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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.

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SUPPLEMENTARY MATERIALS

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TROPHIC CASCADES

Large carnivores make savanna tree communities less thorny

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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 (*Lycan 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 ($F_{2,51} = 0.765$, $P = 0.47$).

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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 less-thorny trees. Hypothesis 3: Predation risk increases the abundance of poorly defended trees in high-risk areas.

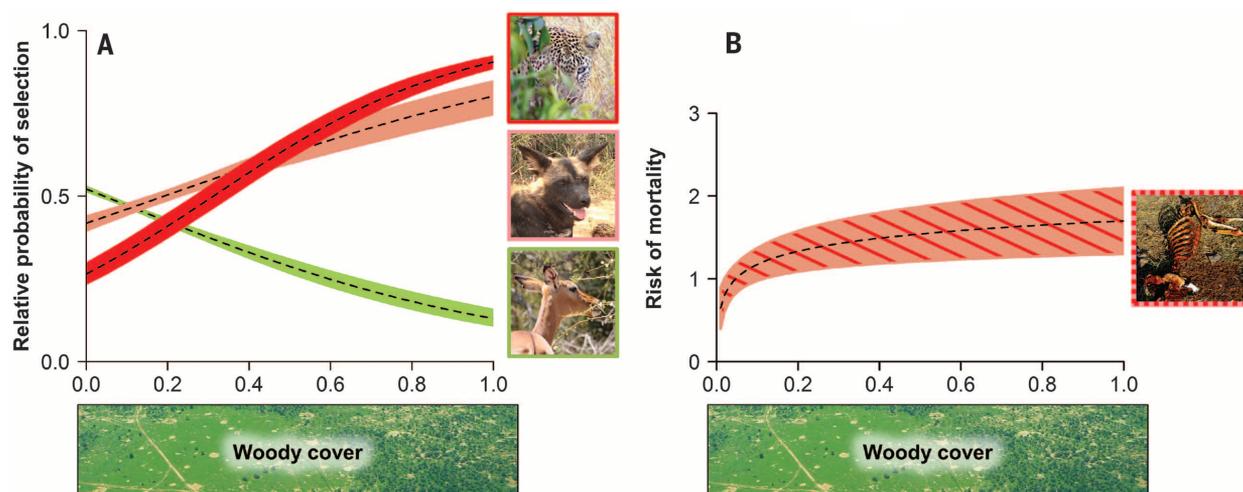
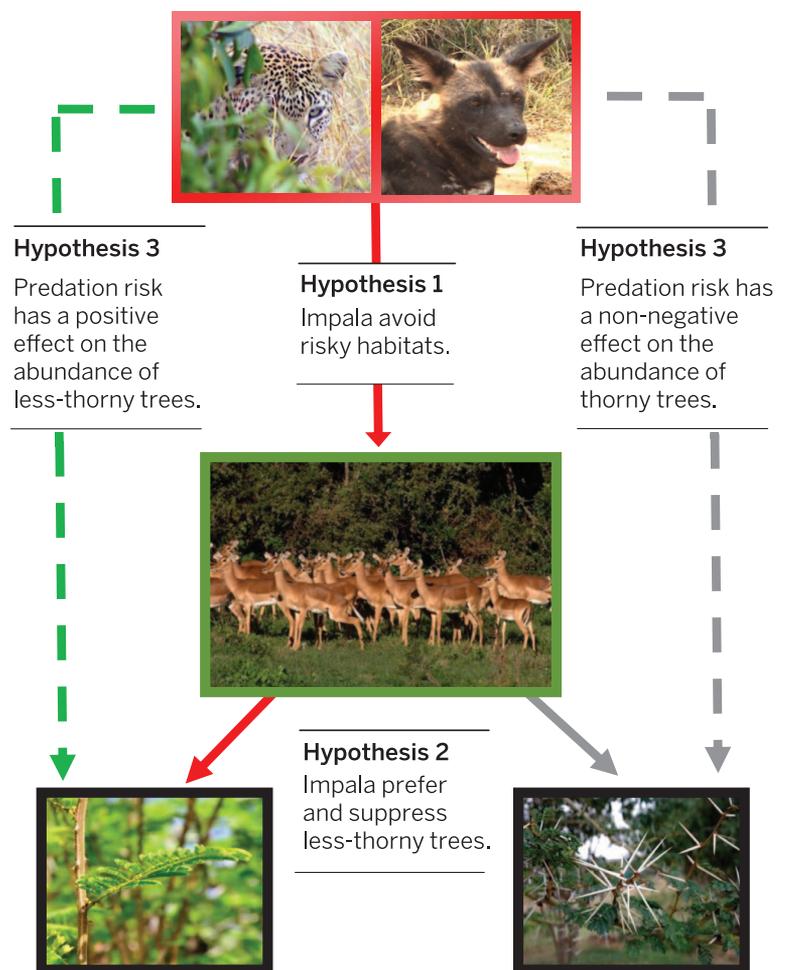
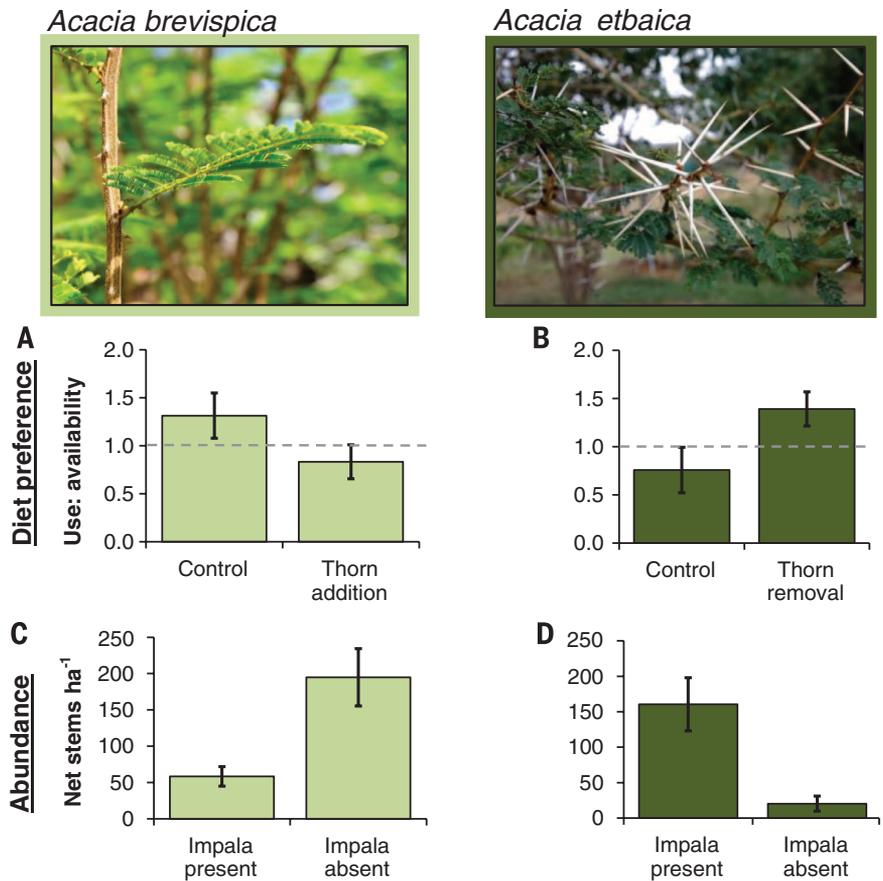


Fig. 2. Impala avoid risky areas, characterized by increasing woody cover. (A) Habitat selection by impala (green, $\beta = -1.99 \pm 0.14$, $n = 20$ impala, $P < 0.001$), leopards (red, $\beta = 3.42 \pm 0.14$, $n = 4$ leopards, $P < 0.001$), and wild dogs (pink, $\beta = 1.64 \pm 0.19$, $n = 5$ wild dogs, $P < 0.001$), where the β s 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 [$1.70 + 0.228 \times \ln(\text{woody cover})$], 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.

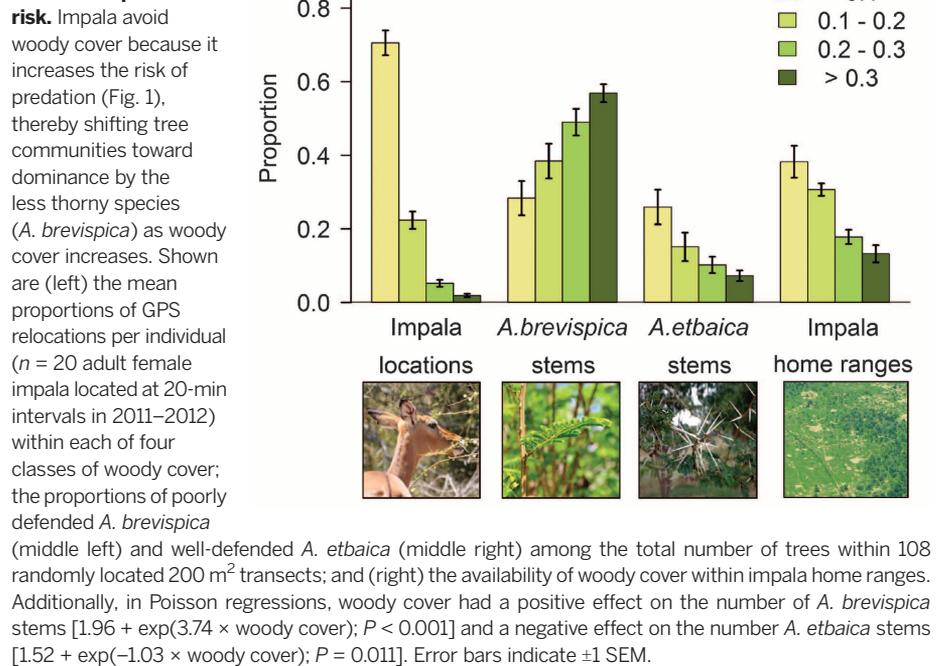
Fig. 3. Impala both preferentially consume and suppress *Acacia* spp. lacking large thorns. The presence of long thorns significantly reduced impala's preference for (A) *A. brevispica* and (B) *A. etbaica* in feeding experiments [likelihood ratio (LR) = 4.76, $P = 0.029$]. The effects of species and species \times 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*



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.

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SUPPLEMENTARY MATERIALS

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CLIMATE CHANGE

Increased variability of tornado occurrence in the United States

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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). Non-meteorological 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

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Supplementary Materials for

Large carnivores make savanna tree communities less thorny

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Figs. S1 to S4
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References

1 **Materials and methods**

2 *Study area and focal species*

3 We conducted our research at the Mpala Research Center (MRC), a 200 km² private wildlife
4 conservancy in Laikipia County, Kenya (0°17' N, 36°53' E). MRC is located in a semi-arid
5 savanna, of which roughly 70% is underlain by well-drained, quartzite soils ('red sands': [13]);
6 we conducted our research entirely on this soil type (fig. S2). Red-sand soils are characterized by
7 a discontinuous overstory layer (~28% total cover) of *Acacia* spp., *Croton* spp., and *Grewia* spp.,
8 within which 40% of stems are *A. brevispica* and 39% are *A. etbaica* (13). Mean annual rainfall
9 across the property is 500-600 mm, falling in a weakly tri-modal annual pattern with marked
10 inter-annual variation (9).

11 MRC contains herds of domestic cattle (*Bos indicus*) that are managed using traditional
12 pastoralist practices in which livestock are secured in a 'boma' or corral at night to protect
13 against depredation from large carnivores. Typically, bomas were constructed from felled trees
14 (*Acacia* spp.), occupied by cattle for several months at a time, and were ≥ 1 ha (S1,17). Over the
15 last 10 years, smaller, portable bomas constructed from chain-link have been used in Laikipia
16 (S2). In both cases, manure deposition inside bomas results in elevated nutrient concentrations
17 within both the soil and the mat-forming grasses that colonize these areas during the wet season
18 (13,14). The elevated nutrient levels in soils and the composition of the herbaceous understory
19 can persist for decades after the cattle herds have abandoned these sites due to the foraging
20 activity of native wildlife (13,14,17, S1,S2). After colonization by grasses, abandoned cattle
21 corrals are known as 'glades', one of the focal habitat features in our study. Thus, glades are
22 created by people and their cattle and maintained by herbivory from wildlife. We also focused on
23 'thickets'—areas spanning 3-100 m on either side of shallow landscape depressions or dry

24 channels, which are characterized by dense woody vegetation. These channels are normally dry
25 (and were for the duration of this study), but occasionally collect water during exceptionally
26 heavy rains; they have a sandy substrate, and can vary in depth from 0.5 m to 2.0 m. In addition
27 to glades and thickets, we analyzed the continuous range of woody cover across the landscape
28 (see below: *Mapping woody cover, glades, and thickets*).

29 We addressed the causes and consequences of habitat selection by impala (*Aepyceros*
30 *melampus*), the second-most abundant species of wild ungulate at MRC (9). Large (>20 kg)
31 carnivores are common in this area, and include leopard (*Panthera pardus*), African wild dog
32 (*Lycaon pictus*), lions (*P. leo*), spotted hyena (*Crocuta crocuta*) and striped hyena (*Hyaena*
33 *hyaena*), which occur at a combined density of about 35 individuals per 100 km² (S3, S4).

34

35 ***Testing Hypothesis 1: Impala habitat selection***

36 *GPS telemetry*: In May and June 2011, twenty adult female impala were captured using drive
37 nets (Kenya Wildlife Service) or net guns deployed from a helicopter (Frontier Helicopters,
38 Whakatane, New Zealand) and fitted with Global Positioning System (GPS) collars (Model:
39 Savannah GPS-UHF, Savannah Tracking Ltd, Nairobi, Kenya). Handling procedures were
40 approved by the University of Wyoming's Institutional Animal Care Committee and the Kenya
41 Wildlife Service, and are in accordance with the guidelines established by American Society of
42 Mammalogists. The amount of data collected from each GPS collar depended on the timing of
43 mortality events ($n = 3$) or variation in battery power, such that monitoring periods ranged from
44 46 to 464 days (258 ± 29 days [mean \pm SEM]), corresponding to 15278 ± 1794 (range: 3800-
45 28000) GPS relocations per impala. GPS collars were programmed to record a location every 20
46 minutes and positions were screened for accuracy prior to analysis using an algorithm presented

47 in Bjørneraas *et al.* (S5). This algorithm removes ‘spikes’ from an animal’s movement trajectory
48 caused by inaccurate GPS relocations. Spikes are formed when a GPS relocation creates a
49 segment of the movement trajectory that is both uncharacteristically fast (i.e., > 500 m/h) and
50 recursive (i.e., cosine of the turning angle between three sequential GPS relocations > 0.999).
51 Inaccurate GPS relocations were flagged and removed from the analysis of habitat selection;
52 however, collar accuracy was not meaningfully affected by habitat type. In an open area, we
53 compared nine days of GPS relocations from a stationary collar with readings from a handheld
54 GPS (accuracy = 12 ± 0.3 m, $n = 847$ from 18-27 January, 2014). We repeated this procedure in
55 an area with high (~30%) woody cover; our estimated accuracy was nearly identical to the open
56 area (accuracy = 11 ± 1.2 m, $n = 275$ from 8-11 April, 2014). GPS receivers in the impala collars
57 were the same model as those used in the leopard collars (see below). Thus, we do not believe
58 there were habitat-specific biases in the accuracy of GPS relocations.

59 For the duration of our study, changes in home-range size and overlap between herds was
60 minimal, and monthly surveys conducted from a field vehicle confirmed that each collared
61 individual was representative of movements of roughly 38 ± 8 individuals per herd. The stability
62 and minimal overlap of impala home ranges (fig. S2) suggests that these herds were cohesive and
63 that their movements were independent of one another. In addition to adult females, these herds
64 typically contained a single adult male and multiple young (i.e., breeding herds). Each of these
65 breeding herds was also associated with a tailing group of <10 bachelor males. Pre-capture
66 surveys indicated that there were approximately 35 breeding herds in MRC, such that our herd-
67 level data are representative of ca. 57% of breeding herds of impala. Impala home-range size
68 averaged 393 ± 47 ha. On average, each home range encompassed 7.7 ± 0.8 glades (totalling 22
69 ± 4 ha, including a 50 m buffer around each glade), along with 37 ± 6 ha of thicket habitat

70 (including a 50 m buffer along each thicket). These 50 m buffers correspond to our measures of
71 habitat use by impala and the composition of tree communities, see below: *Quantifying habitat*
72 *use* and *Distribution of Acacia spp. across the landscape*.

73 *Mapping woody cover, glades, and thickets:* We used a Quickbird satellite image (Digital
74 Globe, Longmont, CO, USA), taken in May 2011, with a resolution of 0.36 m², to create a map
75 of habitat features at MRC. We manually digitized glades and thickets and used automated
76 procedures available in geographic information system (GIS) software to classify overstory
77 cover (ArcMap v10.1, ESRI, Redlands, CA, USA). For the latter, we extracted a five-class
78 principal-components layer from the four multi-spectral bands, single panchromatic layer, and
79 normalized-difference vegetation index layer included with our imagery. We then manually
80 reclassified the principal-components layer into five mutually exclusive cover types: xeric grass,
81 mesic grass, bare ground, canopy and no data (cloud). Because the resolution of this imagery is
82 high relative to the habitat features in which we were interested, because MRC comprises a
83 relatively limited range of vegetation types, and because we are intimately familiar with the site,
84 we used visual inspection to confirm that this procedure accurately classified woody cover. We
85 transformed overstory cover to yield proportional coverage over circular areas with a 40 m
86 radius, which we refer to as ‘woody cover’ (see below: *Quantifying habitat selection*). We refer
87 to glades, thickets, and woody cover as ‘habitat features’.

88 *Quantifying habitat use:* We used GPS telemetry to evaluate shifts in habitat use over
89 seasons and diel periods. Wet seasons were defined as those with > 50 mm rainfall over the
90 preceding 4 weeks; dry seasons were defined as those with ≤ 50 mm rainfall over the preceding 4
91 weeks. Diel periods were defined as day (0800-1800), night (2000-0600), and crepuscular (0600-
92 0800; 1800-2000), corresponding to peaks in activity for leopards (night) and wild dogs

93 (crepuscular) (*S4,S6,S7*). To maximize the resolution of habitat use by impala, we calculated the
94 proportion of relocations within each habitat feature using data from all GPS relocations, which
95 were collected at 20 minute intervals. We summarized the proportion of individual GPS
96 relocations located within 50 m of glades and thickets (table S2) and over a range of classified
97 woody cover (Fig. 4). Using individual impala as the units of analysis, we employed paired *t*-
98 tests to assess the null hypothesis that habitat use did not change across diel periods and seasons
99 (table S2).

100 *Quantifying habitat selection:* We used GPS telemetry to evaluate selection for glades,
101 thickets, and woody cover. We employed a use-availability design to measure resource selection
102 functions (RSFs) for these habitat features (*S8*). RSFs assess the amount of use of a particular
103 habitat feature relative to the availability of that habitat feature; thus, habitat selection more
104 directly measures how impala perceive the quality of a habitat, whereas habitat use is a better
105 measure of the impact (e.g., on vegetation) that impala have in an area.

106 In calculating the RSFs for impala, the area of availability was defined separately for
107 each individual as the 95% minimum convex polygon of observed relocations (hereafter, ‘home
108 range’). We used GPS relocations that were ≥ 4 hours apart (ca. 0000 h, 0400 h, 0800 h, 1200 h,
109 1600 h, 2000h) to minimize serial autocorrelation (prevalent in the 20 minute GPS relocations),
110 which we confirmed using partial-autocorrelation functions (*S9*). We generated a series of
111 random points equal to the number of observed relocations within each home range, then
112 measured woody cover at each observed and random location (hereafter, ‘sample points’).
113 Sample points falling within 50 m of a glade or thicket were considered to occur within that
114 habitat feature. We chose a distance of 50 m to match the plot lengths used in our tree-abundance
115 surveys (see below: *Distribution of Acacia spp. across the landscape*).

116 The satellite image classification depicted overstory cover as a binary variable for each
117 0.36 m^2 pixel. Although we expected habitat selection of impala to manifest over areas larger
118 than 0.36 m^2 , we had no prior expectation for the spatial scale at which impala are most sensitive
119 to variation in cover. Consequently, we defined woody cover as the proportion of 0.36 m^2 pixels
120 classified as overstory over a circular area. We then represented woody cover over circular areas
121 with radii of 10 m (i.e., the approximate accuracy of the GPS collars), 20 m, 40 m, and 80 m,
122 measured impala RSFs for each radius, and used Akaike's Information Criterion corrected for
123 sample size (AICc) to determine the model with the best-fitting radius. Marginal (population-
124 level) RSF coefficients for woody cover were all negative (-1.24 to -1.99) and statistically
125 significant ($P < 0.001$ for all radii), with the model for the 40 m radius ranked highest by > 5
126 AICc compared with the next-best fitting model. Thus, throughout the main text and hereafter,
127 we define woody cover as the proportion of a 5027 m^2 circular area (i.e., one with 40 m radius)
128 occupied by 0.36 m^2 pixels classified as overstory.

129 We used a generalized linear mixed model to estimate RSF coefficients, in which positive
130 values indicate selection for, and negative values indicates avoidance of, a habitat feature. We
131 included a random effect for individual impala in the model and report the marginal (population-
132 level) RSF coefficients for each habitat feature. We created separate models to calculate RSF
133 coefficients for each habitat feature, diel period, and season (table S3). For the crepuscular
134 period only, we used the 20 minute GPS relocation intervals because the 4 h intervals used for
135 the RSFs occurred outside of the crepuscular period. We used the R-package lme4 to analyse
136 these data (R Development Core Team 2013).

137

138 ***Testing Hypothesis 1: Risk of predation***

139 *Quantifying the relative probability of encountering leopards and African wild dogs:* We
140 quantified the relative probability that impala would encounter predators across a continuous
141 gradient of woody cover using RSFs for leopards and wild dogs. All else equal, there is a greater
142 probability of impala encountering wild dogs and leopards in areas selected by these carnivores
143 (as indicated by a positive RSF coefficient) relative to areas that these carnivores avoid (as
144 indicated by a negative RSF coefficient). We note that RSFs quantify neither the actual number
145 of encounters between impala and these large carnivores, nor the density of predators, but rather
146 the relative risk of encounter.

147 From January to March 2014, we captured four adult leopards (three females, one male)
148 using foot snares (*S10*). Following chemical immobilization, leopards were fitted with GPS
149 collars (Model: Savannah GPS-UHF, Savannah Tracking Ltd, Nairobi, Kenya). All procedures
150 were approved by the University of California, Davis IACUC protocol number 15889 and in
151 collaboration with Kenya Wildlife Service, and were conducted in accordance with guidelines
152 established by the American Society of Mammalogists. Through May 2014, the total number
153 of days these collars were functioning ranged from 64 to 87 days (75 ± 4.7 days). We recorded
154 leopard relocations at 30 minute intervals and only used relocation records at night (2000-0600),
155 when leopards typically hunt (*S6*, *S7*). Based on a spatially-explicit capture-recapture study,
156 there are approximately 12 leopards at MRC (*S3*), such that the four collared individuals
157 represent ca. 33% of the population. The combined home ranges of these 4 individuals occupies
158 a 2790 ha portion of our study area.

159 Between 2011-2014, GPS relocations of adult wild dogs were collected from 5 adults (3
160 males, 2 females) at 30 min intervals during crepuscular periods, when wild dogs typically hunt
161 (*S4*, *S6*). The collared animals are members of the only two wild dog packs known to use the

162 study area between 2011-2014 and their combined home ranges occupy a 18934 ha portion of
163 our study area. Wild dogs were captured by darting from a vehicle at distances of 10-20 m,
164 immobilized with medetomidine (Domitor, Pfizer Animal Health; approximately 26 $\mu\text{g}/\text{kg}$) and
165 ketamine (approximately 2.6 mg/kg), and reversed with atipamezole (Antisedan, Pfizer Animal
166 Health; approximately 130 $\mu\text{g}/\text{kg}$). Wild dogs were captured and handled in collaboration with
167 the Kenya Wildlife Service, with permission from the Kenyan Ministry of Science and
168 Technology, according to guidelines of the IUCN/SSC Canid Specialist Group and the American
169 Society of Mammalogists, and following a protocol approved by the Animal Care and Use
170 Committee of the University of California, Davis, and the Ethics Committee of the Zoological
171 Society of London. Wild-dog packs are highly cohesive, and the movements of a single animal
172 give a reliable indicator of the movements of the whole pack. An exception is the roughly three
173 months each year when individuals may guard pups at a den while other pack members hunt.
174 However, because pup guarding is shared among pack members and because dens were typically
175 located outside the study area, only 1% of GPS relocations in this dataset were ≤ 200 m from
176 active dens. The mean size of packs containing a collared animal was 26 ± 5 individuals.

177 Analysis of habitat selection by leopards and wild dogs followed that described above for
178 impala, with area of availability constrained to the portion of MRC encompassed by home ranges
179 (95% minimum convex polygon) of individual leopards or wild-dog packs. For leopards, we
180 applied a random effect in the model for individual, and for wild dogs we included a nested
181 random effect of individual within pack. Wild dogs that were collared from the same pack were
182 not monitored at the same time, such that these random effects conservatively account for pack-
183 specific effects on habitat selection. Thus, we used the leopard ($\beta = 3.42 \pm 0.14$, $P < 0.001$) and

184 wild dog ($\beta = 1.64 \pm 0.19$, $P < 0.001$) RSF coefficients for woody cover in estimating the relative
185 probability of encountering carnivores across the landscape (Fig. 1A).

186 *Per capita risk of mortality:* Between July 2011 and July 2012, security personnel from
187 MRC recorded the location of sites where any impala were killed (hereafter ‘kill sites’) using
188 handheld GPS units (figs. S1, S2). Kill sites were located by foot or vehicle by visually
189 identifying an impala carcass or by following carnivore tracks from where they intersected a
190 road. We recorded 54 kill sites, which were located 120 ± 16 m (range 3 - 520 m) from the
191 nearest road. Areas < 500 m from roads occupy 86% of impala home ranges and wildlife in our
192 study area do not avoid roads (9), so we believe that the spatial distribution of kill sites is an
193 unbiased sample of impala mortalities from predation. Predator identity was assigned based on
194 evidence at the kill location, including tracks, bite marks, and fur-removal. Satellite-derived
195 estimates of woody cover at kill sites from leopards (0.11 ± 0.02), wild dogs (0.08 ± 0.02) and all
196 other carnivores (0.10 ± 0.03) was not statistically significant (ANOVA, $F_{2,51} = 0.765$, $P = 0.47$).
197 Therefore, we pooled the impala kill-site data from all large carnivores to estimate per capita risk
198 of predation for impala as a function of woody cover.

199 The number and distribution of kill sites is constrained by the availability (number and
200 distribution) of prey (S11-S13). Consequently, we were most interested in the risk to individuals
201 associated with varying levels of woody cover after accounting for the distribution of impala
202 across the landscape, which we refer to as the per capita risk of mortality from predation (r). To
203 quantify r , we first partitioned woody cover values into eight classes (0.000 – 0.005; 0.005 –
204 0.020; 0.020 – 0.040; 0.040 – 0.060; 0.060 – 0.080; 0.080 – 0.10; 0.100 – 0.160; 0.160 – 1.000),
205 each of which accounted for 12.5% of GPS relocations (pooled across all 20 impala). We then
206 calculated the proportion of the 54 kill sites occurring within each class of woody cover. Next,

207 we calculated the ratio of the proportion of kill sites to the habitat use by impala for each class of
208 woody cover. A ratio < 1 indicates that, for a given amount of woody cover, the proportion of
209 kill sites was less than expected from impala habitat use, whereas a ratio > 1 indicates that the
210 proportion of kill sites was greater than expected from impala habitat use. Finally, we regressed
211 these ratios against the value of woody cover at the mid-point of each class. This simple model
212 creates a continuous relationship between the occurrence of kill sites relative to impala habitat
213 use and woody cover ($r = 1.70 + 0.228 \cdot \ln(\text{woody cover})$; $n = 8$ classes; $R^2 = 0.792$; $P = 0.003$)
214 and allowed us to estimate the per capita risk of mortality from predation as a function of woody
215 cover across the landscape (Fig. 1B, Fig. S4). Because kill sites are likely more difficult to detect
216 in denser vegetation, we note that this model likely underestimates the steepness of the slope for
217 the relationship between r and woody cover.

218 To interpret r , we extend the work conducted on resource selection that employ
219 use:availability ratios (S8). Here, we are interpreting ‘use’ as the proportion of kill sites in a
220 given class of woody cover, and ‘availability’ as the proportion of impala locations in those same
221 classes. For example, our model predicts the per capita risk of mortality from predation at 5%
222 woody cover to be 1.02, while the value for per capita risk of mortality from predation at 25%
223 woody cover is 1.38 (Fig 1B). When standardized (S8), the relative difference in the per capita
224 risk of mortality in areas with 25% woody cover is 1.36-times greater compared to areas with 5%
225 woody cover.

226 We then validated the predictive model for r . Because r is derived from the regression of
227 a ratio of kill sites to impala habitat use, we can use the product of r and impala density to
228 predict the distribution of kill sites without including woody cover explicitly in the validation
229 effort. This validation predicts that kill sites are most likely to be found in areas where both r and

230 the density of impala are high. This prediction differs from r itself, which increases when the
231 percentage of kill sites is disproportionately higher than the habitat use (%) by impala for a given
232 range of woody cover.

233 To perform this validation, we first identified the subset of impala home ranges in which
234 a kill site was found ($n = 30$ kill sites within 13 home ranges). We then created 500 m buffers
235 around roads in these home ranges, corresponding to the maximum distance from the road where
236 we located a kill site. Within these roadside buffers, we calculated the density of impala GPS
237 relocations (pD) from all collared individuals. The pD provides an actual measure of impala
238 density within roadside buffers, and does not rely on a predictive model based on woody cover.
239 The pD was measured over a circular area with a 40 m radius and assigned to 10 m^2 pixels in a
240 raster map using GIS. Next, we created 300 random points (10 for each observed kill site) within
241 the roadside buffers. Random points were > 40 m from one another, corresponding to
242 independent measures of woody cover. For each of the observed and random points ($n = 330$
243 sample points) we determined r using the satellite-derived estimate of woody cover [$r = 1.7 +$
244 $0.228 \cdot \ln(\text{woody cover})$]. We then measured pD at each sample point using GIS software. Next,
245 we calculated the product of impala density and per capita risk of predation as $v = pD \cdot r$; if r is
246 equivalent to the actual per capita risk of mortality from predation then the probability of kill site
247 occurrence will increase with v . We used a mixed-effects logistic regression, with the
248 observed/random sample point as the binary response variable and v as the predictor. We
249 included a random effect for the home range of the ‘individual impala’ because the maximum-
250 theoretical pD depends on the amount of data collected per individual (which varied with collar
251 performance).

252

253 Our validation procedure predicted a significant increase in the probability of kill site
254 occurrence with increasing v ($\beta = 0.39 \pm 0.15$, $n = 330$, $P = 0.007$), thus confirming that per
255 capita risk of predation predicts one component of actual predation risk to impala. By using an
256 empirical measure of impala density to validate the effect of r on kill sites, our validation is
257 independent of the woody cover term used to create r .

258 *Habitat manipulation:* Because glades contain both lowered risk and nutrient-rich
259 grasses, it was unclear *a priori* which of these two drivers most strongly affected habitat
260 selection by impala. To disentangle the confounding influences of safety (i.e., less woody cover)
261 and forage within glades, we cleared all woody cover from a single 0.5 ha (70 x 70 m) plot in
262 each home range of five individual impala herds (fig. S2). These clearings are equivalent to ~12
263 % more glade area in the average impala home range. Relative to their surroundings, these
264 clearings: (i) reduced risk; (ii) eliminated overstory forage (browse); and (iii) most likely did not
265 change grass quantity or quality over the 60 day course of this experiment. Clearings were
266 established during dry conditions (one clearing in October 2011 and four in February 2012).
267 Prior to this effort, we used the classified satellite image to identify plot locations as areas with a
268 high proportion of woody cover (0.22 ± 0.02 , range 0.13 – 0.31) and low observed use by impala
269 (table S4). We counted the number of impala relocations within 50 m of plot boundaries, and
270 used GPS relocation data from 60 d before and after removal of woody cover to standardize the
271 monitoring period among animals. We report on the proportional change in use of clearings for
272 each individual before vs. after clearing (table S4).

273

274 ***Testing Hypothesis 2: The effect of plant defenses on impala diet preference***

275 *Characteristics of Acacia species:* We tested the hypothesis that thorn morphology—as opposed

276 to chemical defenses and other leaf characteristics (table S5)—deters herbivory by impala. To
277 measure leaf mass, we clipped 10 leaves from randomly selected branches on 10 different trees
278 for a total of 100 leaves. Leaves were dried in a solar oven for 72 h and weighed to obtain an
279 average leaf mass per species. To measure condensed tannins in leaves, we collected and air-
280 dried 10 leaves from 10 trees and used a standard acid–butanol protocol with quebracho as a
281 standard (S14). Results are expressed as percent dry weight in quebracho equivalents (QE).

282 *Cafeteria feeding trials:* We cut 2 m branches from *A. brevispica* and *A. etbaica*, ensuring
283 that these branches had not previously been browsed. Four types of branch cuttings were offered
284 to impala: an unmanipulated branch from each species, an *A. etbaica* thorn-removal
285 manipulation, and an *A. brevispica* thorn-addition manipulation. The *A. etbaica* thorn removal
286 was created by clipping the long thorns of *A. etbaica* at their base with wire cutters. The *A.*
287 *brevispica* spine-addition entailed fixing the long thorns from an *A. etbaica* to an *A. brevispica*
288 branch with wire. Wires were wrapped on all branches to control for handling effects. We placed
289 each branch cutting (two controls, thorn addition, and thorn removal) in separate buckets filled
290 with wet sand and buried the four buckets approximately 1 m apart. We used 10 different glades
291 as experimental sites to maximize the probability of an impala herd encountering the cuttings,
292 and each site was used by a different impala herd (ca. 38 ± 8 individuals per herd), as verified by
293 GPS telemetry.

294 At the beginning of each trial, we marked and then counted the leaves on a randomly
295 selected 30 cm section of each branch in each group. We positioned a motion-activated video
296 camera ~5 m from branch cuttings to identify species of browsers and to monitor preferences by
297 impala. A trial night began in the late afternoon and concluded when we returned to recount
298 leaves on the marked section in the following morning. We then added water to the buckets to

299 reduce desiccation of leaves, and then returned again for a second morning to recount leaves, at
300 which point the trial was terminated. Thus, individual branch cuttings were each exposed to two
301 trial nights in this experiment. Based on video from the motion-activated cameras, impala were
302 responsible for all herbivory events in this experiment.

303 We used standardized selection indices to quantify impala diet preference for each of the
304 four types of branch cuttings (*S8*). The standardized selection index is a ratio of resource use to
305 availability, which we calculated for each type of branch cutting and trial-night as $\widehat{w}_{ij} = o_{it} / \pi_{it}$.
306 Resource use (o_{it}) was calculated as the number of leaves removed from a given branch (i)
307 divided by the total number of leaves removed over a given trial-night (t) from all branch
308 cuttings at a site. Availability (π_{it}) was the number of leaves on a given branch cutting (i) divided
309 by the total number of leaves on all branch cuttings at the start of a trial-night (t). We assumed
310 that the leaves of all branches offered to impala were equally available at each site and for each
311 night, which is supported by the observation that impala readily switched among the types of
312 branch cuttings. Availability was calculated separately for each trial-night to account for leaf loss
313 from previous foraging. Thus, $\widehat{w}_{ij} = 1$ indicates that use (leaf consumption) was proportional to
314 leaf availability, $\widehat{w}_{ij} \geq 1$ indicates selection for, and $\widehat{w}_{ij} \leq 1$ indicates avoidance of, the leaves on
315 a given branch cutting.

316 We used mixed-effects models and treated each trial-night ($n = 20$) as a replicate for each
317 of the four branch-types (i.e., a total of 80 observations), with the selection index as the response
318 variable and both night ($n = 2$) and experimental site ($n = 10$) as random effects. Fixed effects
319 included *Acacia* species, defense (i.e., long thorns present or absent), and an interaction term. We
320 compared nested models of each term (species, defense, species x defense) using a likelihood
321 ratio (*LR*) test with a maximum likelihood estimator. The presence of long thorns ($LR = 4.76$, P

322 = 0.029) was a significant factor in probability of leaf consumption, independent of species (*LR* =
323 = 0.368, *P* = 0.544). The species x thorn interaction was not statistically significant (*LR* =
324 0.305, *P* = 0.581). We used the R-package lme4 to analyse these data (R Development Core
325 Team 2013).

326

327 ***Testing Hypothesis 2: The effect of impala herbivory on the abundance of Acacia spp.***

328 *Experimental herbivore exclosures:* Using data from the Ungulate Herbivory Under Rainfall
329 Uncertainty (UHURU) experiment (15), we asked whether exclusion of impala resulted in
330 changes in stem density for *A. brevispica* and *A. etbaica*. The UHURU experiment consists of
331 experimental plots distributed across our study area (fig. S2); the plots do not encompass any
332 glades or thickets. As such, treatment effects are independent of abiotic variation that may occur
333 between glades and thickets. At each the three sites, there are three blocks of four 1 ha plots (i.e.,
334 36 total 1 ha plots), each of which was randomly assigned a treatment at the onset of the
335 experiment: (i) exclusion of all ungulates ≥ 5 kg and ≥ 0.5 m tall (total exclusion, or ‘TOTAL’);
336 (ii) exclusion of all ungulates ≥ 40 kg and ≥ 1.2 m tall (mesoherbivore exclusion, or ‘MESO’);
337 (iii) exclusion of all ungulates > 2 m tall, namely elephants and giraffes (megaherbivore
338 exclusion, or ‘MEGA’); and (iv) no exclusion (‘OPEN’). Besides impala, other mesoherbivore
339 browsers present in UHURU are eland and gerenuk, although both are extremely rare (15). We
340 attribute mesoherbivore-driven effects on tree density to impala because they account for ~87%
341 of browser biomass in this group (9). Details of the UHURU experimental design can be found
342 in Goheen *et al.* (15).

343 We isolated the effects of impala by calculating the net difference in stems over a five-
344 year period between the 9 MEGA plots (impala present) and the 9 MESO plots (impala absent).

345 Within the center of each 1 ha plot, the number of tree stems was recorded in a 3600 m² area in
346 February/March 2009 and in February/March 2014. We used the net difference in stems (2014-
347 2009) for each 3600 m² plot-center as the response variable in a generalized linear mixed model
348 with a Poisson distribution (S15). We used a Poisson distribution because our response variable
349 is characterized by count data that is non-normally distributed (S15). Because values in a Poisson
350 distribution must be nonnegative, we transformed our response variable to nonnegative integers
351 by adding the absolute value (i.e., 41) of the lowest observed net difference in stems (i.e., -41) to
352 each of the observed responses. We used treatment (presence/absence of impala) as the fixed
353 effect term, and block nested within site as a random effect. To assess significance of the fixed
354 effect term, we compared our main model with a null model (intercept-only) using a likelihood
355 ratio test (S15). In Fig. 3, we scaled the net difference in stems to 1 ha for ease of interpretation.

356

357 ***Testing Hypothesis 3: Quantifying the abundance and proportion of Acacia spp. along a***
358 ***gradient of risk to impala***

359 *Distribution of Acacia spp. across the landscape:* We generated 30 random points across the
360 study area. At each point, we located the nearest glade or thicket that also occurred within the
361 home range of a collared impala. From each point (i.e., ‘location’), we established five 50 m long
362 transects and counted stems of all woody species within 2 m on either side of the 50 m transect
363 line to create 200 m² rectangular plots. These species included *A. brevispica*, *A. etbaica*, *A.*
364 *mellifera*, a single *Croton* sp., and a single *Grewia* sp. Work by Young *et al.* (13) in our study
365 area has demonstrated that the influence of glades on the abundance of *A. etbaica* becomes
366 indistinguishable from background abundances (i.e., across the broader landscape) beyond 50 m
367 from the glade edge. Transects established at glades began at the tree-line on the glade edge and

368 extended away from the center of the glade such that transects did not cross one another. For
369 thickets, we alternated the side of the channel on which transects were established, and oriented
370 transects perpendicularly to the channel. Parallel transects associated with thickets were
371 separated by 50 m.

372 To measure the effect of predation risk to impala on the abundance of *A. brevispica* and
373 *A. etbaica*, we analysed the effect of satellite-derived estimates of woody cover on the abundance
374 (number) of stems for *A. brevispica* and *A. etbaica* using Poisson regressions (Fig. 4, figs. S3,
375 S4). However, woody cover and stem abundance are not independent given that woody cover is
376 derived mostly from the abundance of *A. brevispica* and *A. etbaica* stems. Therefore, to measure
377 the effect of predation risk and impala herbivory on the tree community, we calculated the
378 proportion of *A. brevispica* and *A. etbaica* stems among stems of all woody species at each 200
379 m² plot.

380 To illustrate the spatial dynamics of this trophic cascade (i.e., fig. S4), we depicted: (i)
381 the distribution of woody cover (derived from satellite imagery), (ii) the predicted distribution of
382 per capita risk of mortality from predation (as a function of satellite-derived estimate of woody
383 cover, see above: *Per capita risk of mortality*), and the proportion of (iii) *A. brevispica* and (iv)
384 *A. etbaica* stems in the tree community, using linear regressions that predicted the effect of
385 satellite-derived estimate of woody cover. The proportion of *A. brevispica* (*pACBR*) stems was
386 positively associated with woody cover ($pACBR = 0.257 + 0.850 * \text{woody cover}$, $n = 108$,
387 adjusted $R^2 = 0.191$, $P \leq 0.0001$). The proportion of *A. etbaica* (*pACET*) was negatively
388 associated with woody cover ($pACET = 0.269 - 0.592 * \text{woody cover}$, $n = 108$, adjusted $R^2 =$
389 0.125 , $P = 0.0001$). Using GIS software (ArcMap v10.1, ESRI, Redlands, CA, USA), we used
390 these regression equations to create predictive maps for the species composition of the tree

391 community across our study area.

Table S1. Predictions and methods associated with hypotheses tested in this study. See also Fig. 1.

Hypothesis	Prediction	Methods
(1) Risk of predation from large carnivores drives habitat selection of impala	Impala avoid areas: (i) with high risk of encountering large carnivores (ii) with high per capita risk of mortality from large carnivores	Impala avoidance/selection of habitats: -resource selection for woody cover by impala. - impala habitat use in an experimental manipulation of woody cover. Avoidance by impala of areas selected by large carnivores: - resource selection for woody cover by leopards and wild dogs. Avoidance by impala of areas with high per capita risk of mortality: - effect of woody cover on kill site locations, after controlling for impala habitat use.
(2) Impala prefer and suppress poorly-defended plants	If mechanical defense drives diet preference, impala suppress <i>Acacia brevispica</i> . If chemical defense drives diet preference, impala suppress <i>Acacia etbaica</i> .	Cafeteria feeding trials with: - unmanipulated <i>A. brevispica</i> - unmanipulated <i>A. etbaica</i> - thorn addition <i>A. brevispica</i> - thorn removal <i>A. etbaica</i> Assess changes in plant abundance after experimental exclusion of impala.
(3) Risk of predation from large carnivores drives the abundance and distribution of poorly-defended <i>Acacia</i> spp.	Poorly-defended trees are more abundant in areas of high risk to impala. Well-defended trees are more abundant in areas of low risk to impala.	Analysis relating tree-community composition and abundance to spatial variation in risk across the landscape.

Table S2. Habitat use, defined as the proportion of GPS relocations (mean \pm SEM, $n = 20$) located ≤ 50 m from each habitat feature, by diel period and season, for adult female impala living in distinct herds, May 2011- June 2012. Glades occupy $6.6\% \pm 0.7$ and thickets $8.6\% \pm 0.9$ of the average impala home range (393 ± 47 ha, $n = 20$), measured as the 95% minimum convex polygon of GPS relocations. The crepuscular period coincides with time of day during which the GPS relocations of wild dogs were recorded.

Habitat feature	All	Diel period ⁽¹⁾			$P^{(3)}$	Season ⁽²⁾		
		Crepuscular	Day	Night		Dry	Wet	$P^{(3)}$
Glade	0.28 ± 0.03	0.28 ± 0.04	0.15 ± 0.02	0.41 ± 0.06	<0.0001	0.25 ± 0.04	0.28 ± 0.04	0.220
Thicket	$0.03 \pm <0.01$	$0.03 \pm <0.01$	$0.04 \pm <0.01$	$0.01 \pm <0.01$	<0.0001	$0.02 \pm <0.01$	$0.03 \pm <0.01$	0.050

(1) Diel period: Crepuscular (0600-0800, 1800-2000), Day (0800-1800); Night (2000-0600)

(2) Season: Dry (≤ 50 mm rainfall in previous four weeks); Wet (> 50 mm rainfall in previous four weeks)

(3) P -values show the results of paired t -tests comparing the proportion of impala GPS relocations found within each habitat feature between diel period or season.

Table S3. Habitat selection, defined as the population-level coefficients ($\beta \pm \text{SEM}$; $n = 20$) for resource selection functions of adult female impala living in distinct herds, May 2011- June 2012. Separate models were created for each habitat feature, diel period and season. The values for woody cover shown in Fig. 1 ($\beta = -1.99 \pm 0.14$, $n = 20$, $P < 0.001$) were derived from pooled diel periods, seasons and areas both <200 m and >200 m from the edges of glades and thickets.

Habitat feature	All	Diel period ⁽²⁾			Season ⁽³⁾	
		Crepuscular	Day	Night	Dry	Wet
Glade	0.21 ± 0.02 ***	0.20 ± 0.01 ***	0.07 ± 0.04 *	0.32 ± 0.03 ***	0.21 ± 0.03 ***	0.17 ± 0.03 ***
Thicket	-0.30 ± 0.06 ***	-0.29 ± 0.03 ***	-0.21 ± 0.07 ***	-0.47 ± 0.10 ***	-0.37 ± 0.08 ***	-0.23 ± 0.07 ***
Woody cover ⁽¹⁾	-1.63 ± 0.24 ***	-1.37 ± 0.08 ***	-0.47 ± 0.27 *	-4.17 ± 0.47 ***	-1.51 ± 0.35 ***	-1.49 ± 0.30 ***

(1) Woody cover: excludes sampling locations ≤ 200 m from glades and thickets.

(2) Diel period: Crepuscular (0600-0800, 1800-2000), Day (0800 – 1800); Night (2000 – 0600)

(3) Season: Dry (≤ 50 mm rainfall in previous 4 weeks); Wet (> 50 mm rainfall in previous 4 weeks)

(4) * $P < 0.100$; ** $P < 0.050$; *** $P < 0.001$

Table S4. Use of clearing plots as measured by GPS telemetry of 5 distinct herds of impala, 60 days pre- and post-tree removal.

Animal	Pre-removal		Post-removal		Proportional increase of GPS relocations inside plot
	Relocations per day inside plot	Total observed relocations during 60 d	Relocations per day inside plot	Total observed relocations during 60 d	
A	0.005	3883	0.014	4122	1.60
B	0.016	3963	0.047	257 ⁽¹⁾	1.89
C	0.003	3972	0.019	3897	5.76
D	0.001	4007	0.004	4056	1.96
E	0.007	3903	0.038	2589	4.68
mean ± SEM	0.006 ± 0.002	3946 ± 23	0.024 ± 0.008	2984 ± 737	3.18 ± 0.85

⁽¹⁾ Animal was killed by poachers within 48 h of tree removal.

Table S5. Summary of *A. brevispica* and *A. etbaica* thorn and leaf characteristics (mean \pm SEM) for 10 leaves, each taken from 10 trees.

Trait	<i>A. brevispica</i> (<i>n</i> = 100)	<i>A. etbaica</i> (<i>n</i> = 100)
Condensed tannins (% Quebracho Equivalents \pm SEM)	20.8 \pm 2.6	1.3 \pm 0.3
Leaf mass (g \pm SEM)	0.336 \pm 0.028	0.030 \pm 0.003
Mechanical defenses	Short straight thorns ($<$ 0.6 cm)	Long straight thorns ($<$ 6 cm) and short recurved thorns ($<$ 0.6 cm)

Figure S1

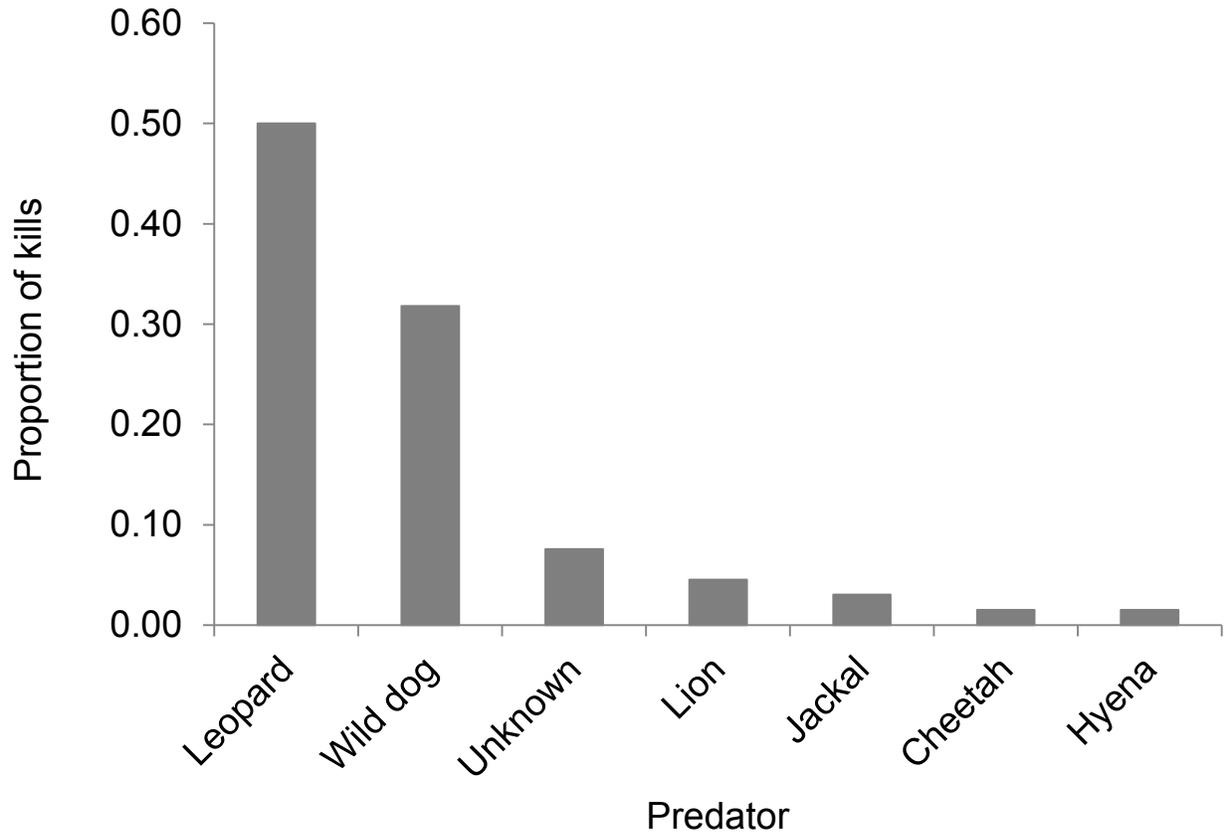


Figure S1. Proportion of impala kills ($n = 54$) attributed to predation by different large carnivores at Mpala Research Center, July 2011 and July 2012. Predator identity was assigned based on evidence at the kill location, including tracks, bite marks, and fur-removal. ‘Jackal’ refers to black-backed jackals and the ‘Hyena’ category encompasses both spotted and striped hyenas. Differences in percent woody cover at kill sites made by leopards ($11\% \pm 2$, $n = 28$), wild dogs ($8\% \pm 2$, $n = 17$), and other large carnivores combined ($10\% \pm 3$, $n = 9$) were non-significant ($F_{2,51} = 0.77$, $P = 0.47$).

Figure S2

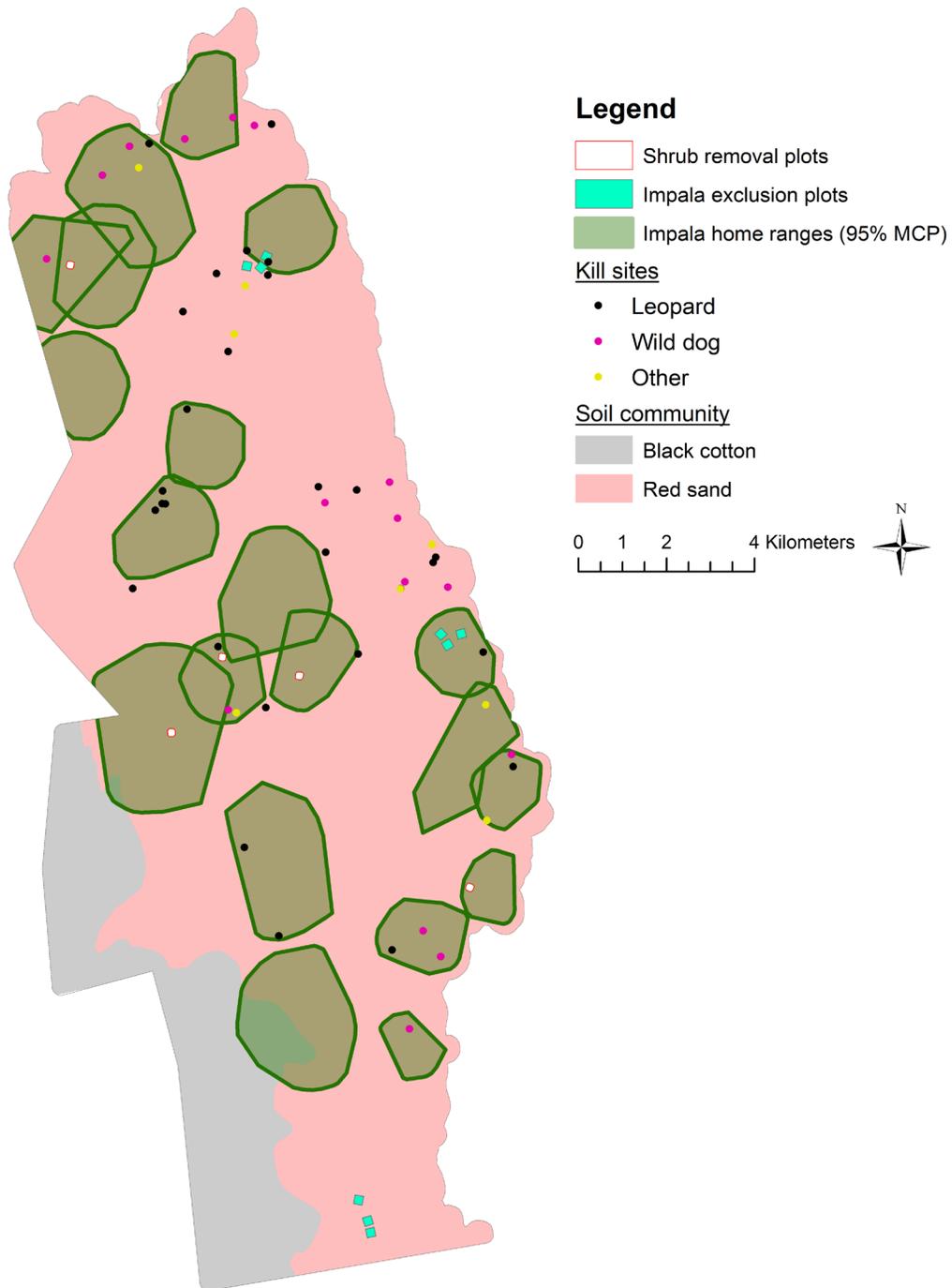


Figure S2. Distribution of home ranges (95% MCP) for GPS-collared impala, impala kill sites, shrub removal plots and impala exclusion plots located across our study area at the Mpala Research Centre, Laikipia, Kenya.

Figure S3.

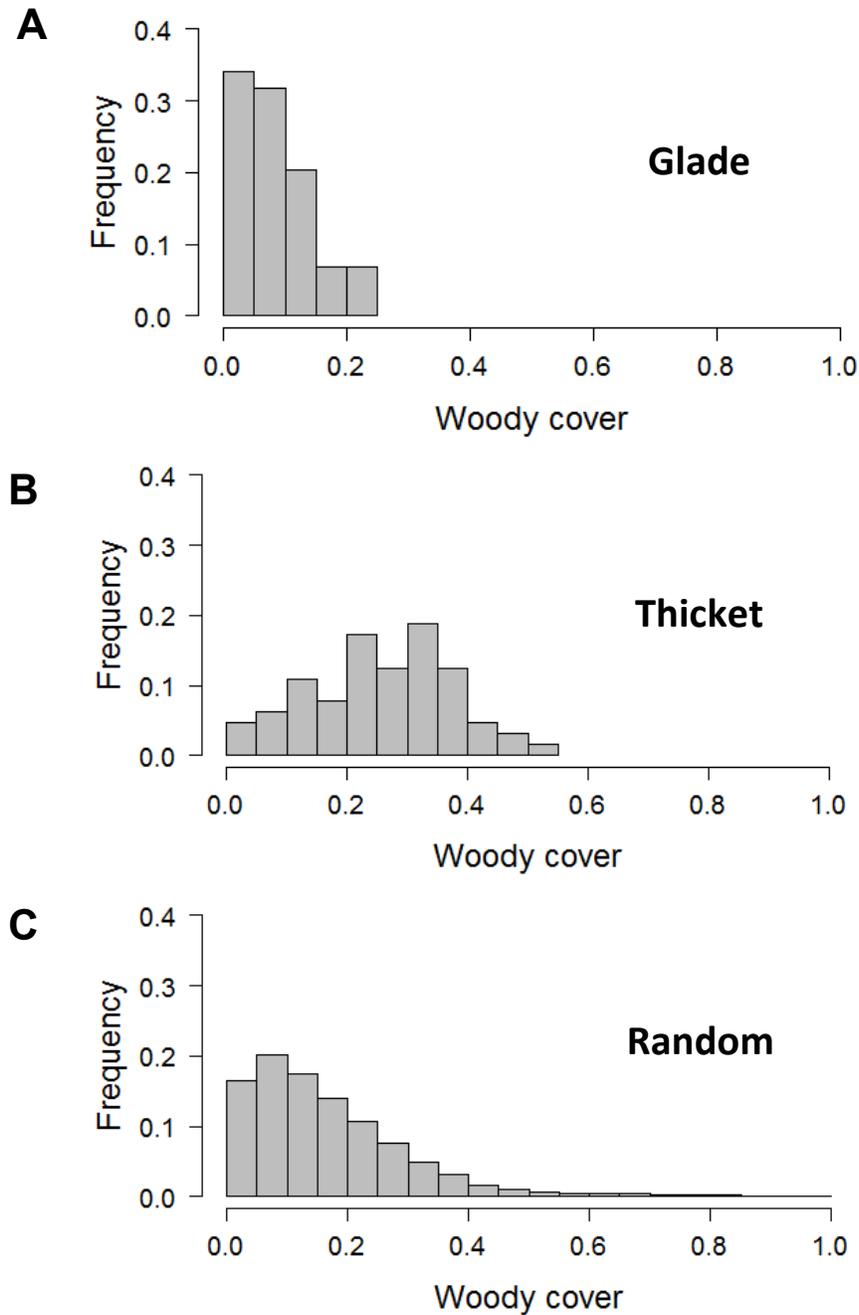


Figure S3. Satellite-derived estimates for woody cover at the mid-points of 200 m² transects located at **(A)** glades ($n = 44$) and **(B)** thickets ($n = 64$); or **(C)** at 1000 random points within each of the 95% minimum convex polygons of 20 adult female impala used in the GPS telemetry study.

Figure S4.

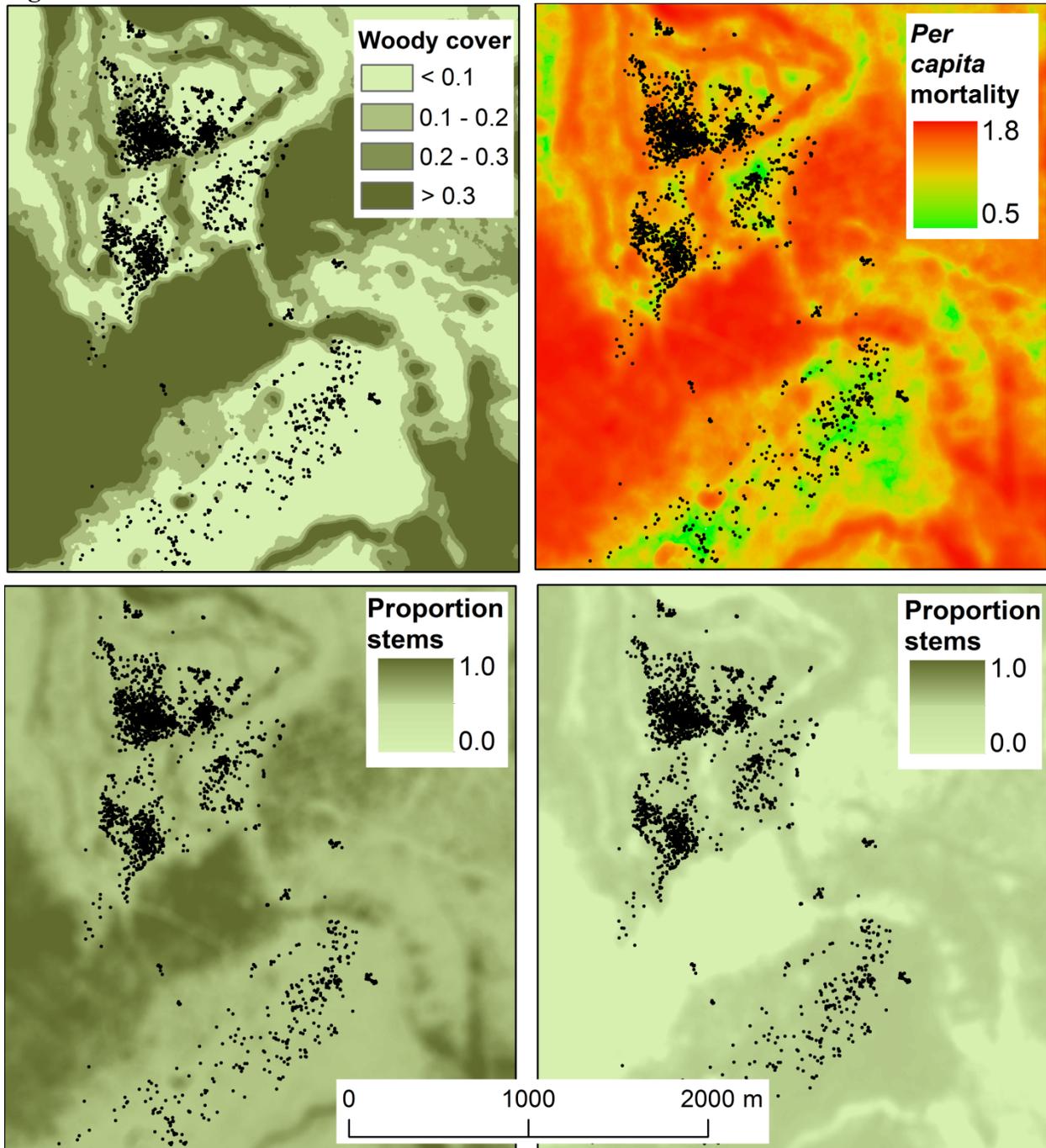


Figure S4. Spatial variation in risk and tree communities within individual impala home ranges. Black points represent a random selection 15% of the locations from a single GPS-collared impala over one year, overlaid on maps of: **(A)** proportion tree cover, classified from satellite imagery; **(B)** per capita risk of mortality from predation (see Fig. 1B); and predicted proportions of stems represented by **(C)** poorly-defended *A. brevispica*; and **(D)** well-defended *A. etbaica*.

References and Notes

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