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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Can an herbivore affect where a top predator kills its prey by modifying woody vegetation structure?

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Abstract

In large mammal communities, little is known about modification of interspecific interactions through habitat structure changes. We assessed the effects of African elephants (*Loxodonta africana*) on features of woody habitat structure that can affect predator–prey interactions. We then explored how this can influence where African lions (*Panthera leo*) kill their prey. Indeed, lions are stalk-and-ambush predators and habitat structure and concealment opportunities are assumed to influence their hunting success. During 2 years, in Hwange National Park, Zimbabwe, kill sites ($n = 167$) of GPS-collared lions were characterized (visibility distance for large mammals, distance to a potential ambush site and presence of elephant impacts). We compared characteristics of lion kill sites with characteristics of random sites (1) at a large scale (i.e. in areas intensively used by lions, $n = 418$) and (2) at the microhabitat scale (i.e. in the direct surrounding available habitat, < 150 m, $n = 167$). Elephant-impacted sites had a slightly higher visibility and a longer distance to a potential ambush site than non-impacted sites, but these relationships were characterized by a high variability. At large scale, kill sites were characterized by higher levels of elephant impacts compared to random sites. At microhabitat scale, compared to the direct nearby available habitat, kill sites were characterized by a reduced distance to a potential ambush site. We suggest a conceptual framework whereby the relative importance of habitat features and prey abundance could change upon the scale considered.

Keywords Ecosystem engineer · Indirect effects · Apex predator · Megaherbivores · Predator–prey relationships

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Introduction

Species within an ecosystem are linked by a network of interspecific interactions (e.g. predation, competition, facilitation), which ultimately drives ecosystem functioning (Wardle et al. 2004). There is an increasing awareness that these interactions are dynamic and can be mediated by abiotic (e.g. climate change—Tylianakis et al. 2008; van der Putten et al. 2010) and biotic factors (e.g. parasitism—Hatcher et al. 2006, non-lethal effects of predators that mediate interspecific prey competition—Preisser and Bolnick 2008). In these cases, the interaction between two species can be modified by a third species (hereafter “interaction modification”, Wootton 1993). This process can arise from a change of a plastic trait of one of the two main species interacting (i.e. trait-mediated interaction modification) or through alteration of the environment in which the interaction takes place (i.e. environment-mediated interaction modification, Wootton 1993, 2002; Dambacher and Ramos-Jiliberto 2007).

Questions have arisen about how habitat changes (diversity and/or physical structure) may affect interspecific interactions (Petren and Case 1998). In the current context of biodiversity loss, many studies have focused on anthropogenic alterations of the habitat (e.g. Tylianakis et al. 2007), but other ecosystem engineer species (Jones et al. 1994) can affect habitats (Crooks 2002), and ultimately interspecific interactions (Marquis and Lill 2007). Arditi et al. (2005) even designated ecosystem engineer species as "interaction modifiers" due to their capacity to modulate their environment. Interaction modifications were shown to drive community dynamics in systems with few species (Werner and Peacor 2003; Preisser et al. 2007; Abrams 2010). There is now growing impetus from other recent works to address the challenges of detecting, measuring and testing the potential role of interaction modifications in complex systems such as natural communities (e.g. Wootton 1994; Peacor and Werner 2001; Okuyama and Bolker 2007). Such an understanding is key to improve our ability to forecast how ecosystems will respond to global changes (Kéfi et al. 2012) as interaction modifications are often identified as the cause of unexpected responses to perturbation (Terry et al. 2017 and references therein).

The African elephant (*Loxodonta africana*) is an ecosystem engineer (Bond 1994). While the effects of elephants on vegetation structure through their foraging activity start to be well understood (review in Guldemond and van Aarde 2008), the consequences of elephant-induced vegetation changes on the whole ecosystem remain unknown as a diversity of indirect effects is documented (Pringle 2008; Valeix et al. 2011; Coverdale et al. 2016). In particular, little is known about the environment-mediated modifications of predator–prey relationships by elephants. Yet, elephants affect the vegetation structure, especially in the understory (Coverdale et al. 2016; Ferry 2018). Further, predation is mediated by physical features of habitats (Bell 1991; Kauffman et al. 2007) and has cascading effects down the food chain (Estes et al. 2011). To our knowledge, two studies highlighted elephant-induced modification of predator–prey relationships. Tambling et al. (2013) showed that elephants, by fragmenting very dense vegetation, improve access for lions, which may ultimately lead to an increased predation by lions on the small prey hiding in this very dense vegetation. Fležar et al. (2019) simulated elephant-induced habitat change at two spatial scales: (1) at the "patch" scale, by comparing high-quality grassland sites with high visibility against ones with low visibility (due to dense woody vegetation) and (2) at the "within-patch" scale by adding coarse woody debris, potential escape impediment for prey, in open areas. They then assessed the perceived predation risk by different herbivores. They revealed different responses of prey at the two scales and argue that depending on the scale, elephants' impact on the risk landscape could be both to hamper kill success (by opening up vegetation, improving visibility and lowering ambush opportunity) as well as facilitate kill success (by dropping woody debris that may lower visibility and create escape impediments). Elephants are thus able to modify predator–prey interactions by altering habitats and different manifestations of elephant-induced changes on the vegetation (e.g. visibility and coarse woody debris) could act at different spatial scales.

Here, we investigated whether elephants, through their impacts on vegetation structure (that lead to changes in visibility distance for large mammals and changes in the distance to a potential ambush site), can influence predator–prey interactions between African lions (*Panthera leo*) and their prey in a woody savanna ecosystem. Lions are stalk-and-ambush predators that rely on features of the habitat providing concealment (typically dense vegetation) to approach and attack their prey (Hopcraft et al. 2005; Loarie et al. 2013; Davies et al. 2016). Therefore, habitat characteristics are expected to play an important role in selecting areas that may increase hunting success (the ambush-habitat hypothesis—Hopcraft et al. 2005). This has been illustrated in Kruger National Park, South Africa, where lions kill their prey within nine metres of a potential ambush site (Loarie et al. 2013). Elephants are thus likely to affect where lions hunt and/or successfully hunt (i.e. kill) their prey.

The aim of this study is twofold: (1) to assess whether elephant impacts on woody vegetation are associated with an increased visibility and a change in the distance to a potential ambush site, and (2) to test the hypothesis that lions kill less in areas impacted by elephants (as we expect them to be more successful hunters in areas with denser vegetation thus greater opportunities for concealment). This second aim was investigated at two different scales: (1) we first compared lion kill sites with random sites in areas intensively used by lions to assess if among all habitats used by lions, kill sites were characterized by denser vegetation and less elephant impacts (the "large" scale hereafter), and (2) we then compared the characteristics of lion kill sites with characteristics of the direct surrounding available habitat (< 150 m) to assess if lions killed more in closed microhabitats that were less impacted by elephants (the "microhabitat" scale hereafter). Together, the results will allow an assessment of the extent to which elephants can induce environment-mediated trophic interaction modification between lions and their prey in woodland savannas and if this modification is scale-dependent.

Materials and methods

Study site

Hwange National Park covers ~ 15,000 km^2 of semi-arid dystrophic (low nutrient soil) savanna in western Zimbabwe

(19° 00′ S, 26° 30′ E). The vegetation is primarily woodland and bushland savanna. The east and southern parts of the park are dominated by open wooded savannas on Kalahari sands, primarily teak woodland (*Baikiaea plurijuga)* and *Combretum/Terminalia* woodlands. Batoka basalt and Karoo sediments in the north and north-west of the park are dominated by *Colophospermum mopane* woodlands interspersed with grassland vleis. The long-term mean annual rainfall is ~ 600 mm, which falls primarily between October and April. The surface water available to animals is found in natural as well as artificial waterholes. The study area is located in the northern region of Hwange National Park (~ 7000 km^2) where lion density is estimated around to be 4.3 individuals/100 km^2 (Loveridge et al. 2016), and elephant density is estimated above two individuals/km^2 (Chamaillé-Jammes et al. 2008).

Data

We collected data between 2014 and 2015 from 12 female and 15 male lions from different coalitions and prides equipped with 2D size AWT GPS radio-collars. The lions' locations were available hourly and for some lions every 2 h, day and night. Potential lion kills were attained by identifying clusters of coordinates that had more than 4 h of sequential locations within a defined proximity (150 m, see also Tambling et al. 2010). In the field, these clusters were searched for a carcass or the remains of a carcass and classified as kill sites based on the evidence of a kill. We confirmed lion kills when the presence of a carcass was associated with indications of a hunt/struggle from animal tracks (observed by skilled field trackers) and/or broken and tramped vegetation and/or from the condition of any remaining hide bearing claw and bite marks typical of lion predation. Carcasses found were classified to species based on the body size of the animal killed and the presence of identifiable material, such as horns, jaws, bones, and hair. We made the assumption that the kill site is a good proxy of the environment within which the lion decided to start the hunt, as lion is a stalk-and-ambush predator attacking and killing prey at short distances (van Orsdol 1984; Haas et al. 2005). This assumption has been made in several previous works (Davidson et al. 2012, 2013; Loarie et al. 2013; Davies et al. 2016). In total, 705 clusters were monitored among which 167 were identified as kill sites and 538 were not (called "non-kill sites" hereafter). For the 167 kill sites and for 251 non-kill sites, we identified a paired random site (with a random direction, a random distance between 50 and 150 m from the kill for kill sites and from the GPS point identified as the start of the cluster for non-kill sites). In total, 418 random sites were characterized and represented habitats intensively used by lions. Among these random sites, 167 were associated to a kill site and represented the direct surrounding available habitat. For each kill site, non-kill site and random site, we measured the distance to a potential ambush site (DPAS hereafter, a potential ambush site was any habitat feature able to conceal a lying lion, i.e. most of the time a dense bush in the study ecosystem) and the visibility. Visibility at each site was assessed by using two 50 cm × 50 cm white boards. The two boards were set so that one board was at 10–60 cm (representative of the height of a crawling lion) and the other was at 100–150 cm (representative of a standing lion). One person stood at the location of the kill or at the centre of the random site, while another person held the boards, walked away from the centre in the four cardinal directions and recorded the distance at which the person at the centre of the site could not see each board anymore. The four distances obtained from the four cardinal directions were then averaged ("visibility" hereafter). As lions are more successful at capturing prey when attacks are launched at short distance (< 7.6 m for Thomson's gazelle, 15 m for wildebeest and zebras, Haas et al. 2005), elephant impacts were assessed within a 25 m radius of the kill for the kill sites, of the random point for the random sites and of the GPS point identified as the start of the non-kill sites. The extent of elephant impact was determined by the definition of five classes of percentage of trees impacted by elephants (broken, coppiced and/or uprooted): class 0: no impact; class 1: [1–25%]; class 2: [26–50%]; class 3: [51–75%]; and class 4: [76–100%].

Analyses

Proximity to water is commonly thought to influence the level of herbivore impacts on the vegetation (i.e. the "piosphere effect", Lange 1969), but this has recently been debated in wild protected areas (Chamaillé-Jammes et al. 2009). We therefore preliminarily checked the existence of a link between distance to water and the existence of elephant impacts on the vegetation and found that sites (random sites and kill sites) impacted by elephants were not located closer to waterholes than sites not impacted by elephants (Kruskal–Wallis test, $\chi^2 = 5.51$, $df = 3$, p value = 0.14).

Effect of elephants on woody habitat structure

Visibility at 100–150 cm was highly correlated to visibility at 10–60 cm ($r = 0.91$, $t = 75$, $df = 1121$, $p < 0.001$), so only results on the visibility at 10–60 cm (visibility hereafter) were considered in the subsequent analyses. We assessed the effect of the level of elephant impacts on (1) the visibility with a simple linear model performed on log-transformed visibility data and on (2) the DPAS with a truncated linear regression as data distribution was left truncated at 0 m on log-transformed DPAS data ('truncreg' package from open source Software R 3.3.1 R Development Core Team 2013).

All kill sites, all non-kill sites and all random sites were included in this analysis to best describe the link between the level of elephant impact and the vegetation characteristics.

Lion kill site characteristics

For the subsequent analyses, non-kill sites were excluded as they could have represented any lion's activity (e.g. resting site). These sites could have been under selection by lions (e.g. habitat with higher woody cover for shadow preferred) and thus led to a bias in our results/interpretation. At the large scale, we compared the characteristics of lion kill sites with characteristics of the habitats of all the random sites (associated to kill sites and to non-kill sites), representing areas intensively used by lions. We used logistic regressions to develop resource selection functions (RSF), with the dependent variable being 1 for kill sites and 0 for random sites. We performed a first logistic regression to assess if lions kill more in low-visibility environments where prey can be closely approached thanks to low DPAS. For this first logistic regression, the explanatory variables are visibility and DPAS. No strong correlation was observed between these two variables, which were therefore kept for the analyses (Pearson's correlation coefficient visibility–DPAS = 0.38). We performed a second logistic regression to assess if the level of elephant impacts on vegetation structure influences lion kill site location. In this second logistic regression, the explanatory variable was the level of elephant impacts. A model selection was performed using the function "dredge" ('MuMin' package) using the Bayesian information criterion (BIC) for a compromise between the explanatory power and the parsimony of the models and model averaging was performed on all the models (Burnham and Anderson 2004). Variables considered as important were those for which $\beta \pm 1.96 \times \mathrm{SE}$ did not include zero. At the microhabitat scale, we compared the characteristics of lion kill sites with the characteristics of the direct surrounding available habitat (represented by the random site associated to each kill site). A paired generalized estimating equation (GEE) model was performed using the package "gee" to remove all the variability between the different pairs and focus only on the variability within each pair (Liang and Zeger 1986). We conducted the same two regression analyses as above. For this analysis, the quasi-likelihood criterion (QIC) was used (Liang and Zeger 1986) and a model averaging was performed on all the models. As no difference between lion sexes was observed (Online Resource 1), all kill sites identified were used and pooled together independently of whether the kill site was found using GPS collar data from a female or a male lion. Further, our data did not allow assessing if the collared individual was the one that made the kill, and male and female lions were regularly observed together (70.1% of all lions' observations) in Hwange National Park at the time of the study.

Results

Kills were not evenly distributed over the different classes of shrub layer cover and over the different prey species (Online Resource 2). The main prey of lions were greater kudu *Tragelaphus strepsiceros* (27%), followed by African buffalo *Syncerus caffer* (20%) and plains zebra *Equus quagga* (12%, Online Resource 2). DPAS and visibility at kills for each prey species are presented in Online Resource 3.

Effect of elephants on woody vegetation structure

For each class of level of elephant impacts (0: no impact; 1: [1–25%]; 2: [26–50%]; 3: [51–75%]; and 4: [76–100%]), the number of study sites (including all kill sites, non-kill sites and random sites) was, respectively, 453, 275, 205, 132, and 55. The log visibility increased as the level of elephant impacts increased (estimate ± SE = 0.14 ± 0.015, $t = 9.04$, $p < 0.001$, Table 1a, Fig. 1a), and the log-transformed DPAS also increased as the level of elephant impacts increased (estimate ± SE = 0.17 ± 0.02, $t = 7.5$, $p < 0.001$), Table 1b, Fig. 1b). On average, there was a difference of 14 m for the visibility ($\mathrm{mean}_{\mathrm{Level\ 0}} = 16.7$ m, $\mathrm{mean}_{\mathrm{Level\ 4}} = 30.7$ m) and 3 m for the DPAS ($\mathrm{mean}_{\mathrm{Level\ 0}} = 2.4$, $\mathrm{mean}_{\mathrm{Level\ 4}} = 5.4$ m) between habitats not impacted by elephants and those with the highest level of elephant impacts. It is noteworthy that there exists a high variability in the visibilities and the DPAS (Fig. 1).

Table 1 Estimated mean and confidence interval at 95% for each level of elephant impacts of (a) the visibility (m) and (b) the distance to a potential ambush site (DPAS) (m)

	% of impacted trees	2.5%	Mean	97.5%
a				
0	0	15.7	16.7	17.8
1	[1, 25]	17.5	20.5	24
2	[26, 50]	20	23.7	28
3	[51, 75]	20.6	24.8	29.9
4	[76, 100]	24	30.7	39.1
b				
0	0	2.1	2.4	2.7
1	[1, 25]	2.5	3.5	4.7
2	[26, 50]	3.5	4.8	6.5
3	[51, 75]	3.2	4.5	6.3
4	[76, 100]	3.5	5.4	8.1

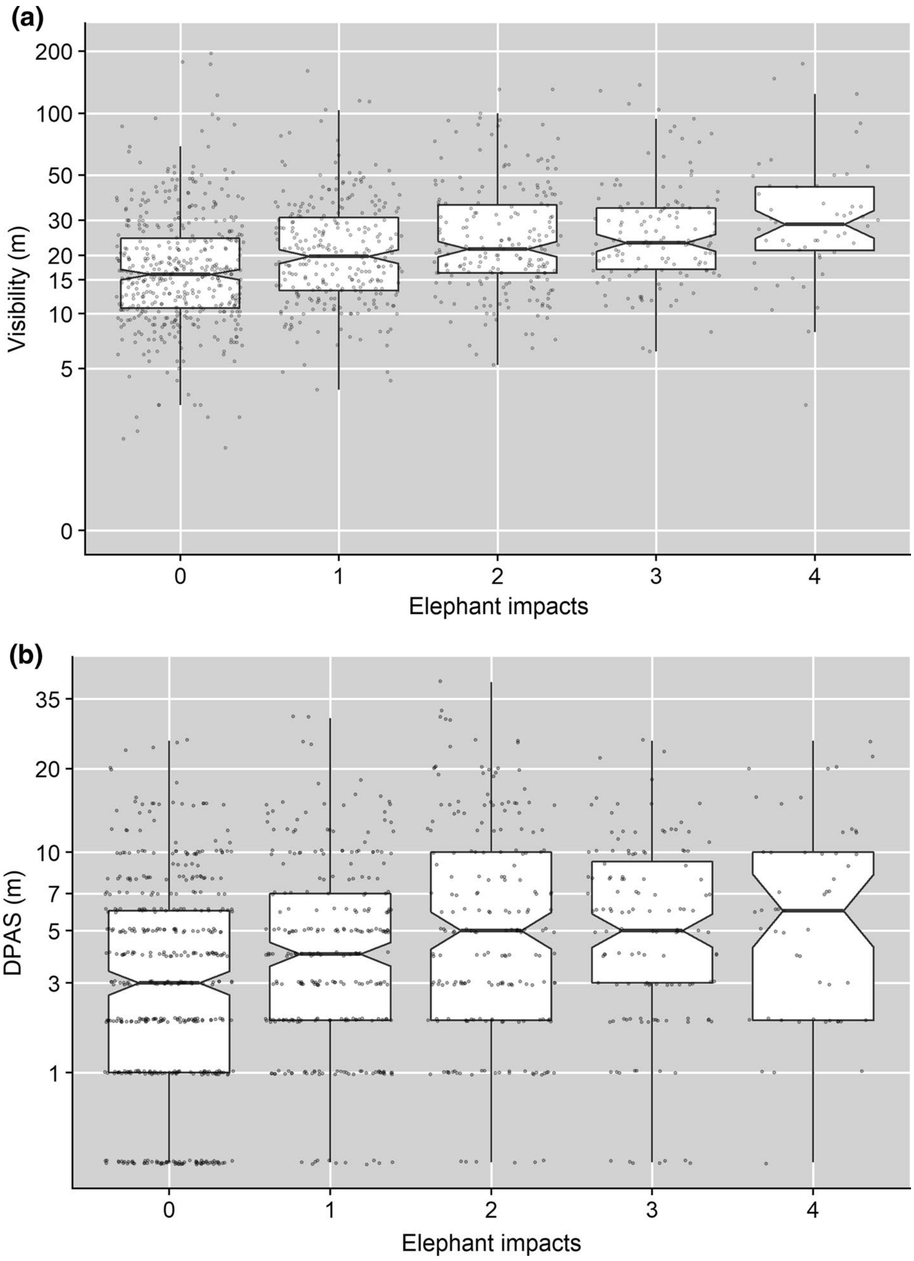


Fig. 1 Boxplot distribution of **a** the visibility and **b** the distance to a potential ambush site (DPAS) according to the five classes of level of elephant impacts, i.e. of percentage of trees impacted by elephants (broken, coppiced and/or uprooted): class 0: no impact; class 1: [1–25%]; class 2: [26–50%]; class 3: [51–75%]; and class 4 [76–100%]. The notch represents the 95% confidence interval of the median. Points represent raw data using geom_jitter function from *ggplot2* package (Wickham 2016)

Lion kill site characteristics

In the first analyses at large scale, comparing kill sites to all the random sites, representing available habitat in areas intensively used by lions, we revealed that the level of elephant impacts was the only variable to explain lion kill site characteristics (Table 2a). Lion kills were located in habitats with higher levels of elephant impacts (estimate ± SE = 0.27 ± 0.09, Fig. 2a, see Online Resource 4 for raw data). At the microhabitat scale, when we compared the characteristics of lion kill sites to the characteristics of the direct surrounding habitat (within-pair comparison approach), we revealed that the DPAS was the only variable to explain lion kill site characteristics (Table 2b). Lion kill sites w7ere preferentially located in habitats characterized by a reduced DPAS compared to the direct nearby available habitat (estimate ± SE = − 0.44 ± 0.19, Fig. 2b). In the kill sites, the mean DPAS value was 5.86 m, whereas it was 7.56 m in the random sites representing a decrease of 1.7 m (22% of the mean DPAS value of random sites).

Discussion

In this study, we first assessed the effects of elephants on features of woody habitat structure that can be key for the ecology of predator–prey interactions, i.e. visibility and

Table 2 Logistic models examining (1) the effect of visibility (Vis) and distance to a potential ambush site (DPAS) on lion kill site location and (2) the effect of the level of elephant impacts (Ele) on lion kill site location

(a) Large scale—kill sites vs all random sites

(1) Kill sites/random sites ~ DPAS + Vis

	Candidate models	*df*	BIC	Δ*i*	w_i	bcc w_i
1	Null	1	702.2	0.00	0.453	0.453
2	DPAS	2	702.7	0.45	0.361	0.814
3	Vis + DPAS	3	704.3	2.06	0.162	0.976
4	Vis	2	708.1	5.89	0.024	1

Variable	Average β	SE
Vis	0.22	0.25
DPAS	−0.06	0.13

(2) Kill sites/random sites ~ Ele

	Candidate models	*df*	BIC	Δ*i*	w_i	bcc w_i
1	Ele	2	696.6	0	0.943	0.943
2	Null	1	702.2	5.62	0.057	1

Variable	Average β	SE
Ele	0.25	0.09

(b) Microhabitat scale—kill site vs paired random site

(1) Kill site/paired random site ~ DPAS + Vis

	Candidate models	QIC	Δ*i*	w_i	bcc w_i
1	Vis + DPAS	310.5	0.00	0.436	0.436
2	DPAS	310.6	0.13	0.408	0.844
3	Vis	312.7	2.22	0.144	0.988
4	Null	317.6	7.1	0.013	1

Variable	Average β	SE
Vis	−0.33	0.27
DPAS	−0.44	0.19

(2) Kill site/paired random site ~ Ele

	Candidate models	QIC	Δ*i*	w_i	bcc w_i
1	Null	317.6	0	0.596	0.596
2	Ele	318.4	0.78	0.404	1

Variable	Average β	SE
Ele	0.004	0.07

(a) Approach at the large scale, comparing the characteristics of kill sites to characteristics of all random sites in areas intensively used by lions. (b) Approach at the microhabitat scale, comparing the characteristics of kill sites to characteristics of paired random site representing the direct surrounding available habitat (< 150 m). Models are ranked according to their BIC or QIC. Model-averaged estimates for the variables ± standard error are shown at the bottom of each table. Variables considered as important were those for which $\beta \pm 1.96 \times \mathrm{SE}$ did not include zero

distance to a potential ambush site. Elephant-induced vegetation changes tended to be associated with an increase in visibility (as observed by Valeix et al. 2011). Regarding distance to a potential ambush site, elephants could either increase it (e.g. by removing large bushes or by reducing the crown diameter of bushes—see Ferry 2018) or reduce it (e.g. by uprooting or breaking trees, which can create ambush sites behind the trunk, branches and foliage on the ground). Overall, in Hwange National Park, elephant-induced vegetation changes tended to be associated with an increase in distance to a potential ambush site. Even though these average differences were not very large, they can make a

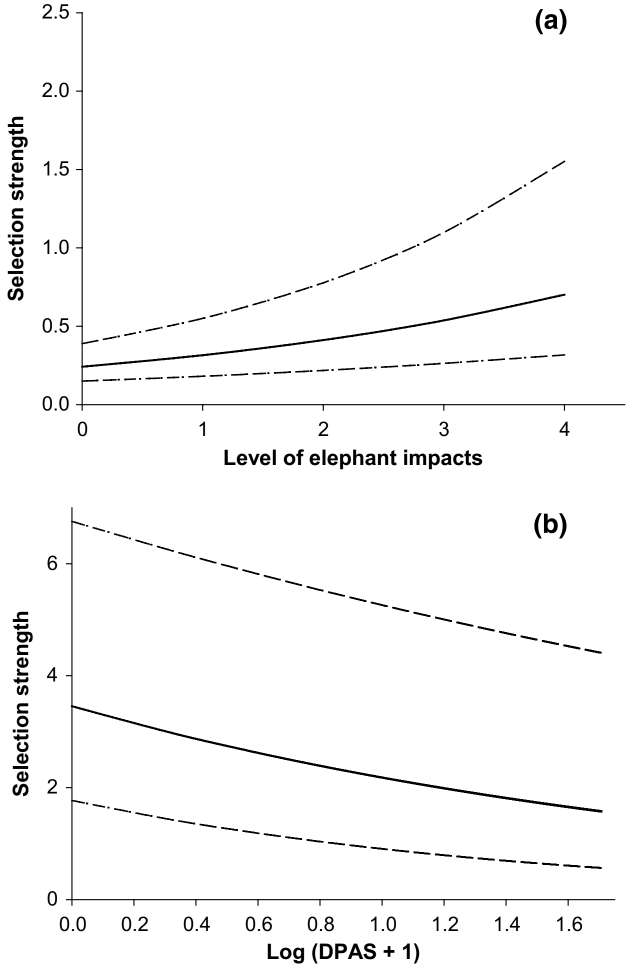
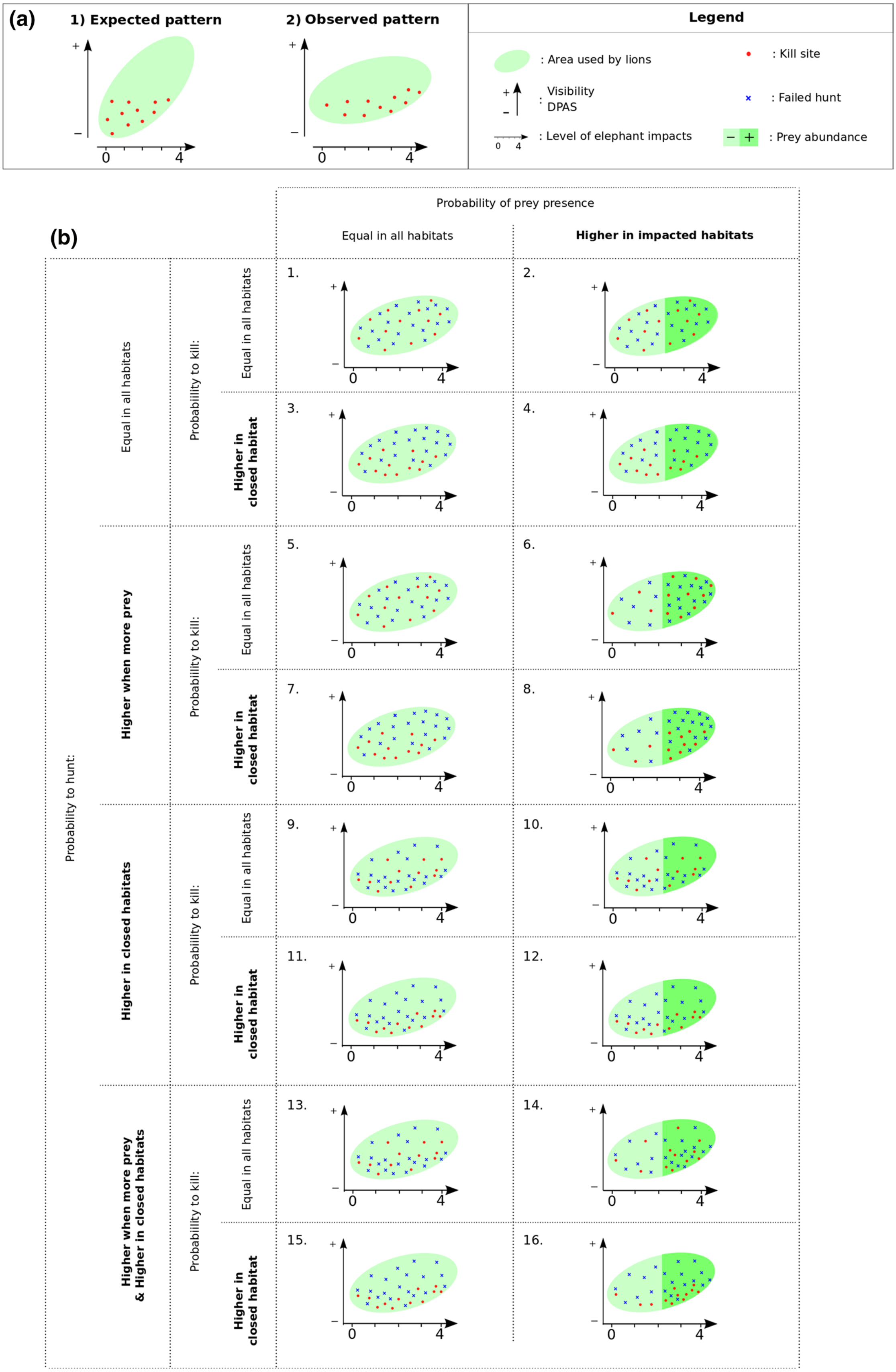


Fig. 2 **a** Relationship between the level of elephant impacts and the strength of this factor on lions' kill site location at the large scale. **b** Relationship between the log-transformed DPAS (for DPAS ranging from 0 to 50 m) and the strength of this factor on lions' kill site location at the microhabitat scale. The selection strength is exp ($\beta0 + \beta1 \times$ level of elephant impacts) at the large scale and exp ($\beta0 + \beta1 \times \log(\text{DPAS} + 1)$) at the microhabitat scale, where $\beta0$ is the intercept estimate and $\beta1$ is the estimated coefficient for the level of elephant impacts at the large scale and for log(DPAS + 1) at the microhabitat scale. Dotted lines represent the standard errors

difference in dense habitats considering the hunting behaviour of lions, which kill their prey close to dense vegetation (e.g. within 9 metres of a potential ambush site—Loarie et al. 2013). Hence, elephants, by altering visibility and distance to potential ambush site, are likely to affect where lions choose to hunt and/or where they hunt successfully in woodland. Following the ambush-habitat hypothesis (Hopcraft et al. 2005), we initially expected lions to kill more in habitats with lower level of elephant impacts and characterized by lower visibility and a shorter distance to potential ambush site, thus more favourable to lion hunting success (Fig. 3a—expected pattern). This assumption can appear to be in opposition with the results from Tambling et al. (2013) and Davies et al. (2016). This can be explained by the fact that, in these studies, habitats not impacted by elephants were actually so dense (average distance to cover < 1 m) that lions were not able to move and hunt inside this dense vegetation, which could be therefore used as a refuge by small prey species (e.g. the duiker *Sylvicapra grimmia*).

In this study, we were limited on the inferences we could make because of two main limitations in our data. The first one is that we were not able to identify hunts in which lions failed, which prevented us from assessing whether there were more kills in a habitat because lions hunted more in this habitat or had a higher hunting success there. The second limitation is the lack of information about the contextual abundance and distribution of herbivores during the hunt, which could influence the kill site location as expected under the prey-abundance hypothesis. To partly fill these gaps, we suggest a conceptual framework with different scenarios that could explain the patterns observed based on three different parameters: the probability of prey presence, the probability to hunt (depending either on prey presence or on habitat openness), and the probability to kill a prey (i.e. to hunt successfully) (Fig. 3b). Patterns 3,9 and 11 represent our initial hypothesis, without assumption on prey distribution and with the probability to hunt and/or kill being linked to habitat features only (following the ambush-habitat hypothesis, with more hunt/kills in habitats less impacted by elephants, less open).

Contrary to our expectations, at the large scale, when we compared the characteristics of lion kill sites to the characteristics of random sites in areas intensively used by lions, kills were more located in woody habitats characterized by higher levels of elephant impacts, but we did not detect a selection for a lower visibility and a shorter distance to a potential ambush site. This result suggests that other factors than habitat structural features drive lion hunting behaviour at this scale, such as the presence and abundance of prey (i.e. the prey-abundance hypothesis, Hopcraft et al. 2005). If this is the case, it assumes that herbivores select habitats impacted by elephants (representing all the even numbered patterns in Fig. 3). This selection pattern may arise from (1) a coincidence with elephants and other herbivores using the same habitats, (2) a reduced perceived risk of predation in elephant-impacted habitats due to the higher visibility caused by elephants in these habitats for all herbivore species (Underwood 1982; Valeix et al. 2011), and/or (3) a facilitative effect of elephants that may increase browse availability at lower heights within reach of smaller browsers by stimulating tree coppicing, a mechanisms known as "browsing lawns" (Rutina et al. 2005; Fornara and du Toit 2007). Hence, the fact that lion kills were preferentially found in elephant-impacted habitats at the large scale could be explained by a selection for areas where prey are abundant (patterns 6, 8, 14 and 16, Fig. 3) and elephants could


(a)
1) Expected pattern
2) Observed pattern
Legend
: Area used by lions
: Kill site
Visibility
DPAS
: Failed hunt
: Level of elephant impacts
: Prey abundance
(b)
Probability of prey presence
Equal in all habitats
Higher in impacted habitats
Probability to hunt:
Equal in all habitats
Higher when more prey
Higher in closed habitats
Higher when more prey & Higher in closed habitats
Probability to kill:
Equal in all habitats
Higher in closed habitat
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◀**Fig. 3** **a** Representation of the expected pattern under our initial hypotheses and the observed pattern. (1) Expected pattern—under our initial hypotheses, we expected higher visibilities and DPAS in habitats with higher levels of elephant impacts, as well as more lion kill sites in habitats characterized by a lower visibility and a shorter DPAS, and thus more kills in non-impacted habitats. (2) Observed pattern—an increased visibility and DPAS were effectively observed with the increase of the level of elephant impacts but not as strongly as expected (see the shape of the green area). At the large scale, lion kills were, unexpectedly, more in highly elephant-impacted habitats. At the microhabitat scale, lion kill sites were more in habitat characterized by a shorter DPAS. **b** Representation of the different scenarios envisaged to explain the observed pattern. We played on the combination of three variables: the probability of prey presence, the probability that a hunt will occur (with lions hunting more in high prey abundance habitat and/or with lions hunting more in closed habitats), and (3) the probability of a kill, i.e. of a successful hunt (with lions having a higher success rate in closed habitat). Patterns 8, 14 and 16 appear to be the most likely to explain the observed pattern

be considered as interaction modifiers if they influence prey habitat selection. Evidences about the role of elephants in other herbivore woody habitat selection at this scale still need to accumulate (e.g. herbivore distribution data thanks to camera traps placed on contrasted elephant-impacted habitats).

At the microhabitat scale (the within-pair comparison between a kill site and its paired random site), results revealed that lion kills were not preferentially located in habitats impacted by elephants anymore. At this scale, lion kill sites were preferentially located in habitats characterized by a shorter distance to a potential ambush site (patterns 3, 4, 7–16, Fig. 3), supporting here our hypothesis of the role of prey catchability (ambush-habitat hypothesis). Interestingly, the visibility did not seem to be a factor as important as the distance to a potential ambush site. An explanation could be that, whatever the visibility, the presence of a few large bushes/broken trees as potential ambush sites is sufficient to lead to a higher probability of kill even in woody habitats with a high visibility. Finally, when combining the two different scales, the only patterns to explain the observed pattern (Fig. 3a—observed pattern) with both more kills in impacted habitat at the large scale and more kills in closed habitat at the microhabitat scale are patterns 8, 14 and 16. These patterns share the same processes: prey select elephant-impacted habitats and a higher probability to hunt in habitat with more prey (prey-abundance hypothesis). However, they differ in terms of probability to hunt or to kill in closed habitats. Pattern 8 needs a higher probability to kill in closed habitats, pattern 14 needs a higher probability to hunt in closed habitats and pattern 16 needs both of them, suggesting therefore that lions are influenced by habitat structure during the hunting process at the microhabitat scale (ambush-habitat hypothesis).

Therefore, our results suggest that the main driver of kill site location for lions is likely to be prey abundance at a first scale of selection, and prey catchability at the scale of the direct nearby available habitat (< 150 m). As suggested in previous studies, the prey-abundance and the ambush-habitat hypotheses are not exclusive and could interact with one another to explain lion hunting behaviour (Davidson et al. 2012). Therefore, by affecting the woody vegetation structure, elephants could play an important role in the intensity of predator–prey relationships although in complex ways, as they could act on both predators and prey's behaviour, with different mechanisms involved depending on the scale considered (as suggested by Fležar et al. 2019). We encourage future research to confirm that herbivores select woody habitats impacted by elephants because of the elephant's engineering process and not because of simple coincidence or shared resources. Further, a focus on identifying unsuccessful hunts will be needed to disentangle the roles of the probability to hunt and the probability to kill in closed habitats. This would ultimately help to know which process is influenced by the vegetation structure during the lion hunting behaviour in woodland areas. This task is both conceptually and practically a challenging one, although perhaps it can be accomplished through the deployment of GPS collars with integrated tri-axial accelerometer–magnetometer (see for example Fröhlich et al. 2012; Wilmers et al. 2017).

Despite remaining questions regarding the underlying mechanisms, our study suggests that elephants have the potential to influence predator–prey interactions in their ecosystem. In a context of rapidly changing elephant populations worldwide (Chase et al. 2016), it is of importance to understand their indirect role on interspecific interactions. Our results reinforce the idea that elephants, through ecosystem engineering, could act on a multitude of broad-scale ecological processes in wooded savannas (Kerley and Landman 2006). Further, whereas previous studies of ecosystem engineers have highlighted their effects on other species abundance and richness (Jones et al. 1997), our findings demonstrate the importance of their indirect effect on interspecific interactions (see also Arditi et al. 2005; Marquis and Lill 2007 and references therein). Finally, we highlighted the importance of multi-scale consideration in interspecific interactions and their modification (see also Fležar et al. 2019). We therefore hope these findings will promote studies on interaction modification, with a multi-scale component (Tylianakis and Morris 2017) in large mammal communities.

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References

Abrams PA (2010) Implications of flexible foraging for interspecific interactions: lessons from simple models. Funct Ecol 2(4):7–17. https://doi.org/10.1111/j.1365-2435.2009.01621.x

Arditi R, Michalski J, Hirzel AH (2005) Rheagogies: modelling non-trophic effects in food webs. Ecol Complex 2:249–258. https://doi.org/10.1016/j.ecocom.2005.04.003

Bell WJ (1991) Searching behavior: the behavioural ecology of finding resources. Chapman & Hall, New York

Bond WJ (1994) Keystone species. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Springer, Berlin, pp 237–253

Burnham KP, Anderson DR (2004) Multimodel inference. Sociol Methods Res 33:261–304. https://doi.org/10.1177/0049124104268644

Chamaillé-Jammes S, Fritz H, Valeix M, Murindagomo F, Clobert J (2008) Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. J Anim Ecol 77:135–144. https://doi.org/10.1111/j.1365-2656.2007.01307.x

Chamaillé-Jammes S, Fritz H, Madzikanda H (2009) Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. Ecography 32:871–880. https://doi.org/10.1111/j.1600-0587.2009.05785.x

Chase MJ et al (2016) Continent-wide survey reveals massive decline in African savannah elephants. PeerJ 4:e2354. https://doi.org/10.7717/peerj.2354

Coverdale TC et al (2016) Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. Ecology 97:3219–3230. https://doi.org/10.1002/ecy.1557

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Dambacher JM, Ramos-Jiliberto R (2007) Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. Q Rev Biol 82:227–250. https://doi.org/10.1086/519966

Davidson Z, Valeix M, Loveridge AJ, Hunt JE, Johnson PJ, Madzikanda H, Macdonald DW (2012) Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. J Mammal 93:677–685. https://doi.org/10.1644/10-mamm-a-424.1

Davidson Z, Valeix M, Van Kesteren F, Loveridge AJ, Hunt JE, Murindagomo F, Macdonald DW (2013) Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. PLoS One 8:e55182. https://doi.org/10.1371/journal.pone.0055182

Davies AB, Tambling CJ, Kerley GI, Asner GP (2016) Effects of vegetation structure on the location of lion kill sites in African Thicket. PLoS One 11:e0149098. https://doi.org/10.1371/journal.pone.0149098

Estes JA et al (2011) Trophic downgrading of planet earth. Science 333:301–306. https://doi.org/10.1126/science.1205106

Ferry N (2018) Processes involved in the functioning of large mammal communities: the role of the African elephant in the ecology of predator–prey relationships. University of Lyon, Lyon

Fležar U et al (2019) Simulated elephant-induced habitat changes can create dynamic landscapes of fear. Biol Conserv 237:267–279. https://doi.org/10.1016/j.biocon.2019.07.012

Fornara DA, du Toit JTD (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. Ecology 88:200–209. https://doi.org/10.1890/0012-9658(2007)88%5b200:blroan%5d2.0.co;2

Fröhlich M, Berger A, Kramer-Schadt S, Heckmann I, Martins Q (2012) Complementing GPS cluster analysis with activity data for studies of leopard (*Panthera pardus*) Diet. S Afr J Wildl Res 42:104–110. https://doi.org/10.3957/056.042.0208

Guldemond R, van Aarde R (2008) A meta-analysis of the impact of African Elephants on savanna vegetation. J Wildl Manag 72:892–899. https://doi.org/10.2193/2007-072

Haas SK, Hayssen V, Krausman PR (2005) Panthera leo. Mamm. Species 762:1–11. https://doi.org/10.1644/1545-1410(2005)762[0001:PL]2.0.CO;2

Hatcher MJ, Dick JT, Dunn AM (2006) How parasites affect interactions between competitors and predators. Ecol Lett 9:1253–1271. https://doi.org/10.1111/j.1461-0248.2006.00964.x

Hopcraft JGC, Sinclair ARE, Packer C (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. J Anim Ecol 74:559–566. https://doi.org/10.1111/j.1365-2656.2005.00955.x

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. https://doi.org/10.2307/3545850

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957. https://doi.org/10.1890/0012-9658(1997)078%5b1946:paneoo%5d2.0.co;2

Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS (2007) Landscape heterogeneity shapes predation in a newly restored predator–prey system. Ecol Lett 10:690–700. https://doi.org/10.1111/j.1461-0248.2007.01059.x

Kéfi S et al (2012) More than a meal integrating non-feeding interactions into food webs. Ecol Lett 15:291–300. https://doi.org/10.1111/j.1461-0248.2011.01732.x

Kerley GI, Landman M (2006) The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets: elephant conservation. S Afr J Sci 102:395–402

Lange RT (1969) Piosphere—sheep track and dung patterns. J Range Manag 22:396–400

Liang KY, Zeger SL (1986) Longitudinal data analysis using generalized linear models. Biometrika 73:13–22. https://doi.org/10.1093/biomet/73.1.13

Loarie SR, Tambling CJ, Asner GP (2013) Lion hunting behaviour and vegetation structure in an African savanna. Anim Behav 85:899–906. https://doi.org/10.1016/j.anbehav.2013.01.018

Loveridge AJ, Valeix M, Chapron G, Davidson Z, Mtare G, Macdonald DW (2016) Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. Biol Conserv 204:247–254. https://doi.org/10.1016/j.biocon.2016.10.024

Marquis RJ, Lill JT (2007) Effects of arthropods as physical ecosystem engineers on plant-based trophic interaction webs. In: Ohgushi T (ed) Ecological communities. Cambridge University Press, Cambridge, pp 246–274. https://doi.org/10.1017/cbo9780511542701.012

Okuyama T, Bolker BM (2007) On quantitative measures of indirect interactions. Ecol Lett 10:264–271. https://doi.org/10.1111/j.1461-0248.2007.01019.x

Peacor SD, Werner EE (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. Proc Natl Acad Sci USA 98:3904–3908. https://doi.org/10.1073/pnas.071061998

Petren K, Case TJ (1998) Habitat structure determines competition intensity and invasion success in gecko lizards. Proc Natl Acad Sci USA 5:11739–11744. https://doi.org/10.1073/pnas.95.20.11739

Preisser EL, Bolnick DI (2008) The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. PLoS One 3:e2465. https://doi.org/10.1371/journal.pone.0002465

Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. Ecology 88:2744–2751. https://doi.org/10.1890/07-0260.1

Pringle RM (2008) Elephants as agents of habitat creation for small vertebrates at the patch scale. Ecology 89:26–33. https://doi.org/10.1890/07-0776.1

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org. Accessed 2018

Rutina LP, Moe SR, Swenson JE (2005) Elephant Loxodonta africana driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. Conserv Biol 11:207–213. https://doi.org/10.2981/0909-6396(2005)11%5b207:eladwc%5d2.0.co;2

Tambling CJ, Cameron EZ, du Toit JT, Getz WM (2010) Methods for locating African lion kills using global positioning system movement data. J Wildl Manag 74:549–556. https://doi.org/10.2193/2009-010

Tambling CJ, Minnie L, Adendorff J, Kerley GI (2013) Elephants facilitate impact of large predators on small ungulate prey species. Basic Appl Ecol 14:694–701. https://doi.org/10.1016/j.baae.2013.09.010

Terry JCD, Morris RJ, Bonsall MB (2017) Trophic interaction modifications: an empirical and theoretical framework. Ecol Lett 20:1219–1230. https://doi.org/10.1111/ele.12824

Tylianakis JM, Morris RJ (2017) Ecological networks across environmental gradients. Annu Rev Ecol Evol Syst 48:25–48

Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445:202–205. https://doi.org/10.1038/nature05429

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Underwood R (1982) Vigilance behaviour in grazing African antelopes. Behaviour 79:81–107. https://doi.org/10.1163/156853982x00193

Valeix M, Fritz H, Sabatier R, Murindagomo F, Cumming D, Duncan P (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biol Conserv 144:902–912. https://doi.org/10.1016/j.biocon.2010.10.029

Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos Trans R Soc Lond B Biol Sci 365:2025–2034. https://doi.org/10.1098/rstb.2010.0037

Van Orsdol KG (1984) Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. Afr J Ecol 22:79–99. https://doi.org/10.1111/j.1365-2028.1984.tb00682.x

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van Der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304(5677):1629–1633. https://doi.org/10.1126/science.1094875

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100. https://doi.org/10.1890/0012-9658(2003)084%5b1083:arotii%5d2.0.co;2

Wickham H (2016). *ggplot2*: Elegant graphics for data analysis. Springer-Verlag, New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org. Accessed 2019

Wilmers CC, Isbell LA, Suraci JP, Williams TM (2017) Energetics-informed behavioral states reveal the drive to kill in African leopards. Ecosphere 8:e01850. https://doi.org/10.1002/ecs2.1850

Wootton JT (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. Am Nat 141:71–89. https://doi.org/10.1086/285461

Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. Annu Rev Ecol Evol Syst 25:443–466. https://doi.org/10.1146/annurev.es.25.110194.002303

Wootton JT (2002) Indirect effects in complex ecosystems: recent progress and future challenges. J Sea Res 48:157–172. https://doi.org/10.1016/S1385-1101(02)00149-1