xylem sap were high under N-starved conditions but lower under N-rich conditions.

Altogether, the available evidence from molecular and physiological analyses of CEP–CEPR ligand receptor pairs suggests that CEP acts as a root-derived ascending N-demand signal to the shoot, where its perception by CEPR leads to the production of a putative shoot-derived descending signal that up-regulates nitrate transporter genes in the roots. This mechanism supports N acquisition, especially when NO_3^- is unevenly distributed within the soil. CEP family peptides induced on one side of the roots by local N starvation mediate up-regulation of nitrate transporter genes in the distant part of the roots exposed to N-rich conditions to compensate for N deficiency.

The systemic mode of action of CEP family peptides in N-demand signaling is reminiscent of that of *Rhizobium*-induced, xylem-mobile CLE peptides that suppress excess nodulation in legume plants, although CEP plays a role opposite to that of CLE in terms of lateral organ formation (*5, 12, 13*). Plants, as sessile organisms, continuously face a complex array of environmental fluctuations and have evolved sophisticated responses to cope with them. Given that CEP family peptides are conserved throughout vascular plants except for ferns (*8, 9*), peptide-mediated root-to-shoot-to-root long-distance signaling is likely to be a general strategy employed by all higher plants for environmental adaptation.

REFERENCES AND NOTES

1. B. G. Forde, *Annu. Rev. Plant Biol.* **53**, 203–224 (2002).
2. X. Gansel, S. Muños, P. Tillard, A. Gojon, *Plant J.* **26**, 143–155 (2001).
3. S. Ruffel *et al.*, *Plant Physiol.* **146**, 2020–2035 (2008).
4. S. Ruffel *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 18524–18529 (2011).
5. D. E. Reid, B. J. Ferguson, S. Hayashi, Y. H. Lin, P. M. Gresshoff, *Ann. Bot. (Lond.)* **108**, 789–795 (2011).
6. Y. Matsubayashi, *Annu. Rev. Plant Biol.* **65**, 385–413 (2014).
7. K. Ohyama, M. Ogawa, Y. Matsubayashi, *Plant J.* **55**, 152–160 (2008).
8. I. Roberts *et al.*, *J. Exp. Bot.* **64**, 5371–5381 (2013).
9. C. Delay, N. Imin, M. A. Djordjevic, *J. Exp. Bot.* **64**, 5383–5394 (2013).
10. A. C. Bryan, A. Obaidi, M. Wierzba, F. E. Tax, *Planta* **235**, 111–122 (2012).
11. E. A. Vidal, R. A. Gutiérrez, *Curr. Opin. Plant Biol.* **11**, 521–529 (2008).
12. N. Imin, N. A. Mohd-Radzman, H. A. Ogilvie, M. A. Djordjevic, *J. Exp. Bot.* **64**, 5395–5409 (2013).
13. S. Okamoto, H. Shinohara, T. Mori, Y. Matsubayashi, M. Kawaguchi, *Nat. Commun.* **4**, 2191 (2013).

Large carnivores make savanna tree communities less thorny

Adam T. Ford,[1,2]* Jacob R. Goheen,[2,3] Tobias O. Otieno,[2] Laura Bidner,[2,4] Lynne A. Isbell,[2,4] Todd M. Palmer,[2,5] David Ward,[6] Rosie Woodroffe,[2,7] Robert M. Pringle[2,8]

Understanding how predation risk and plant defenses interactively shape plant distributions is a core challenge in ecology. By combining global positioning system telemetry of an abundant antelope (impala) and its main predators (leopards and wild dogs) with a series of manipulative field experiments, we showed that herbivores' risk-avoidance behavior and plants' antiherbivore defenses interact to determine tree distributions in an African savanna. Well-defended thorny *Acacia* trees (*A. etbaica*) were abundant in low-risk areas where impala aggregated but rare in high-risk areas that impala avoided. In contrast, poorly defended trees (*A. brevispica*) were more abundant in high- than in low-risk areas. Our results suggest that plants can persist in landscapes characterized by intense herbivory, either by defending themselves or by thriving in risky areas where carnivores hunt.

The observation that most ecosystems support abundant plant life, despite the existence of herbivores that eat plants, has motivated a great deal of research and debate in ecology. Two broad hypotheses have been advanced to explain this phenomenon. The green world hypothesis (*1*) posits that predators indirectly benefit plants by suppressing herbivory; such trophic cascades occur when carnivores consumptively reduce herbivore densities or trigger risk-avoidance behaviors (such as increased vigilance or refuge-seeking) that reduce plant consumption (*2, 3*). In contrast, the plant defense hypothesis contends that the world is green because plants have evolved structural and chemical defenses that inhibit consumption (*4, 5*), often at a cost to their growth and competitive ability (*6, 7*). Although traditionally viewed as alternatives, these hypotheses are no longer thought to be mutually exclusive (*7, 8*). A key challenge for contemporary ecology is to understand how plant defense and predation interact across landscapes to shape a green world (*8*).

We evaluated how the combination of plant defense and risk avoidance by a common African ungulate (impala, *Aepyceros melampus*) determined the outcome of a trophic cascade in an East African savanna. Impala consume a mixture of grasses and trees ("browse") (*9*) and are preyed upon by several carnivores, especially leopards (*Panthera pardus*) and African wild dogs (*Lycaon pictus*) (fig. S1). We tested three hypotheses (Fig. 1)

to explain the structure of this food web: (i) Predation risk drives habitat selection by impala; (ii) impala prefer to eat less-thorny tree species, thereby suppressing their abundance; and (iii) predation risk thus differentially influences the distribution of thorny versus less-thorny *Acacia* trees (table S1).

To test our first hypothesis, we quantified habitat selection by impala, using resource selection functions, global positioning system (GPS) telemetry, and high-resolution (0.36-m²) satellite imagery (*10*) (fig. S2). Specifically, we quantified the selection of woody cover, which represents forage for impala (*9*) but could also increase risk by concealing predators (*11, 12*). We also tracked how impala used two discrete habitat features typified by low versus high woody cover (fig. S3): (i) "glades," which are ~0.5-ha clearings (with 8% mean tree cover) derived from abandoned cattle corrals, covered with nutrient-rich grasses, and maintained through grazing by wildlife (*13, 14*); and (ii) "thickets," which are <100-m-wide strips of woody vegetation (with 25% cover) along the edges of dry channels. We then quantified the relationship between woody cover and two components of risk: (i) relative probability of encountering predators, assessed using resource-selection functions of leopards and wild dogs for woody cover; and (ii) per-capita risk of mortality from predation, measured as the spatial distribution of kill sites relative to the spatial distribution of impala (*10*).

Impala avoided woody cover (Fig. 2A) and aggregated in glades and other open habitats, especially during times of the day when their predators are most active (tables S2 and S3). Both the relative probability of encountering predators (Fig. 2A) and the per-capita risk of mortality from predation (Fig. 2B) increased with increasing woody cover. Leopards and wild dogs accounted for 83% of impala kills (52 and 31% respectively; fig. S1), and kill sites from all carnivore species occurred in areas with similar amounts of woody cover ($F_{2,51} = 0.765$, $P = 0.47$).

[1]Department of Zoology, University of British Columbia, Vancouver, BC, Canada. [2]Mpala Research Centre, Post Office Box 555, Nanyuki, Kenya. [3]Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA. [4]Department of Anthropology, University of California, Davis, CA, USA. [5]Department of Biology, University of Florida, Gainesville, FL, USA. [6]School of Life Sciences, University of KwaZulu-Natal, Scottsville, South Africa. [7]Institute of Zoology, Zoological Society of London, Regent's Park, London, UK. [8]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA.
*Corresponding author. E-mail: atford@zoology.ubc.ca

Thus, a single cue—woody cover—integrated two components of risk (encounters and mortalities) arising from the two major predators of impala.

Although impala avoided risky areas, this behavior might be explained by selection for the nutrient-rich grasses that characterize glades and open habitats (*14*). We tested this alternative hypothesis by experimentally removing all woody cover from five 0.5-ha plots, thereby

Fig. 1. Food web hypotheses tested in our study. Solid and dashed arrows represent direct and indirect effects, respectively. Red arrows represent negative effects, green arrows represent positive effects, and gray arrows represent either neutral or positive effects. Hypothesis 1: The risk of predation from large carnivores drives habitat selection of impala. Hypothesis 2: Impala both prefer and suppress the densities of poorly defended plants. Hypothesis 3: Predation risk increases the abundance of poorly defended trees in high-risk areas.
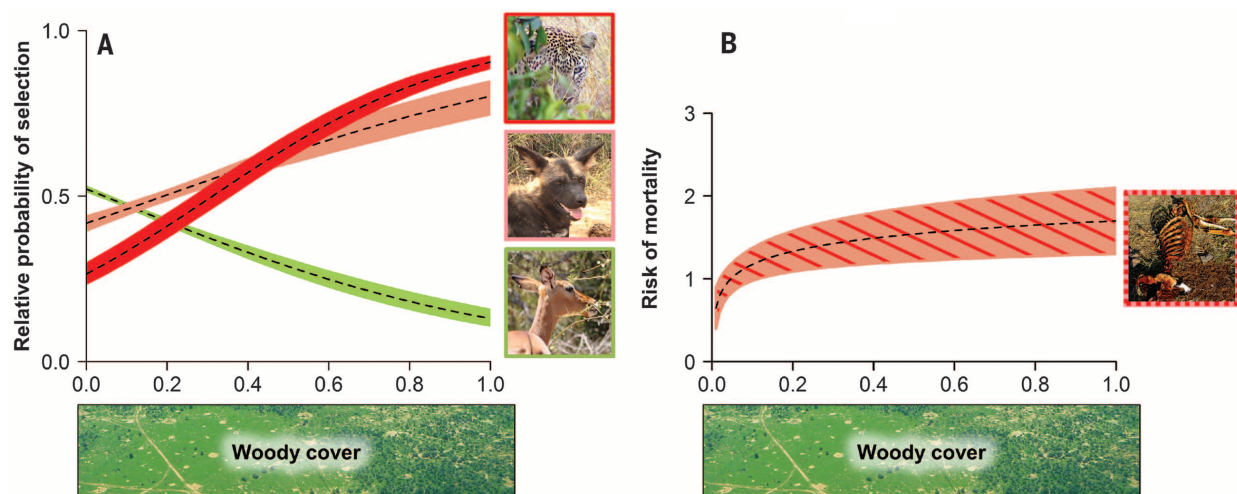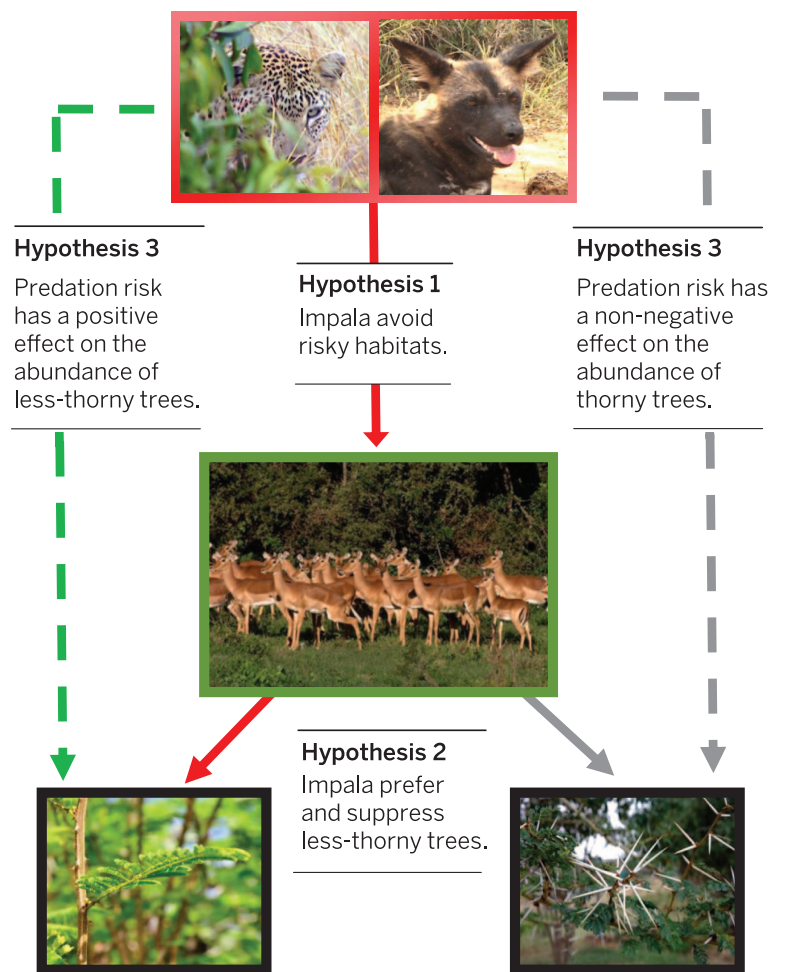
Hypothesis 3
Predation risk has a positive effect on the abundance of less-thorny trees.

Hypothesis 1
Impala avoid risky habitats.

Hypothesis 3
Predation risk has a non-negative effect on the abundance of thorny trees.

Hypothesis 2
Impala prefer and suppress less-thorny trees.

Fig. 2. Impala avoid risky areas, characterized by increasing woody cover. (**A**) Habitat selection by impala (green, β = −1.99 ± 0.14, *n* = 20 impala, *P* < 0.001), leopards (red, β = 3.42 ± 0.14, *n* = 4 leopards, *P* < 0.001), and wild dogs (pink, β = 1.64 ± 0.19, *n* = 5 wild dogs, *P* < 0.001), where the βs represent population-level coefficients from resource selection functions for woody cover. Positive and negative coefficients indicate selection and avoid-ance of woody cover, respectively. (**B**) The predicted per-capita risk of mortality from predation [1.70 + 0.228 × ln(woody cover)], coefficient of determination based on pooled kill sites from all large carnivores (fig. S2). Values <1 and >1 indicate that kill sites occur less or more than expected, respectively, relative to the spatial distribution of impala. Shading indicates 95% prediction intervals.
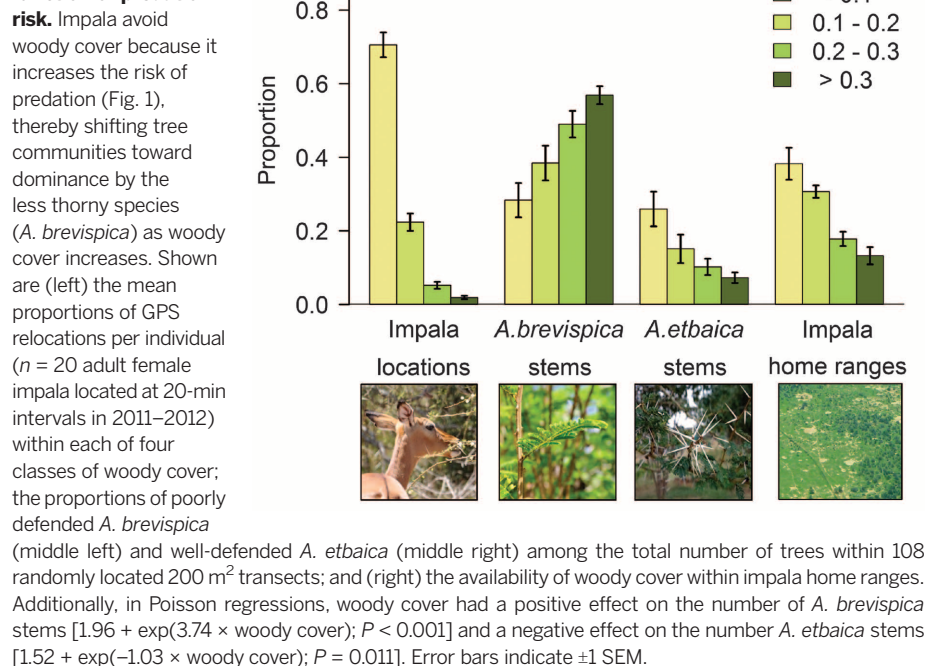
Fig. 3. Impala both preferentially consume and suppress *Acacia* spp. lacking large thorns. The presence of long thorns significantly reduced impala's preference for (**A**) *A. brevispica* and (**B**) *A. etbaica* in feeding experiments [likelihood ratio (LR) = 4.76, $P = 0.029$)]. The effects of species and species × thorns on preference were nonsignificant (*10*). A value of 1 (dashed line) indicates that diet preference (leaf consumption) occurred randomly among the four treatments, whereas values >1 indicate selection and values <1 indicate avoidance. Over a 5-year impala exclusion experiment, the net density (stems/ha) of (**C**) *A. brevispica*, which lacks long thorns, increased in plots where impala were absent (LR: $\chi^2_1 = 127.13$, $P < 0.001$); in contrast, (**D**) *A. etbaica* decreased in plots where impala were absent (LR: $\chi^2_1 = 158.88$, $P < 0.001$). Error bars indicate ±1 SEM.
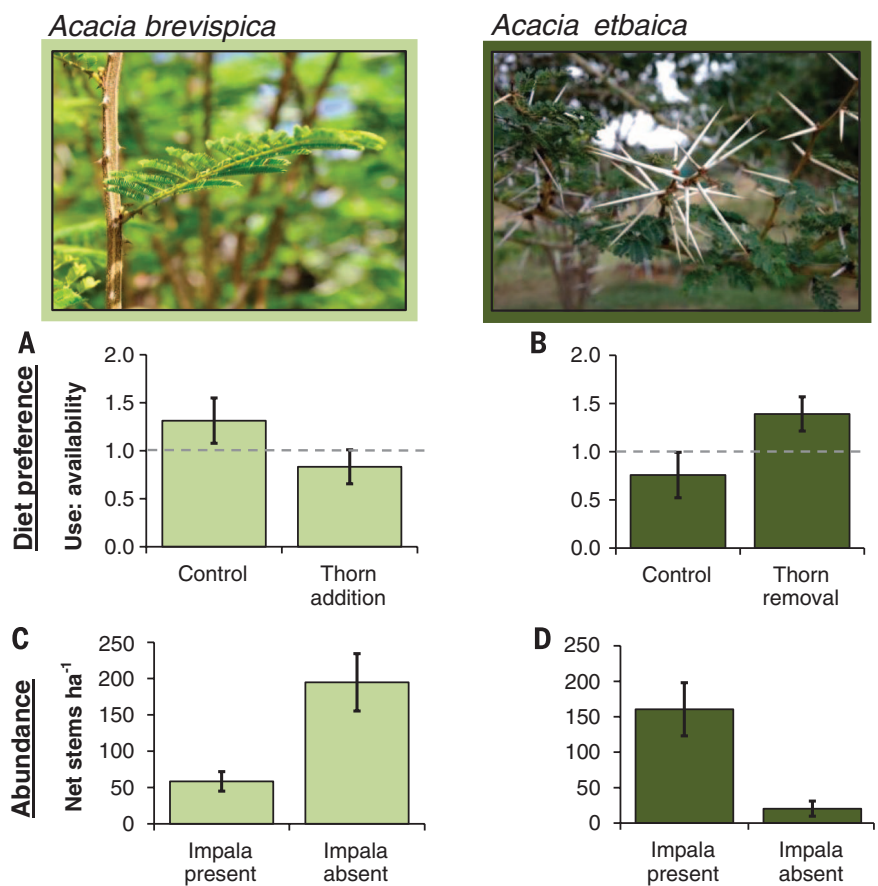
mimicking the lowered risk of glades, but without potential confounds associated with forage quality. We monitored the movements of five GPS-collared impala herds for 60 days before and after creating these clearings. Impala's use of these areas increased by 160 to 576% after the removal of woody cover (table S4), indicating that forage quantity and quality cannot fully explain impala's selection of open areas. Additionally, impala typically increase their consumption of woody plants during the dry season when grass quality is poor (*9*), yet we detected no significant influence of season on their use of open habitat (tables S2 and S3). Hence, risk avoidance appears to drive habitat selection by impala.

We next tested our second hypothesis: that impala prefer and consequently reduce the abundance of poorly defended plants. We started by quantifying the effect of plant defenses on diet preference, focusing on two common *Acacia* species (*A. brevispica* and *A. etbaica*) that together constitute ~80% of trees in the study area (*13*) and differ in traits that may affect the diet preference of herbivores (*4–8*): *A. brevispica* has shorter thorns (≤0.6 cm versus ≤6.0 cm) but higher condensed-tannin concentrations than *A. etbaica* (table S5). To measure the impact of these traits on diet preference, we removed thorns from *A. etbaica* branches and attached them to *A. brevispica* branches; we then presented both types of manipulated branches alongside unmanipulated controls of each species to free-ranging

Fig. 4. Tree-community composition as a function of predation risk. Impala avoid woody cover because it increases the risk of predation (Fig. 1), thereby shifting tree communities toward dominance by the less thorny species (*A. brevispica*) as woody cover increases. Shown are (left) the mean proportions of GPS relocations per individual (*n* = 20 adult female impala located at 20-min intervals in 2011–2012) within each of four classes of woody cover; the proportions of poorly defended *A. brevispica*

(middle left) and well-defended *A. etbaica* (middle right) among the total number of trees within 108 randomly located 200 m² transects; and (right) the availability of woody cover within impala home ranges. Additionally, in Poisson regressions, woody cover had a positive effect on the number of *A. brevispica* stems [1.96 + exp(3.74 × woody cover); $P < 0.001$] and a negative effect on the number *A. etbaica* stems [1.52 + exp(−1.03 × woody cover); $P = 0.011$]. Error bars indicate ±1 SEM.

impala in a cafeteria-style feeding experiment. Mean leaf selection by impala was 1.4 times greater for unmanipulated *A. brevispica* branches

than for unmanipulated *A. etbaica* (Fig. 3, A and B). This preference for *A. brevispica* was due to differential thorniness: The removal of

A. etbaica's long thorns increased leaf selection to levels commensurate with that of unmanipulated *A. brevispica*, whereas selection for thorn-addition *A. brevispica* was roughly equal to that of unmanipulated *A. etbaica* (Fig. 3, A and B). Thus, we conclude that *A. brevispica* is preferred relative to *A. etbaica* and that this preference is determined by thorns rather than tannins or other species-specific attributes.

Next, we considered whether the diet preference of impala could alter the abundance of *Acacia* species. We therefore measured the net change in the density of tree stems from 2009–2014 within nine replicate sets of 1-ha herbivore exclosures that independently manipulated megaherbivores [elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*)], mesoherbivores [impala and eland (*Taurotragus oryx*)], and small browsers [dik-dik (*Madoqua guentheri*)], using electrified wires at different heights (*15*). We isolated the effects of impala on *Acacia* species by comparing the megaherbivore and mesoherbivore-exclusion treatments; we attributed mesoherbivore-driven effects on tree density to impala because they account for ~87% of browser biomass in this size class (*9*). The exclusion of impala increased the net stem density of the preferred and poorly defended *A. brevispica* by 233% (Fig. 3C). Conversely, net stem density of well-defended *A. etbaica* increased by 692% in plots accessible to impala as compared to impala-exclusion plots (Fig. 3D). This increase in *A. etbaica* in plots where impala were present is perhaps due to reduced competition with *A. brevispica* (*15*, *16*). Thus, although impala consumed leaves from both *Acacia* species (Fig. 3, A and B), the long thorns of *A. etbaica* enabled them to avoid suppression by impala.

To evaluate our third and final hypothesis, we related spatial patterns in the abundance of these two *Acacia* species to satellite-derived estimates of woody cover. We counted all trees in 108 transects (200 m²) located near randomly selected glades and thickets throughout our 140-km² study area. The abundance of *A. brevispica* increased monotonically with satellite-derived estimates of woody cover (i.e., risk) across these transects, whereas *A. etbaica* became scarcer as woody cover increased (Fig. 4 and fig. S4). Risk avoidance by impala (Fig. 2) was functionally analogous to impala exclusion by electrified fences (Fig. 3, C and D): Our results consistently showed that the absence of impala herbivory increased the prevalence of poorly defended trees but not the prevalence of well-defended trees. Thus, tree communities became less thorny as predation risk arising from large carnivores increased (Fig. 4).

Collectively, our results show that the nature of trophic control is contingent on biotic context: namely predation risk and plant defenses (Fig. 1). Both mechanisms enable plants to thrive in different parts of the landscape: Where risk is high, poorly defended trees are released from browsing, resulting in a trophic cascade; where risk is low, intense herbivory increases the benefit of defenses, creating communities dominated by thorny trees. Consequently, the thorniness of tree communities decreased across the landscape because of the way in which impala responded to spatial variation in predation risk, and also because of the way plant defenses affected impala's diet preference.

Human activities—both past and present—exert a major influence on the interactions between carnivores, impala, and the tree community. Glades represent the legacy of traditional livestock production (*17*), generating a constellation of refugia that has shaped the spatial distribution of impala herbivory. However, the loss of large carnivores will make landscapes less risky (*18*), decoupling the spatial interplay of risk avoidance and herbivory. The loss of carnivores will also render obsolete the need for pastoralists to corral their cattle nightly, eliminating the formation of glades. Consequently, human-driven extirpation of large carnivores from African savannas (*2*) will reduce spatial variation in plant communities, leading to a world that is thornier, but still green. As large-carnivore populations continue to decline globally, understanding the context in which predators shape key ecosystem processes is an urgent priority (*19*). Studies integrating risk of predation and plant defenses will constitute a major step toward this goal.

REFERENCES AND NOTES

1. N. G. Hairston, F. E. Smith, L. B. Slobodkin, *Am. Nat.* **94**, 421 (1960).
2. J. A. Estes *et al.*, *Science* **333**, 301–306 (2011).
3. E. L. Preisser, D. I. Bolnick, M. F. Benard, *Ecology* **86**, 501–509 (2005).
4. W. W. Murdoch, *Am. Nat.* **100**, 219 (1966).
5. S. L. Pimm, *The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities* (Univ. of Chicago Press, Chicago, 1991).
6. O. J. Schmitz, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 5364–5367 (1994).
7. K. A. Mooney, R. Halitschke, A. Kessler, A. A. Agrawal, *Science* **327**, 1642–1644 (2010).
8. O. J. Schmitz, *Resolving Ecosystem Complexity*, vol. 47 of *Monographs in Population Biology*, S. A. Levin, H. S. Horn, Eds. (Princeton Univ. Press, Princeton, NJ, 2010).
9. D. J. Augustine, *Afr. J. Ecol.* **48**, 1009–1020 (2010).
10. Materials and methods are available as supplementary materials on *Science* Online.
11. R. Underwood, *Behaviour* **79**, 81–107 1982).
12. M. Thaker *et al.*, *Ecology* **92**, 398–407 (2011).
13. T. P. Young, N. Patridge, A. Macrae, *Ecol. Appl.* **5**, 97 (1995).
14. D. J. Augustine, *J. Wildl. Manage.* **68**, 916–923 (2004).
15. J. R. Goheen *et al.*, *PLOS ONE* **8**, e55192 (2013).
16. J. L. Orrock, R. D. Holt, M. L. Baskett, *Ecol. Lett.* **13**, 11–20 (2010).
17. K. E. Veblen, *J. Arid Environ.* **78**, 119–127 (2012).
18. J. Berger, J. E. Swenson, I.-L. Persson, *Science* **291**, 1036–1039 (2001).
19. W. J. Ripple *et al.*, *Science* **343**, 1241484 (2014).

CLIMATE CHANGE

Increased variability of tornado occurrence in the United States

Harold E. Brooks,[1]* Gregory W. Carbin,[2] Patrick T. Marsh[2]

Whether or not climate change has had an impact on the occurrence of tornadoes in the United States has become a question of high public and scientific interest, but changes in how tornadoes are reported have made it difficult to answer it convincingly. We show that, excluding the weakest tornadoes, the mean annual number of tornadoes has remained relatively constant, but their variability of occurrence has increased since the 1970s. This is due to a decrease in the number of days per year with tornadoes combined with an increase in days with many tornadoes, leading to greater variability on annual and monthly time scales and changes in the timing of the start of the tornado season.

Separating nonmeteorological effects in the official database of tornadoes in the United States from actual meteorological ones has made interpreting the existence and causes of long-term physical changes in tornado occurrence extremely difficult (*1*). Nonmeteorological effects in the database result from changes in the emphasis on, and methodology of, collecting reports, and from how tornadoes are observed. The mean occurrence of well-reported aspects of the database, such as the mean annual

¹National Oceanic and Atmospheric Administration (NOAA)/National Severe Storms Laboratory, Norman, OK 73072, USA. ²NOAA/National Weather Service Storm Prediction Center, Norman, OK 73072, USA.
*Corresponding author. E-mail: harold.brooks@noaa.gov

Science

Large carnivores make savanna tree communities less thorny

Adam T. Ford, Jacob R. Goheen, Tobias O. Otieno, Laura Bidner, Lynne A. Isbell, Todd M. Palmer, David Ward, Rosie Woodroffe and Robert M. Pringle

A thorny defense keeps grazers at bay

Fear and avoidance of predators are known to influence how and where herbivore prey species, such as impala, forage. This in turn has cascading effects on plant morphologies and communities. Plants, however, have their own defenses, and so may not just be hapless victims of the predator-prey "dance." Ford *et al.* found that thorny Acacia trees are more common in areas where impala experience a low risk of predation by wild dogs. A related *Acacia*, without thorns, is most abundant in areas where risk of predation is high, and so the number of hungry impala is low.
Science, this issue p. 346

ARTICLE TOOLS	http://science.sciencemag.org/content/346/6207/346
SUPPLEMENTARY MATERIALS	http://science.sciencemag.org/content/suppl/2014/10/15/346.6207.346.DC1
REFERENCES	This article cites 16 articles, 5 of which you can access for free http://science.sciencemag.org/content/346/6207/346#BIBL
PERMISSIONS	http://www.sciencemag.org/help/reprints-and-permissions

Use of this article is subject to the Terms of Service