

# Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey

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Mutualisms often define ecosystems, but they are susceptible to human activities. Combining experiments, animal tracking, and mortality investigations, we show that the invasive big-headed ant (*Pheidole megacephala*) makes lions (*Panthera leo*) less effective at killing their primary prey, plains zebra (*Equus quagga*). Big-headed ants disrupted the mutualism between native ants (*Crematogaster* spp.) and the dominant whistling-thorn tree (*Vachellia drepanolobium*), rendering trees vulnerable to elephant (*Loxodonta africana*) browsing and resulting in landscapes with higher visibility. Although zebra kills were significantly less likely to occur in higher-visibility, invaded areas, lion numbers did not decline since the onset of the invasion, likely because of prey-switching to African buffalo (*Syncerus caffer*). We show that by controlling biophysical structure across landscapes, a tiny invader reconfigured predator-prey dynamics among iconic species.

**M**utualisms are among the most widespread and economically important species interactions, creating and maintaining terrestrial, aquatic, and marine ecosystems (1, 2). Because virtually every species on Earth participates in one or more mutualisms, their disruption can erode biodiversity through a combination of the direct loss of species, altered flows of mass and energy through ecological communities, and the inhibition of evolutionary trajectories (3). Although the loss of mutualisms is a global phenomenon (3), empirical studies linking mutualism disruption to broader community dynamics, particularly those across expansive areas, remain scarce.

The potential for mutualism disruption to reverberate across entire landscapes is especially strong when mutualism underpins the persistence of foundation species, i.e., spatially dominant and highly connected species within ecological networks that can amplify diversity and modulate critical ecosystem processes (4–6). Mutualisms involving these foundation species (or “foundational mutualisms”) create and maintain habitats through biophysical structure [e.g.,

corals and their dinoflagellate associates (7), seagrasses and sulfide-oxidizing lucinid bivalves (8), and whistling-thorn trees (*Vachellia drepanolobium*) and their protective ant associates (9)]. As such, foundational mutualisms may modify species interactions through nontrophic pathways; for example, by generating refugia for competitors or prey species and cover or vantage points for predators. In the aftermath of disrupted foundational mutualisms, shifts in trophic dynamics may occur where biophysical structure shapes the frequency and outcomes of encounters among predators and their prey. Within such systems, spatially structured interactions, encompassing landscapes of fear (in which spatial variation in predation risk affects prey distributions) (10, 11), predator-prey shell games (in which predators attempt to anticipate locations of prey, and prey respond by attempting to be spatially unpredictable) (12), and competition (13), should hinge on foundation species, and thus on foundational mutualisms.

## Effects of ant invasion on defenses of a foundation tree

Across tens of thousands to hundreds of thousands of square kilometers in East Africa (14, 15), the foundational whistling-thorn tree forms near-monocultures, comprising >70% (and often 98 to 99%) of woody stems where it occurs (9, 16) (Figs. 1 and 2A). The whistling-thorn tree is a myrmecophyte, providing food (extrafloral nectar) and shelter (swollen-thorn domatia) in exchange for defense by a guild of native acacia ants (*Crematogaster* spp.) (17). Protection by acacia ants is particularly effective at deterring lethal herbivory by elephants (*Loxodonta africana*), thereby stabilizing savanna tree cover across entire landscapes (9). Over the past two decades, invasion of the big-

headed ant (*Pheidole megacephala*), thought to originate from an island in the Indian Ocean, has disrupted this foundational mutualism in Laikipia, Kenya (18). Where big-headed ants encounter whistling-thorn trees, they numerically overwhelm and completely exterminate *Crematogaster* spp. ants, killing adult ants and consuming eggs, larvae, and pupae (18). However, big-headed ants do not protect whistling-thorn trees from herbivory, thus increasing the vulnerability of invaded trees to browsing by elephants. Consequently, in invaded areas, elephants browse and break trees at five to seven times the rate of that in uninvaded areas (18) (Figs. 1 and 2B).

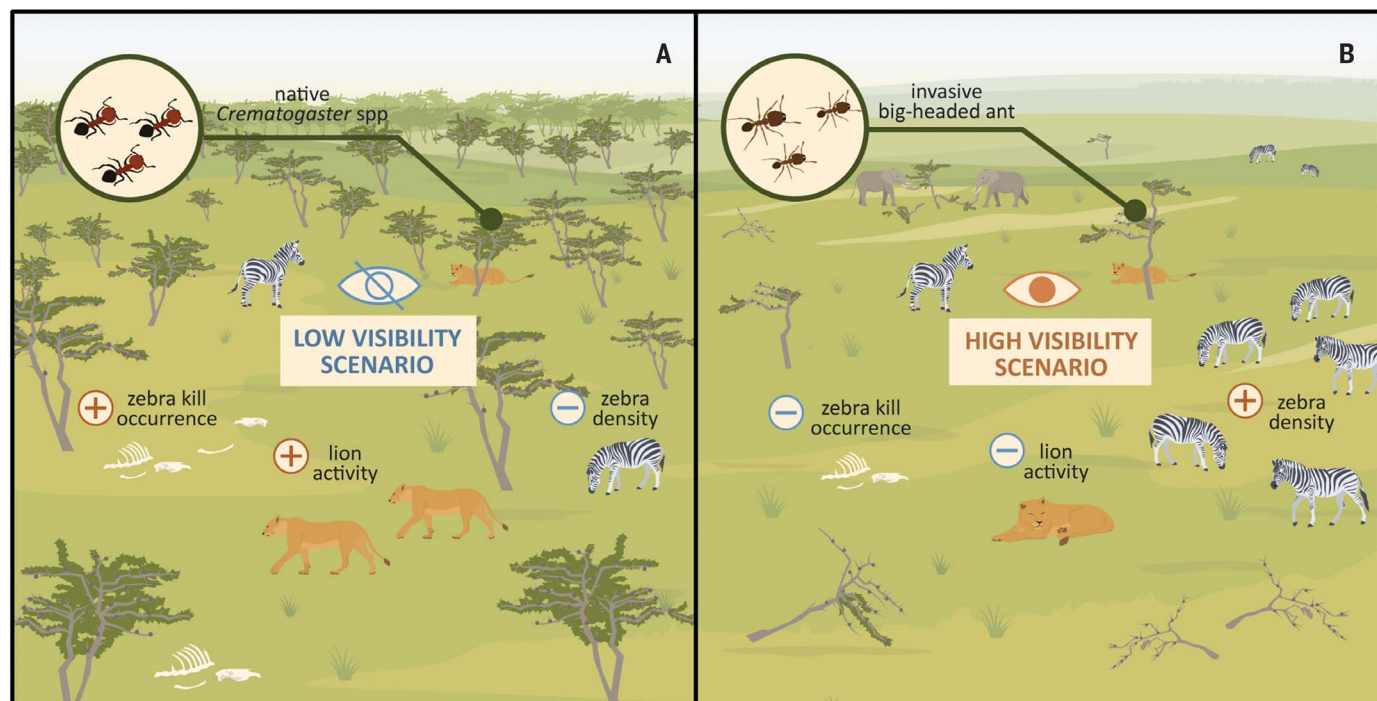
We hypothesized that disruption of this foundational ant-tree mutualism would affect interactions between lions (*Panthera leo*) and their most common prey, plains zebra (hereafter referred to as “zebra”; *Equus quagga*). Zebra are unselective grazers (19) that require large volumes of grass to meet their nutritional needs, and they comprise around 50% of wild ungulates killed by lions on Ol Pejeta Conservancy in Laikipia (figs. S1 and S2). We tested two predictions regarding lion-zebra dynamics and mutualism disruption by means of big-headed ant invasion (Fig. 1): (i) Big-headed ant invasion increases browsing by elephants, thereby generating greater visibility or “openness” relative to uninvaded areas, and (ii) greater visibility, mediated by big-headed ant invasion, shapes interactions between lions and zebra through some combination of increased selection for visibility by zebra (if zebra choose habitats on the basis of perceived safety) (20), avoidance of increased visibility by lions (if lions choose habitats on the basis of prey accessibility) (21), or a reduction in the hiding cover necessary for lions to hunt successfully (22). Additionally, we sought to quantify whether and how any changes in the catchability of zebra triggered by big-headed ant invasion manifested as changes in lion population size through time.

## Effects of mutualism disruption on savanna openness

To test our first prediction, we measured differences in visibility across a 364-km<sup>2</sup> landscape that varied in both tree cover and in the occurrence of big-headed ants. We measured visibility associated within three blocks of four replicated 2500-m<sup>2</sup> plots (fig. S1A). For each replicate block, a pair of plots was established on each side of a big-headed ant invasion front; one plot in each pair experimentally excluded “megaherbivores” [elephants, giraffes (*Giraffa camelopardalis*), and rhinoceros (*Diceros bicornis* and *Cerotherium simum*)] with electrified fencing. Big-headed ant invasion fronts advance ~50 m per year (23). Therefore, we established “uninvaded” plots 0.5 to 2.5 km in front of invasion fronts (fig. S1, A and B) to ensure that uninvaded plots would not be

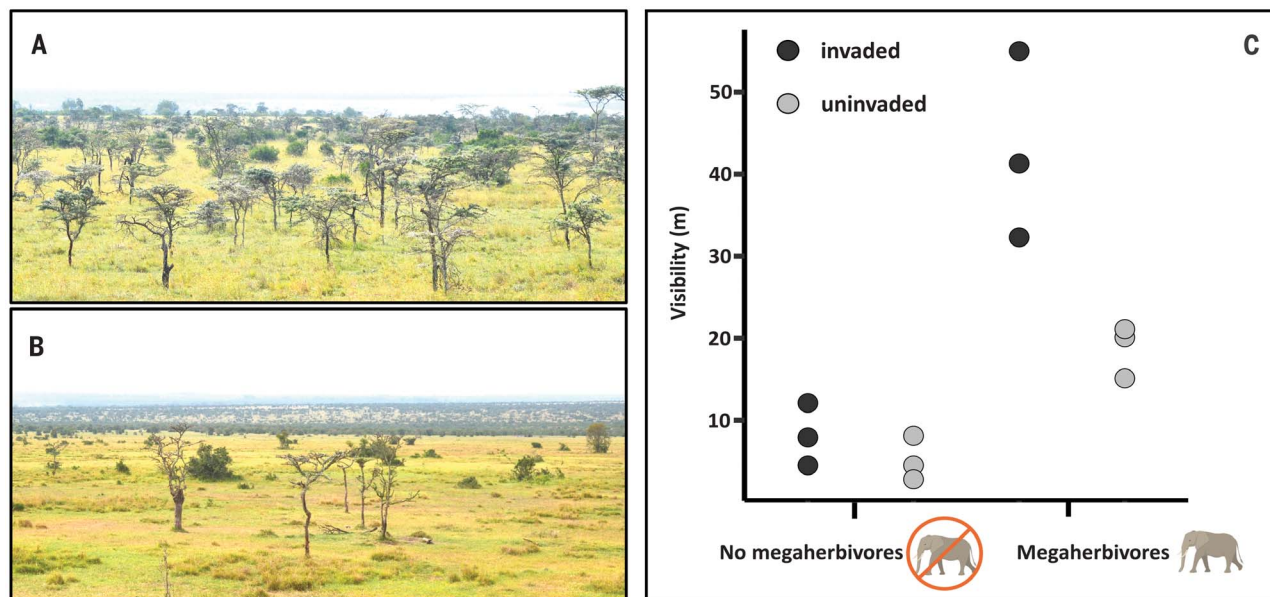
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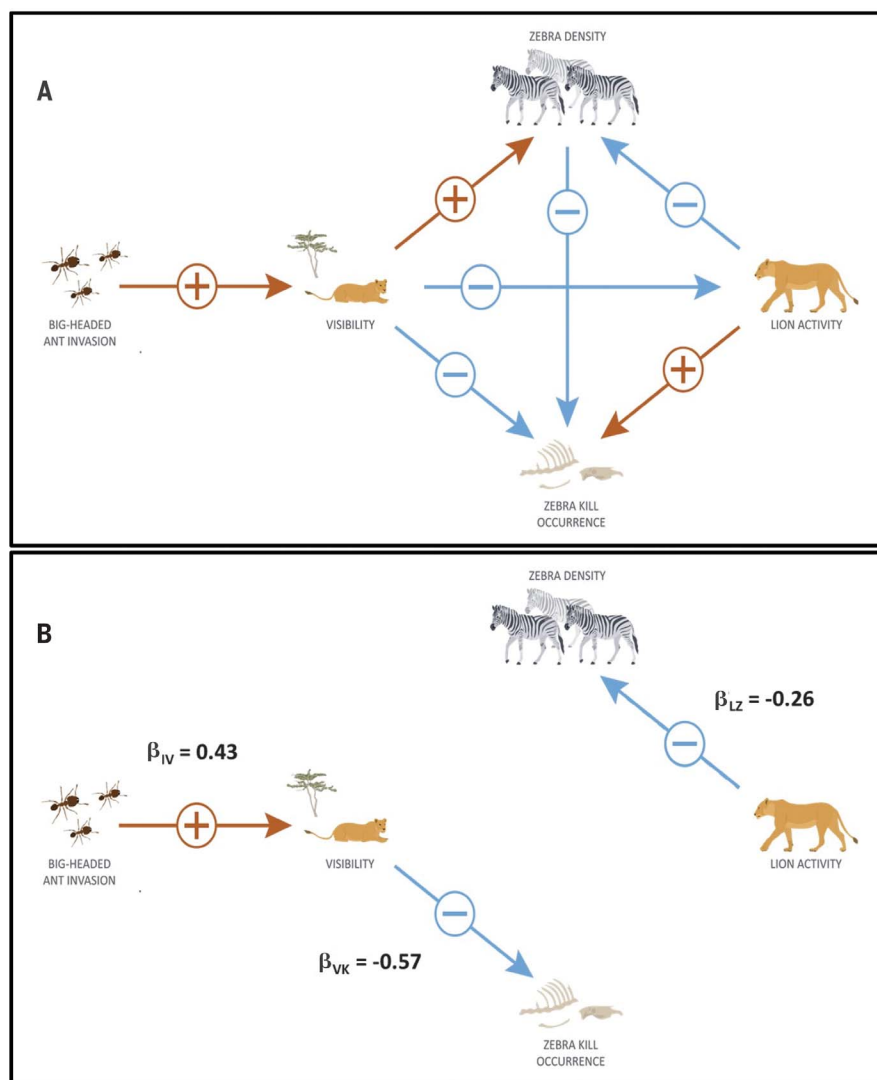


**Fig. 1. Illustrated predictions by which disruption of the foundational ant-plant mutualism shapes spatial patterns of lion predation.** (A) In uninvaded whistling-thorn tree savanna, native acacia ants defend whistling-thorn trees against browsing by elephants, such that tree density is high and visibility is low. In turn, lower visibility is predicted to be associated with zebra kills through some combination of reduced zebra density (if lower densities increase risk of predation via delayed detection of lions), increased lion activity (if lions are more active in denser stands of whistling-thorn trees), and increased hunting success of lions (if hunting success is predicated on the hiding cover afforded

by whistling-thorn trees). (B) In invaded whistling-thorn tree savanna, big-headed ants kill acacia ants, rendering trees vulnerable to browsing by elephants and resulting in higher visibility. Higher visibility is predicted to be associated with reduced occurrence of zebra kills through some combination of increased zebra density (if lower densities increase risk of predation through delayed detection of lions), reduced lion activity (if lions are more active in denser stands of whistling-thorn trees), and reduced hunting success of lions (if hunting success is predicated on the hiding cover afforded by whistling-thorn trees).



**Fig. 2. Big-headed ant invasion increases visibility.** (A) An uninvaded whistling-thorn tree savanna. (B) An invaded landscape in which elephants have browsed, broken, and killed whistling-thorn trees. (C) After a 3-year period in open (unfenced) plots accessible to megaherbivores, visibility was 2.67 times higher in plots invaded by big-headed ants relative to uninvaded plots accessible to megaherbivores (two-way ANOVA invasion-megaherbivore interaction:  $F_{1,8} = 8.14$ ,  $P = 0.02$ ).



**Fig. 3. Zebra kill occurrence is reduced in areas invaded by big-headed ants because of heightened visibility stemming from disruption of the foundational mutualism. (A)** The full model depicting hypothesized relationships among big-headed ant invasion, visibility, zebra density, lion activity, and zebra kill occurrence. Orange and blue arrows represent hypothesized positive and negative effects among variables, respectively. Within this full model, 21 paths were nested and evaluated using *d*-separation and subsequent model selection (figs. S8 and S9 and tables S8 and S9). **(B)** The best-supported nested path model (nested path model 17) is illustrated. This model was statistically indistinguishable (i.e., within 2 AIC<sub>c</sub> units) from nested path models 19 and 9, each of which contained an additional linkage from zebra density to zebra kill occurrence (tables S8 and S9). In both cases, and contrary to our inferred hypothesis, the path coefficient for zebra density to zebra kill occurrence was positive, although its 95% confidence limits for both nested path models 19 and 9 encompassed zero. Similarly, nested path model 9 contained an additional linkage from lion activity to zebra kill occurrence, but the 95% confidence limits on this path coefficient encompassed zero. Confidence limits for path coefficients for each linkage in nested path model 17 did not encompass zero (big-headed ant invasion and visibility: unstandardized  $\beta_{IV} = 13.45 \pm 2.75$  SE; visibility and zebra kill occurrence: unstandardized  $\beta_{VK} = -0.09 \pm 0.02$  SE; lion activity and zebra density: unstandardized  $\beta_{LZ} = -1.07 \pm 0.39$  SE). Standardized  $\beta$  coefficients are reported next to each arrow.

invaded during our 3-year study. Over the course of our experiment, changes in tree cover could arise in two ways. First, and within megaherbivore exclusion (fenced) plots, any differences relative to baseline conditions (i.e., those from uninvaded, open plots in 2017) would

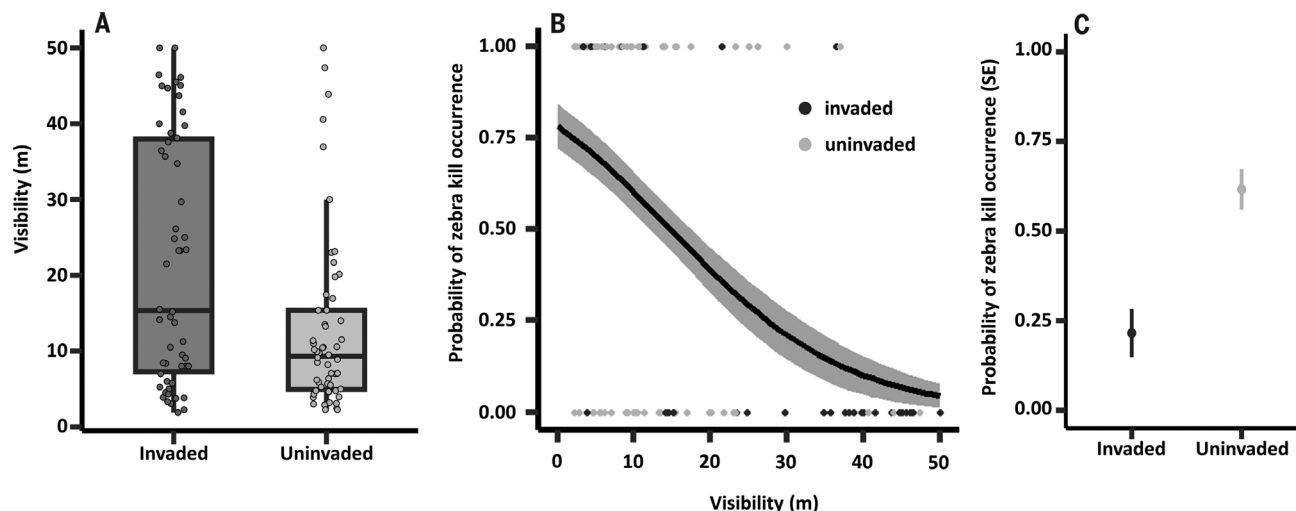
reflect differences in tree growth and survival in the absence of megaherbivores for both invaded and uninvaded areas (24). Second, within open (unfenced) plots, megaherbivore browsing (which we predicted would be higher in invaded areas) would reduce tree growth

and survival (24). We expected both processes in tandem to result in the highest visibility within invaded, open plots and the lowest visibility within megaherbivore exclusion plots (regardless of invasion status), with intermediate visibility within uninvaded, open plots. We attributed differences in visibility caused by megaherbivore exclusion and big-headed ant invasion to elephant browsing (as opposed to other megaherbivores) for the following reasons: (i) Acacia ants are especially effective at deterring browsing by elephants, such that browsing rates increase by nearly an order of magnitude on branches from which acacia ants have been experimentally removed (9); (ii) elephants are singular in their ability to promote visibility by breaking and knocking over adult trees; and (iii) elephants comprise around 60 to 70% of the biomass density of megaherbivores at Ol Pejeta Conservancy and in Laikipia, more generally (25). In open plots, big-headed ant invasion was associated with 2.67 times higher visibility after 3 years (uninvaded, open mean =  $18.06 \text{ m} \pm 3.00$  SE; invaded, open mean =  $48.17 \text{ m} \pm 6.80$  SE) (Fig. 2C). By contrast, visibility did not differ as a function of big-headed ant invasion for megaherbivore exclusion plots (Fig. 2C). Relative to uninvaded, open plots (reflecting baseline conditions of a “natural” savanna), changes in visibility were driven by a combination of greater growth and survival of trees within megaherbivore exclusion plots, and reduced growth and survival of trees in invaded, open plots (fig. S3 and tables S1 and S2). Thus, big-headed ant invasion rendered whistling-thorn trees largely defenseless against elephants, leading to higher browsing rates and more open landscapes characterized by higher visibility (Fig. 2).

### Savanna openness and predation risk to zebra

Testing our second prediction entailed quantifying zebra density, lion activity, big-headed ant occurrence, and visibility at zebra kills. To quantify zebra density, we built time-varying, spatially explicit density surfaces from resource selection functions to measure habitat selection and population density of zebra (26). We incorporated three habitat features into these resource selection functions: glades (nutrient-rich lawns arising from old livestock corrals), water sources, and human settlements (in the event that zebra selected for such settlements as protection against lions; i.e., the “human shield” hypothesis) (27), in addition to a distance to glade–distance to water source interaction. To quantify lion activity, we captured and fit GPS collars to six lionesses from distinct prides representing approximately 50 adult individuals and 30 cubs (or 95% of the lions at our study site) (26). In Laikipia, lions form cohesive groups, such that movements of a single lioness are representative of pride-level movements (28, 29). Estimates of zebra density and





**Fig. 4. Pairwise relationships underlying zebra kill occurrence from the best-supported nested path model. (A)** Visibility and big-headed ant invasion, **(B)** probability of zebra kill occurrence and visibility, and **(C)** predicted probability of zebra kill occurrence by invasion status. The shading in (B) indicates 95% confidence limits. Visibility was higher in areas invaded by big-headed ants, and

probability of zebra kill occurrence was lower where visibility was higher. At the median level of visibility for invaded (29.69 m) versus uninvaded (9.31 m) whistling-thorn tree savanna, the probability of zebra kill occurrence was 2.87 times higher in uninvaded than in invaded savanna ( $0.62 \pm 0.06$  SE versus  $0.22 \pm 0.07$  SE).

lion activity were then incorporated with visibility as predictors of kill occurrence. Within nested path models, visibility was modeled as an outcome of big-headed ant invasion and as a predictor of kill occurrence, zebra density, and lion activity (Fig. 3A).

To quantify big-headed ant occurrence and visibility at zebra kills, we first assessed spatial variation in the distribution of lion-killed zebra using a clustering algorithm from GPS-collared lions (26). Because lions at our study site and elsewhere in East Africa ambush their prey (as opposed to chasing them over long distances) (21, 22), the locations of kills are reasonable proxies for locations of successful hunts (29). Within whistling-thorn tree savanna, we identified 55 zebra kill sites by investigating GPS “clusters,” which are defined as  $\geq 2$  successive GPS relocations occurring within 100 m of each other (given that pride members feed together at kills, we were able to identify kill sites from the movement patterns of telemetered individuals, even if they did not make the kill themselves) (29). Within 5 to 10 days, we visually confirmed the prey species at each GPS cluster (26). At each zebra kill site, we collected data on visibility and the presence of big-headed ants (26), as well as estimated zebra density (from resource selection function-derived density estimates; fig. S4) and lion activity (from telemetry-derived utilization distributions; fig. S6). Across the broader landscape, patterns of visibility mirrored our experimental results, such that the visibility of invaded locations was  $13.45 \text{ m} \pm 2.75$  SE greater than that of uninvaded locations (Fig. 4A).

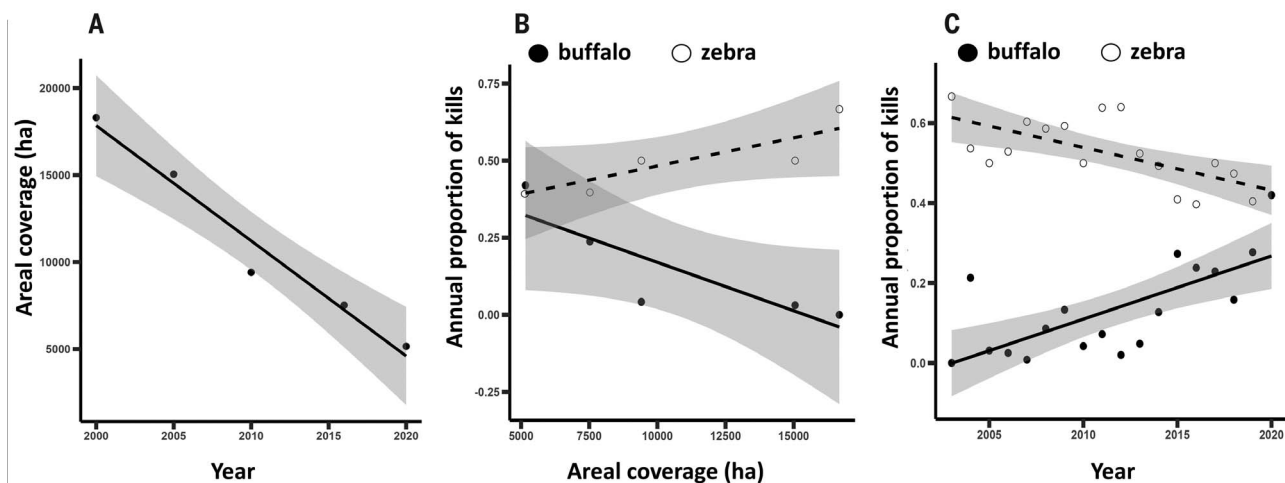
We expected zebra to aggregate in high-visibility areas, including areas invaded by big-

headed ants and other openings in the tree layer. Further, lion activity is known to be correlated with tree cover (or visibility) in our study system and elsewhere (21, 22, 29). Thus, several potential predictors (big-headed ant invasion, visibility, zebra density, and lion activity) of predation risk to zebra were correlated, making it challenging to test whether big-headed ants were associated with safety for zebra. Similarly, both density of whistling-thorn trees (and thus, visibility) and zebra density can vary because of a whole host of environmental variables (30–32), making it difficult to attribute changes in visibility solely to big-headed ants.

To test whether and how big-headed ant invasion shifted spatial variation in lion predation of zebra, we conducted nested path analysis (33, 34). We tested 21 path models nested within our full model (Fig. 3A), representing a series of ecological linkages by which increased visibility could shift spatial variation in predation risk to zebra (figs. S8 and S9 and table S8). Nested path models represented different combinations of relationships among big-headed ant invasion, visibility, zebra density, and lion activity, as well as the influence of such relationships on zebra kill occurrence. We did not attempt to formulate and test an exhaustive set of nested path models within the full model; rather, our nested path models were based on our inferred understanding of this ecosystem. Our nested path analysis provided a test of our second prediction: that greater visibility, mediated by big-headed ant invasion, shapes the spatial distribution of lion-killed zebra.

Of the 21 path models nested within our full model, Fisher’s C (a combined test of condi-

tional independence among linkages in nested path models) (33) revealed that 14 were statistically viable, with correlation structures that represented the observed data (fig. S8 and table S8). The correlation structure proposed through seven nested path models (models 2, 5, 6, 8, 13, 14, and 16) differed from the observed data; each of these models included a linkage from visibility to zebra density, did not include a linkage from big-headed ant invasion to visibility, or both (fig. S8 and table S8). Through a model selection procedure on the remaining 15 path models (14 nested path models, plus the full model), there was statistical support for the hypothesis that big-headed ant invasion reduced the occurrence of zebra kills by increasing the visibility of lions to their prey (nested path models 17, 19, and 9) (Fig. 3 and tables S8 and S9) (26). Each of these three nested path models included linkages from big-headed ant invasion to visibility (Fig. 4A), from visibility to zebra kill occurrence (Fig. 4B), and from lion activity to zebra density, with path coefficients whose 95% confidence limits did not encompass zero for each linkage (Fig. 3B and table S9). Consequently, zebra kill occurrence was 2.87 times higher in uninvaded areas relative to areas invaded by big-headed ants (Fig. 4C). Nested path models 19 and 9 also included a linkage from zebra density to zebra kill occurrence, and nested path model 9 included a linkage from lion activity to zebra kill occurrence, but the 95% confidence limits for path coefficients from these linkages encompassed zero (Fig. 3B and table S9). Of the 10 remaining viable nested path models, those that did not include a linkage from big-headed ant invasion to visibility were  $>19$  Akaike’s information



**Fig. 5. Over 18 years, lion diets shifted toward buffalo as whistling-thorn tree cover declined.** (A) Since the onset of big-headed ant invasion, areal coverage of habitats classified as whistling-thorn monoculture (in which >98% of stems were whistling-thorn trees) or whistling-thorn dominant (in which whistling-thorn trees were the most common woody species) (26) declined through time ( $R^2 = 0.86$ ,  $P < 0.01$ ). (B) The annual proportion of kills made by lions that were zebra tended to increase with increasing whistling-thorn tree cover in each of 5 years (2000, 2005, 2010, 2016, and 2020;  $R^2 = 0.72$ ,  $P = 0.07$ ), and the annual proportion of kills made by lions that were buffalo tended to decline

with increasing whistling-thorn tree cover in the same 5 years ( $R^2 = 0.74$ ,  $P = 0.06$ ). For each relationship, areal coverage of whistling-thorn trees in 2003 was calculated as the midpoint of whistling-thorn tree coverage in 2000 and in 2005. (C) From 2003 to 2020, the annual proportion of kills made by lions that were zebra declined from 67 to 42% ( $R^2 = 0.42$ ,  $P < 0.01$ ), whereas the annual proportion of kills made by lions that were buffalo increased from 0 to 42% ( $R^2 = 0.47$ ,  $P < 0.001$ ). The shading on all panels represents 95% confidence limits. Kill proportions were calculated from kills discovered opportunistically by antipoaching patrols at Ol Pejeta Conservancy from 2003 to 2020 (fig. S2).

criterion (AIC) points higher than the best-supported model (table S8).

#### Can lions compensate for less-catchable zebra?

Invasion by big-headed ants is ongoing in Laikipia. Big-headed ants continue to expand at approximately 50 m per year (23), a rate comparable to that of other invasive ants (35). Although mutualism disruption shaped the spatial distribution of lion predation, we cannot know the extent to which lions will respond as big-headed ants continue to expand across this region. We consider two scenarios by which lions might compensate in a landscape with increasingly less-catchable zebra.

First, and by promoting visibility, big-headed ants may reduce the catchability of zebra in invaded areas, but not reduce the overall rate at which zebra are killed. This scenario requires that lions concentrate their hunting activity in uninvaded portions of their home ranges, an expectation that is not supported by our data. Mean lion activity was statistically indistinguishable between invaded and uninvaded areas (fig. S10). Further, the number of adult and subadult lions at Ol Pejeta Conservancy ( $53.31 \pm 2.64$  SE) has remained remarkably stable for the 13 years that it has been monitored (26), implying that this population is at or near carrying capacity (consistent with results from other fenced reserves across sub-Saharan Africa) (36). Taken together, this strongly suggests that lions are persisting despite losing habitat in which they can efficiently kill zebra.

The second scenario entails a functional response by lions, through which big-headed ant invasion leads to prey switching toward more catchable or energetically rewarding prey (37). Given that the distribution of big-headed ants is not at equilibrium on Ol Pejeta Conservancy, the progression of time since their introduction to Laikipia (estimated to be in the early 2000s) (18) should be a reasonable proxy for the area occupied and any corresponding impacts on zebra catchability. From 2000 to 2020, areal coverage of whistling-thorn trees declined (Fig. 5A), and whistling-thorn cover was marginally correlated with the proportion of lion kills that were zebra versus buffalo (*Synceus caffer*, the second most commonly killed wild ungulate) (Fig. 5B) (26). From 2003 to 2020, the proportion of kills made by lions that were zebra declined from 67 to 42%, whereas the proportion of kills that were buffalo increased from 0 to 42% (Fig. 5C) (26). There were no directional changes in zebra or buffalo densities from 2014 to 2020 (no data were available on zebra or buffalo densities prior to 2014) (fig. S11).

#### Redirected trophic flows following mutualism disruption

Our results show that interactions between lions and their primary prey, the plains zebra, are mediated by a foundational ant-plant mutualism. Lions and other large carnivores use tree cover to conceal themselves, such that their success in hunting plains zebra was higher where visibility was lower (11, 21). By disrupting the foundational mutualism between whistling-

thorn trees and native acacia ants, invasion by big-headed ants renders trees more vulnerable to browsing by elephants, thereby reducing tree cover and increasing visibility. Contrary to our expectation, we found no evidence that higher visibility triggered by big-headed ant invasion changed zebra density, and zebra density itself was a weak predictor of zebra kill occurrence. Similarly, there was no evidence for a linkage between increased visibility and lion activity. Instead, big-headed ant invasion reduced the occurrence of zebra kills by increasing openness across the landscape, thereby limiting the frequency with which lions killed zebra.

Confronted with declining numbers or catchability of preferred prey, prey switching has long been recognized as theoretical basis for stabilizing populations (38). Yet, empirical evidence for prey switching among large mammals is scant, perhaps because prey are not uniformly vulnerable to predation (39). Dangerous prey tend to be avoided by predators, even when populations of preferred prey decline (40). Elsewhere in East Africa, larger groups (i.e., subsets of prides involved in hunts) of lions are required to kill buffalo, and male lions are significantly more likely to participate in buffalo kills than those of zebra (41, 42), although large groups of lions still prefer zebra when zebra are abundant (perhaps to reduce injuries during hunts) (42, 43). Although the invasion of big-headed ants has shaped the spatial distribution of zebra kills, and the frequency of zebra kills has declined over time, prey switching by lions to more formidable prey seems to

have (thus far) prevented any cascading effects on lion numbers. The role of behavioral adjustments (i.e., size and composition of hunting groups) in underlying the population stability of lions, plus the degree to which such stability can be maintained as big-headed ants advance across the landscape, remain open questions for future investigation.

Foundational mutualisms structure some of the most iconic environments on Earth, including coral reefs, kelp forests, and, as evidenced in this work, African savannas (7–9, 44, 45). When such mutualisms are disrupted, their effects can reverberate across landscapes, to the detriment of some species and to the benefit of others. We show that the spread of the big-headed ant, one of the globe's most widespread and ecologically impactful invaders (35, 46), has sparked an ecological chain reaction that reduces the success by which lions can hunt their primary prey. The disruption of foundational mutualisms could be an underappreciated contributor to predator-prey dynamics and trophic restructuring of the world's ecosystems.

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