, R. Gordon, A.L.V. Davis, J. DeWaard, and T. Simoes for taxonomic insights; D. Corcoran, J. Pansu, J. DeWaard, A. Jacobsen, and D. Yu for technical advice; and J. Abraham, E. Phillips, H. Watson, the Pringle lab, C. Tarnita, and three peer reviewers for feedback. **Funding:** This work was supported by the following: US National Science Foundation: 1355122, 1457697, 1656527, 2225088, 2303836 (to R.M.P.); US National Science Foundation: 1547679, 1930763, 2018405, 2132265 (to J.R.G.); Mohammed bin Zayed Species Conservation Fund: 212525091 (to F.G.); Rufford Foundation: 38617-1 (to F.G.); American Philosophical Society (to F.G.); Society of Systematic Biologists (to F.G.); High Meadows Environmental Institute at Princeton University: Mary & Randall Hack '69 Award (to F.G.); Currie C. and Thomas A. Barron Biodiversity Challenge (to R.M.P.); Carbon Mitigation Initiative (to R.M.P.); Princeton Institute for International Relations (to F.G.); Smithsonian Institute Barcode Network (to F.G. and S.E.M.); Natural Sciences and Engineering Research Council: Research Tools and Instruments (to J.R.G.); University of Wyoming (to J.R.G.); Iowa State University (to J.R.G.); Collegium Helveticum: Senior Fellowship (to R.M.P.);

John Simon Guggenheim Memorial Foundation: Guggenheim Fellowship (to R.M.P.).
Author contributions: Conceptualization: F.G. and R.M.P. Methodology: F.G., J.R.G., T.M.P., and R.M.P. Investigation: F.G., C.M.N., F.L.O.O., F.M.K., S.E.M., and R.M.P. Formal analysis: F.G., M.C.H., and R.M.P. Visualization and data presentation: F.G. and R.M.P. Funding acquisition: F.G., J.R.G., R.M.P., and S.E.M. Project administration: F.G. and R.M.P. Supervision: R.M.P. Writing – original draft: F.G. and R.M.P. Writing – review & editing: F.G., F.M.K., F.L.O.O., M.C.H., C.M.N., T.M.P., J.R.G., S.E.M., and R.M.P. **Competing interests:** The authors declare that they have no competing interests. **Data, code, and materials availability:** DNA sequences are in BOLD (74) and GenBank. Accession numbers and the data and code to reproduce all analyses are on Dryad (75). No new materials were created in this study. **License information:** Copyright © 2026 the authors, some rights

reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/content/page/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.aeb7062](https://doi.org/10.1126/science.aeb7062)
Materials and Methods; Figs. S1 to S12; Tables S1 to S16; References (77–108); Reproducibility Checklist
Submitted 22 August 2025; accepted 17 April 2026

10.1126/science.aeb7062



Importance of elephants for dung beetle biodiversity and ecosystem functions

Finote Gijssman, Ciara M. Nutter, Fathiya M. Khamis, Fidelis L. O. Ombura, Matthew C. Hutchinson, Todd M. Palmer, Jacob R. Goheen, Scott E. Miller, and Robert M. Pringle

Science **392** (6801), eaeb7062. DOI: 10.1126/science.aeb7062

Editor's summary

Large mammalian herbivores play key roles in ecosystems and are vulnerable to extinction from hunting and global environmental change. Loss of such species is expected to cause further extinctions, but this pattern has mainly been shown through simulations. Gijssman *et al.* combined simulations with experimental evidence to show that loss of elephants would lead to coextinctions of dung beetles and decreases in the dung decomposition and secondary seed dispersal that beetles provide (see the Perspective by Lewis and Slade). In the field, excluding elephants reduced dung beetle abundance and diversity, whereas excluding other mammalian herbivores had little additional effect. These results aligned with the central role of elephants in an empirically derived ecological network and support the designation of elephants as a keystone species in African savannas. —Bianca Lopez

View the article online

<https://www.science.org/doi/10.1126/science.aeb7062>

Permissions

<https://www.science.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of service](#)

Science (ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.

Copyright © 2026 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works