



Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna

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ABSTRACT

African elephants can affect the quality of the habitat of other species by breaking or uprooting trees and shrubs in savannas. Their effect on vegetation has been widely studied but less is known about the effects of such vegetation changes on other animals. We studied how changes in the vegetation caused by elephants influence the selection of microhabitats by five African herbivore species (giraffe, kudu, steenbok, impala, and zebra) in Hwange National Park, Zimbabwe. There was no clear significant effect of overall elephant-induced vegetation changes on microhabitat selection except for the small species (steenbok and impala) that used vegetation modified by elephants preferentially. This is consistent with a medium-term browsing facilitation hypothesis. More subtle possible effects were detected for larger browsers (giraffe and kudu). They selected areas with broken and uprooted plants and avoided coppiced areas. All of the browsers selected sites characterized by plants uprooted and broken by elephants, which were associated with a higher visibility, and ultimately a better probability of detecting an approaching predator, suggesting that perceived predation risk plays an important role in microhabitat selection. These results illustrate how elephants can initiate indirect effects that influence microhabitat selection by other herbivores. Understanding the indirect effects of elephants through changes in food availability and predation risk thus needs further investigation. The results of this study do not provide support for the hypothesis that elephant-induced changes in the structure of habitats have caused the declines in the populations of the other herbivores in the study area.

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1. Introduction

Habitat selection is driven by factors as different as the abundance of high quality food resources (e.g. Duncan, 1983), intra- and interspecific competition (e.g. Fritz et al., 1996) and facilitation (e.g. van Der Wal et al., 2000), predation risk (e.g. Valeix et al., 2009), thermoregulation (e.g. Dussault et al., 2005) and parasite

avoidance (Hart, 1990). Some species, by changing the physical environment, modulate these factors (e.g. availability of resources to other species or the risk of predation), hence ultimately mediating competition and predation: these have been defined as ecosystem engineers (Jones et al., 1994). The importance of the scales of space and time in understanding the importance of ecosystem engineering has been underlined (Hastings et al., 2007). Physical ecosystem engineering is considered an important mechanism generating heterogeneity and thus potentially high species richness at the landscape scale (Jones et al., 1997; Wright et al., 2002). However, modified patches may have higher (e.g. Pringle, 2008) or lower (e.g. Bratton, 1975) species richness than unmodified patches.

African elephants (*Loxodonta africana*) are ecosystem engineers (Bond, 1993; Jones et al., 1994) because they have complex, scale-dependent effects on habitat structure. Elephant-induced changes in the structure and composition of vegetation have been studied in the field (e.g. Ben-Shahar, 1993; de Beer et al., 2006) and by modelling (e.g. Baxter and Getz, 2005; Holdo, 2007). Generally,

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elephant impact on woody vegetation leads to a decreasing number of trees, and consequently to larger number of open or coppiced areas (review in Conybeare, 2004). This may also lead to the local extirpation of some woody plant species (O'Connor et al., 2007). Further, much of the work on elephants as agents of habitat change revolves around concerns that high densities of elephants maintain open savannas (i.e. with reduced habitat complexity) and ultimately cause habitat degradation and loss of biodiversity (e.g. Cumming et al., 1997; Guldemond and van Aarde, 2008). However, high elephant abundance is not always associated with lower woody cover (Chamaillé-Jammes et al., 2009a).

Surprisingly, less is known about the effects of elephant-induced vegetation changes on other animals (but see Pringle, 2008) and particularly on other large herbivores. The few existing studies on the influence of elephants on other herbivores have provided contrasting results. Some have suggested a competitive influence of elephants on other herbivore species, and more specifically on browsers. For example, a negative correlation between elephant biomass and browser biomass exists across ecosystems (Fritz et al., 2002), and trends in elephant populations are often correlated with opposite trends in browser populations (e.g. Valeix et al., 2008). It had been suggested that the prime mechanism underlying the observed patterns in these studies is a deleterious change in habitat conditions. Conversely, other studies show that elephants may facilitate smaller browsers. Some heavily browsed plants develop tolerance traits such as high regrowth abilities in shoots and leaves, high annual growth rates, and extensive tree branching (browsing lawns, Fornara and du Toit, 2007). It has been suggested that other browsers generally benefit from increased food availability in areas of elephant high abundance (medium-term facilitation hypothesis, Rutina et al., 2005; Makhabu et al., 2006). Changes in canopy cover resulting from the uprooting and breaking of trees and shrubs by elephants can also influence the species composition and structure of the herbaceous layer, and thus affect grazers (e.g. Belsky and Canham, 1994). Indirect mechanisms of facilitation have also been suggested (Young et al., 2005). The issue of the impact of high densities of elephants on habitat structure and hence on habitat selection by other herbivores, and ultimately on the sizes of the populations of other species, is of more than academic interest, especially in regions where increasing elephant populations have been accompanied by a decrease in some other large herbivores.

The importance of predation in influencing habitat selection by herbivores has been established (Creel et al., 2005; Valeix et al., 2009) and is characterised by a “landscape of fear” (Laurdré et al., 2001). Habitat features, particularly the amount of cover and visibility, have the potential to affect the perceived predation risk by herbivores. Elephants regularly break and uproot trees and shrubs, and hence may affect the capacity of other herbivores to detect a predator through changes in visibility and cover (Lima and Dill, 1990; Hopcraft et al., 2005), or the ability of prey to escape predators through changes in obstructions to flight (Lima, 1992). However, nothing is known on the indirect effects of elephant-induced vegetation changes on predation risk for other herbivores. Understanding the role of elephants as ecosystem engineers, and particularly their indirect effects through changes in predation risk as well as food availability, thus needs attention.

In this study, we assess whether other large herbivores select or avoid sites (microhabitat scale) in which elephant-induced structural changes in woody vegetation have occurred. We explore whether the herbivores' responses to elephant-induced changes were driven by changes in food availability, or changes in visibility, or both. We discuss the implications of the effects for the dynamics of populations of the other herbivores in the study area where a doubling of the elephant population has been accompanied by a

decrease in the populations of most of the other herbivore species (Valeix et al., 2007, 2008).

2. Material and methods

2.1. Study site

The study site is located in the northern sector (Main Camp area) of Hwange National Park (Hwange hereafter), which covers 14,651 km² of semi-arid savanna in northwestern Zimbabwe (19°00'S, 26°30'E). The long-term mean annual rainfall in this sector is 645 mm, which falls between October and April. The vegetation is primarily woodland savanna (64%) and vegetation communities are dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers, 1993). The average elephant population density is c. 2 indiv/km² over the whole park (Chamaillé-Jammes et al., 2008) but inside the park local densities during the dry season can be as high as above 5 indiv/km² (Chamaillé-Jammes et al., 2009b). The potential influence of elephant-induced vegetation changes was studied for the five herbivores most frequently seen in the wooded habitats in Hwange where elephants do most of their feeding. These were three browsers (giraffe (*Giraffa camelopardalis*) – average body mass 750 kg, greater kudu (*Tragelaphus strepsiceros*) – 135 kg, and steenbok (*Raphicerus campestris*) – 8 kg), a mixed-feeder (impala (*Aepyceros melampus*) – 45 kg), and a grazer (plains zebra (*Equus quagga*) – 200 kg).

Potential predators for these herbivores in the study site are lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), and wild dogs (*Lycaon pictus*). The most common predators are spotted hyaenas with a density estimated around 8.5 hyaenas/100 km² (Drouet-Hoguet, 2007) and lions with a density estimated around 2.7 lions/100 km² (Loveridge et al., 2007a). In the study site, kudu, giraffe and zebra account for 18%, 9%, and 6% of lion diet respectively (Loveridge et al., 2007b). Impala and steenbok represent minor prey items for lions (Loveridge et al., 2007b). Kudu, steenbok, giraffe, impala and zebra account respectively for 12%, 8%, 7%, 5% and 4% of hyaena diet (Drouet-Hoguet, 2007). Kudu and impala are known to be the two major prey for wild dogs (Rasmussen, unpublished data). No data exist on leopard and cheetah diets in the study site. However, impala and steenbok are expected to be the main prey for these two predators (Owen-Smith and Mills, 2008).

2.2. Observations

The study took place in 2004 (annual rainfall = 776 mm) and 2005 (annual rainfall = 330 mm). The observations were made every second week throughout the year, along two transects (30 km each). An observation was made when a herbivore was seen to use a site (i.e. feeding or resting, but not moving) in a bushy or woody area (open grasslands were not included). Care was taken to spread the observations evenly during the day. After the animal(s) had left the site, we recorded different attributes of their microhabitat, defined as a 25-m radius circle centred on the position at which the first animal of the herd was first observed. When the animal was located within 25 m from the road, the plot was moved perpendicularly until it was 25 m from the road.

First, we recorded information about the structure of the woody vegetation (plants hereafter) defined as trees (>3 m) and shrubs (30 cm < height < 3 m); seedlings (<30 cm) were not included. Within each site, along 2 m-large strips heading in the four cardinal directions, we recorded the number of intact plants, the number of uprooted plants (e.g. Fig. 1A), the number of plant stumps

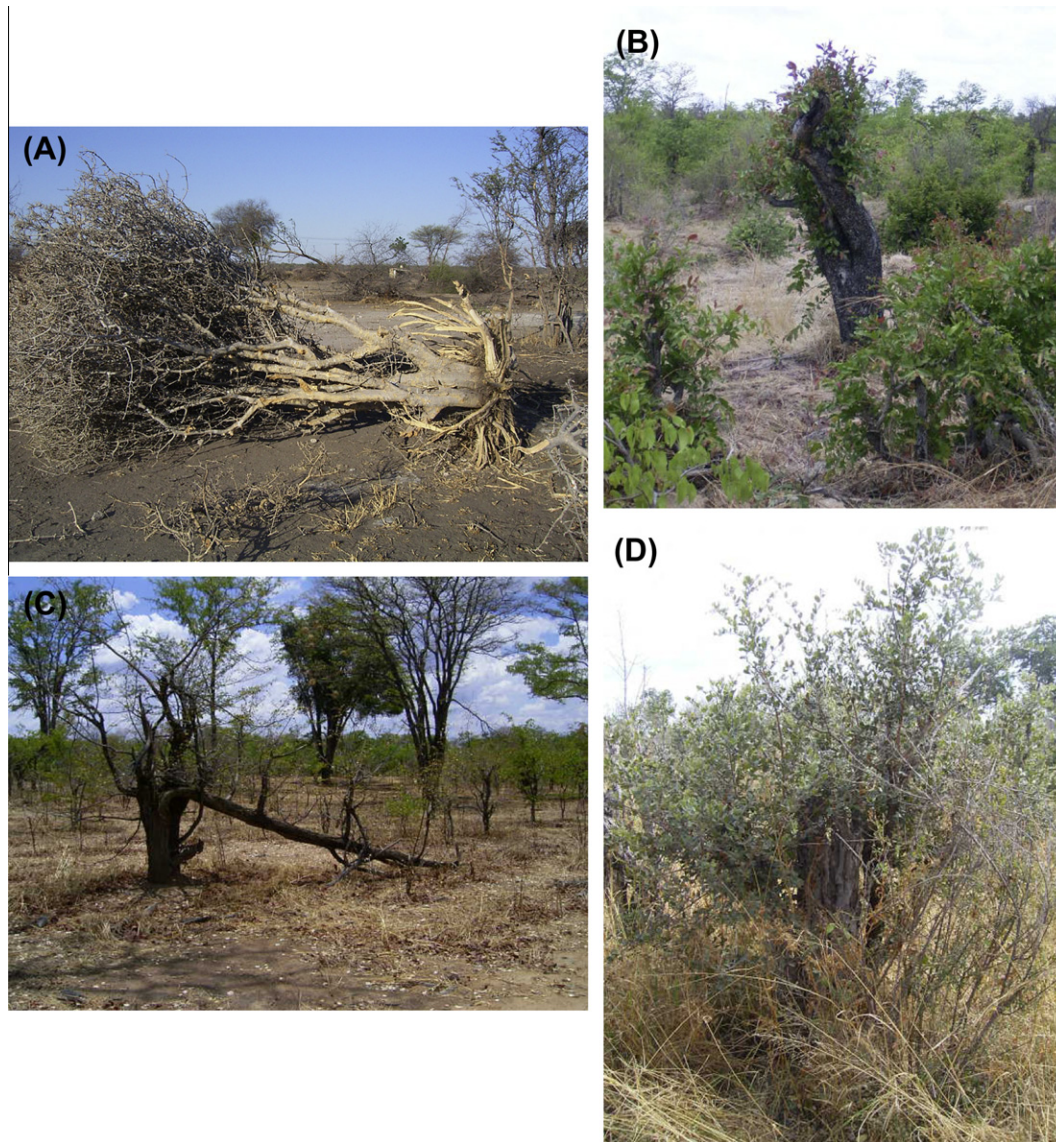


Fig. 1. Pictures of the different elephant-induced vegetation structural changes found in Hwange National Park, Zimbabwe: (A) uprooted tree, (B) tree stump, (C) broken tree, and (D) coppiced tree. Coppiced trees are characterized by a very high number of new shoots and branches, which contrasts with the low number of new shoots on stumps that have been recently broken by elephants.

(e.g. Fig. 1B), the number of broken plants where the upper lodged part of the plant is still attached (broken plants hereafter, e.g. Fig. 1C), the number of coppiced trees (e.g. Fig. 1D). The differentiation between stumps and coppiced trees was made as follows: whereas stumps (recently broken by elephants) may have started producing a few new shoots, coppiced trees (generally broken by elephants some time ago) are characterized by a very high number of shoots and branches. The number of plants recorded was used as an index of plant density (plant density hereafter) since numbers of plants were consistently recorded over the same area.

Second, we recorded food-related information regarding both the woody layer and the grass layer. For the woody layer, which is relevant for browsers and mixed-feeders, we recorded information about the leaves of shrubs and trees. We visually assigned each plant to one leaf abundance category (0: no leaf, 1: less than 50% of the potential leaves; 2: more than 50% of the potential leaves; 3: all potential leaves) and to one leaf greenness category (0: only dry leaves; 1: less than 50% of the leaves were green; 2: 50% of the leaves were green and 50% were dry; 3: more than 50% of the leaves were green; 4: only green leaves), which allowed

us to estimate an index of leaf abundance and of leaf greenness for each plot. For each plot, the leaf abundance index represents the sum of the values of leaf abundance category over all plants, and the leaf greenness index represents the sum of the values of leaf greenness category over all plants. These indices were calculated differently depending on the animal species to take into account the relevant availability for the animals: for giraffe all plants were considered, for impala and kudu only plants whose total height did not exceed 3 m were considered, and for steenbok only plants whose total height did not exceed 1 m were considered. For the grass layer, which is relevant for zebras and impalas, we estimated visually the grass cover and the proportion of green grass in five quadrats of 1 m². One quadrat was located at the centre of the plot and the four others were located 15 m from the centre of the plot in the four cardinal directions. Within each quadrat, we directly measured the grass height at five points (each corner and the centre of the quadrat) by placing a hand lightly on the vegetation at the level below which about 80% of the vegetation is estimated by eye to be growing (Stewart et al., 2001), and we then calculated the average grass height. For each site, the mean value of the five

quadrats was used as the index of grass cover, grass greenness and grass height.

Third, we assessed visibility at each plot, using a panel with two 50 cm × 50 cm grey boards (Appendix A). The two boards were set so that one board was at 25–75 cm (representative of the height stratum below 1 m) and the other was at 125–175 cm (representative of the height stratum between 1 and 2 m). One person held the panel in the centre of the plot and another person walked away from this panel in the four cardinal directions and recorded the distance at which each board could not be seen any more. The distance at which the top board could not be seen any more was recorded from a standing position, whereas the distance at which the bottom board could not be seen any more was recorded from a sitting position. We calculated the mean and the minimum visibility for each height stratum. Finally, the eight dominant tree species and the eight dominant shrub species were recorded for each plot.

In order to estimate the characteristics of available microhabitats, the same attributes were measured in control plots, every 2 km along each transect, at c. 50 m from the road. The distances to water, which influence herbivore habitat selection (Redfern et al., 2003; Smit et al., 2007; Valeix et al., 2009), were extracted from GIS for each plot, 'used' and 'available'.

2.3. Analyses

2.3.1. The probability of detecting animals

As our capacity to detect animals depends on the openness of a habitat, which is potentially modified by the impact of elephants, we estimated the detection probability function of the herbivores along the study transects. We used data from road transect counts carried out in 2004 and 2005 on the same roads, applying the Line Transect method and Distance Sampling theory (Buckland et al., 1993). Distance Sampling software was used to estimate the most likely detection probability function model using the Akaike Information Criterion. In order to eliminate the potential bias linked to differences among the habitats in our ability to detect animals, we calculated the distance at which the detection probability is 0.95. In the following analysis of the selection of microhabitats, we used only the sightings closer to the road than the value which gave a detection probability of over 0.95 (giraffe = 70 m; kudu = 80 m; impala = 50 m; steenbok = 25 m; zebra = 70 m). Sample sizes were $n_{\text{giraffe}} = 70$; $n_{\text{kudu}} = 51$; $n_{\text{impala}} = 24$; $n_{\text{steenbok}} = 35$; $n_{\text{zebra}} = 29$.

2.3.2. Floristic composition

Our goal was to study the effects of the structure of the vegetation; nonetheless we began by testing whether microhabitat selection could also be driven by the floristic composition of the plots. For microhabitats selected by each herbivore species and for the control plots, we ranked the 22 most common plant genera by their frequency of occurrence and we performed Spearman rank tests. The ranks of the plant genus in the selected and control plots were highly correlated (Spearman correlation, for all tests $N = 22$ / Giraffe: $r = 0.747$; $p < 0.0001$; Kudu: $r = 0.798$; $p < 0.0001$; Impala: $r = 0.429$; $p = 0.0465$; Steenbok: $r = 0.929$; $p < 0.0001$; Zebra: $r = 0.672$; $p = 0.0006$). This preliminary analysis suggested that the dominant plant genera in the plots selected by herbivores were similar to the ones in control plots; hence we focused on the vegetation structure characteristics only in the following analyses.

2.3.3. Influence of elephant-induced vegetation changes on microhabitat selection

The aim of this section is to test whether herbivores selected or avoided sites modified by elephants. The distribution of animal observations revealed that impala and zebra preferentially used areas close to waterholes and areas with low densities of woody

plants whereas giraffe, kudu and steenbok used a wider range of sites with giraffe and kudu tending to use sites less dense than average (Appendix B). We therefore included these environmental data in the models of microhabitat selection. We used logistic regressions to develop resource selection functions (RSF are proportional to the probability of use of a resource by an animal, Manly et al., 1993) for each herbivore species. The dependent variable was 1 for herbivore sightings, and 0 for control points. We first modelled the probability of selecting a microhabitat (1 vs. 0) as a function of the distance to water, the plant density, the proportion of plants impacted by elephants (whatever the type of impact), the interaction between the plant density and the proportion of impacted plants, and the interaction between distance to water and the proportion of impacted plants. Herbivore microhabitat selection may be influenced differently by different elephant impacts. We then modelled the probability of selecting a microhabitat (1 vs. 0) as a function of the distance to water, the plant density, the proportion of plant stumps, the proportion of broken and uprooted plants, the proportion of coppiced trees, the interactions between the plant density and these proportions, and the interactions between distance to water and these proportions. All proportions were arcsine transformed. Preliminary analyses revealed that some variables included in these models were significantly correlated but with low to very low coefficients of correlation ($0.12 < \rho < 0.30$), hence we considered that there was no collinearity between variables. Distance to water and plant density had to be controlled for to account for their effect on herbivore habitat selection so we used a Type I error approach and distance to water and plant density were the first covariates to be entered in the model to control for their effect before testing for the other variables. Control points for a given analysis were randomly selected from the pool of control points to achieve a 1:1 ratio of used-to-available sites. Statistical analyses used generalized linear models performed with SAS software (version 8.2), using the LOGISTIC procedure. Backward variable selection was used with successive removal of non-significant variables. We performed a likelihood ratio test to assess whether the general models differed significantly from a model with a random distribution of used and available plot characteristics. We also performed a Hosmer and Lemeshow goodness-of-fit test to evaluate whether the fitted models were adequate for describing the data (Hosmer and Lemeshow, 2000). Because herbivores may respond differently to the proportion and to the density of impacted plants, we also carried out the analyses with the density of impacted plants. Both approaches led to similar results and conclusions, consequently only results on proportions are presented hereafter.

2.3.4. Influence of elephant-induced vegetation changes on food availability and visibility

The aim of this section is to assess what characteristics of a site (food availability, visibility as a proxy for predation risk) are modified by elephant-induced vegetation changes. To explore which microhabitat characteristics were influenced by the different types of elephant-induced vegetation change, food-related indices (indices of leaf abundance, leaf greenness, grass cover, grass greenness, and grass height) and visibility indices (the mean and the minimum visibility for each height stratum >1 m and <1 m) were modelled in function of the plant density, proportion of broken and uprooted plants, proportion of plant stumps, and proportion of coppiced trees, using data from the control plots only. We performed linear models with SAS software (version 8.2), using the GLM procedure. The plant density had to be controlled for to account for its effect on site characteristics so we used a Type I error approach and the plant density was the first covariate to be entered in the model to control for its effect before testing for the other variables. All proportions were arcsine transformed.

2.3.5. Influence of food availability and visibility on microhabitat selection

The aim of this section is to test whether herbivores selected or avoided sites characterized by elephant-modified food availability or visibility. We used data from the control plots to check for collinearity between the different indices. The leaf abundance index and the leaf greenness index were highly correlated for each height stratum (Pearson: $N = 480$; $\rho = 0.96$ (for height stratum >3 m), 0.96 (for intermediate height stratum) and 0.94 (for height stratum <1 m); $p < 0.0001$) so we considered the leaf abundance index only for the food-related information for browsers. The grass cover index was correlated with the grass greenness index (Pearson: $N = 480$; $\rho = 0.48$; $p < 0.0001$) and with the grass height index (Pearson: $N = 480$; $\rho = 0.53$; $p < 0.0001$) so we considered the grass cover index only for the food-related information for grazers. For impala, a mixed-feeder, we considered both the leaf abundance index and the grass cover index. In the two height strata, the mean visibility was highly correlated with the minimum visibility (Pearson: $N = 480$; $\rho = 0.80$ (for height stratum >1 m) and 0.75 (for height stratum <1 m); $p < 0.0001$) and consequently only the mean visibility was considered. Additionally, there was a correlation between the mean visibility in the higher stratum (>1 m) and in the lower stratum (<1 m) (Pearson: $N = 480$; $\rho = 0.82$; $p < 0.0001$). Consequently, we used the mean visibility for the stratum above 1 m for all species, except for the steenbok for which we used the mean visibility for the stratum below 1 m. Logistic regressions were used for each herbivore species (dependent variable = 1 for herbivore sightings, and 0 for control points) to model the probability of selecting a site as a function of the distance to water, the plant density, the relevant food-related information (see above for details), the relevant visibility-related information (see above for details), the interaction between the plant density and the relevant indices, and the interaction between distance to water and the relevant indices. Statistical analyses used generalized linear models performed with SAS software (version 8.2), using the LOGISTIC procedure. We also performed a likelihood ratio test and a Hosmer and Lemeshow goodness-of-fit test.

3. Results

3.1. Description of elephant impact

Control sites data revealed that 96.2% of the sites are impacted by elephants and on average $19.9 \pm 15.4\%$ (maximum = 71.9%) of

the plants are impacted (Appendix C). Coppiced trees are the most common elephant impact in the study area (Appendix D). In control sites, the proportion of plants impacted by elephants did not decrease linearly with distance to water (Appendix E). Though the extent to which vegetation is impacted by elephants is rather homogeneous, the area located within 1 km of water is more affected (Appendix E). The density of plants does not appear to influence the proportion of plants impacted by elephants, even though the impact may be less at low and high plant densities (Appendix E).

3.2. Influence of elephant-induced vegetation changes on microhabitat selection

Logistic regressions were significant for all species (likelihood ratio test: $P < 0.05$) and they provided good fits (Hosmer and Lemeshow goodness-of-fit test: $P > 0.05$). Environmental variables (distance to water and woodiness of sites) played a significant role in microhabitat selection by the study herbivores: impala and zebra selected sites close to water whereas kudu and steenbok tended to select sites further from water, and giraffe, impala and zebra selected less woody sites (Table 1). These results corroborated the preliminary findings revealed in Appendix B. The overall impact of elephants on the vegetation did not influence microhabitat selection by the study herbivores except steenbok, which selected sites impacted by elephants (Table 1), and impala, which selected sites impacted by elephants but only at a certain distance from water (Table 1 and Fig. 2). At a significance level of 0.05, the different elephant-induced vegetation changes influenced microhabitat selection by steenbok, which selected sites characterized by broken plants, uprooted plants and plant stumps, impalas, which selected sites characterized by coppiced trees at a certain distance from water, and kudu, which select sites characterized by broken and uprooted plants in woody sites (Table 2 and Fig. 3). If the effects significant at the significance level of 0.10 are considered, then microhabitat selection by all the browsers and impala was influenced by the nature of elephant-induced vegetation changes. They all selected plots characterized by higher proportions of broken and uprooted plants (Table 2 and Fig. 3). For giraffe and kudu, the interaction between the plant density and the proportion of broken and uprooted plants indicated that they selected for sites with a high proportion of broken and uprooted plants more strongly in woodier areas (Fig. 3). Sites with coppiced trees were avoided by giraffe and kudu whereas they were selected by impala (Table 2 and Fig. 3). For kudu, the interaction between the plant density and the proportion of coppiced trees indicated that their

Table 1
Results of the logistic regressions modelling the probability of selecting a microhabitat depending on the environmental variables and the overall impact of elephants on the vegetation measured as the proportion of woody plants impacted. Proportions are arcsine transformed. The results are presented as slope estimates (\pm standard error) when significant at $p < 0.10$, and results are also provided for variables that did not have a significant effect alone, but in interaction with another variable. See also Fig. 2 for interpretation of the interaction results.

Species	Significant variable	Estimate \pm SE	df	χ^2	p
Giraffe	Plant density	-0.0227 ± 0.0059	1, 138	18.64	<0.0001
Kudu	Distance to water	0.0002 ± 0.0001	1, 100	3.10	0.0784
Steenbok	Distance to water	0.0004 ± 0.0002	1, 67	3.13	0.0770
	Proportion of impacted plants	0.0679 ± 0.0285	1, 67	6.47	0.0110
Impala	Distance to water	-0.0030 ± 0.0017	1, 43	7.07	0.0078
	Plant density	-0.0250 ± 0.0122	1, 43	4.63	0.0314
	Proportion of impacted plants	-0.0967 ± 0.0719	1, 43	0.16	0.6896
	Distance to water * proportion of impacted plants	0.0001 ± 0.0001	1, 43	3.87	0.0491
Zebra	Distance to water	-0.0002 ± 0.0002	1, 55	6.20	0.0128
	plant density	-0.0514 ± 0.0151	1, 55	19.77	<0.0001

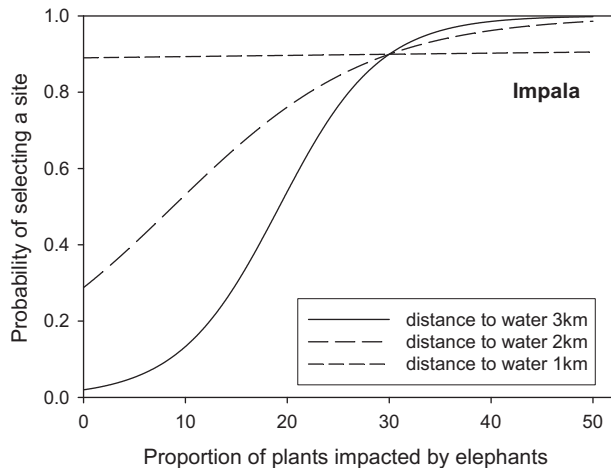


Fig. 2. Relationship between the proportion of plants impacted by elephants and the probability of selecting a site (results from logistic regressions) for impala. The interaction distance to water * proportion of plants impacted by elephants was significant at the p level of 0.05. Proportions are arcsine transformed.

avoidance of sites characterized by a high proportion of coppiced trees was more pronounced in open areas (Fig. 3).

3.3. Influence of elephant-induced vegetation changes on food availability and visibility

Sites with higher densities of plants were characterized by high food-related indices for browsers (more and greener leaves), low food-related indices for grazers (less and drier grass), and less visibility (Table 3). Once controlled for this effect, microhabitats with many broken and uprooted plants had less and poorer quality leaves above 1 m, and a higher visibility. In contrast, plots with coppiced trees had more and better quality leaves in the intermediate height stratum ($1\text{ m} \ll 3\text{ m}$), but visibility was lower

(Table 3). Plots characterized by plant stumps had more and better quality leaves below 1 m (Table 3).

3.4. Influence of food availability and visibility on microhabitat selection

Logistic regressions were significant (likelihood ratio test: $P < 0.05$) and they provided good fits (Hosmer and Lemeshow goodness-of-fit test: $P > 0.05$) for all species. The food indices did not appear to play a significant role in microhabitat selection by the study herbivores (leaf abundance did not influence microhabitat selection by giraffe and kudu, it influenced microhabitat selection by impala negatively, and grass cover did not influence microhabitat selection by impala or zebra). The only exception was steenbok, which tended to select sites characterized by higher leaf abundance (slope estimate \pm SE = 0.0501 ± 0.0213 ; $\chi^2_{1,66} = 3.34$; $p = 0.0674$). In contrast, the indices of visibility influenced microhabitat selection in all study species, except steenbok ($\chi^2_{1,66} = 1.83$; $p = 0.1759$). Once the effect of the plant density on microhabitat selection had been controlled for, giraffe selected sites with higher visibility (slope estimate \pm SE = 0.0227 ± 0.0109 ; $\chi^2_{1,137} = 4.60$; $p = 0.0320$; Fig. 4). Once the distance to water had been controlled for, kudu selected sites with higher visibility (slope estimate \pm SE = 0.0405 ± 0.0118 ; $\chi^2_{1,99} = 14.47$; $p = 0.0001$; Fig. 4). Once the distance to water and the plant density had been controlled for, impala selected sites with higher visibility (slope estimate \pm SE = 0.0275 ± 0.0153 ; $\chi^2_{1,44} = 3.51$; $p = 0.0611$; Fig. 4), as did zebras (slope estimate \pm SE = 0.0376 ± 0.0177 ; $\chi^2_{1,54} = 5.35$; $p = 0.0207$; Fig. 4).

4. Discussion

A major goal of ecology is to understand the causes of variations in the distribution and abundance of species, in particular how organisms interact with other species and their environment. A

Table 2

Results of the logistic regressions modelling the probability of selecting a microhabitat depending on the nature of the elephant-induced vegetation changes. Proportions are arcsine transformed. Results are presented as slope estimates (\pm standard error) when significant at the level $p < 0.10$, and results are also provided for variables that did not have a significant effect alone, but in interaction with another variable. See also Fig. 3 for interpretation of the interaction results.

Species	Significant variable	Estimate \pm SE	df	χ^2	p
Giraffe	Plant density	-0.0352 ± 0.0097	1, 135	18.64	<0.0001
	Proportion of broken and uprooted plants	-0.0715 ± 0.0600	1, 135	0.76	0.3830
	Proportion of coppiced trees	-0.0373 ± 0.0210	1, 135	3.15	0.0760
	Plant density * proportion of broken and uprooted plants	0.0017 ± 0.0010	1, 135	3.29	0.0697
Kudu	Distance to water	0.0002 ± 0.0001	1, 95	3.10	0.0784
	Plant density	-0.0282 ± 0.0114	1, 95	0.99	0.3195
	Proportion of broken and uprooted plants	-0.0613 ± 0.0627	1, 95	1.77	0.1828
	Proportion of coppiced trees	-0.1040 ± 0.0481	1, 95	1.00	0.3166
	Plant density * proportion of broken and uprooted plants	0.0023 ± 0.0012	1, 95	4.23	0.0398
	Plant density * proportion of coppiced trees	0.0012 ± 0.0005	1, 95	3.56	0.0591
Steenbok	Distance to water	0.0003 ± 0.0002	1, 66	3.13	0.0770
	Proportion of broken and uprooted plants	0.0811 ± 0.0439	1, 66	4.17	0.0413
	Proportion of plant stumps	0.0690 ± 0.0317	1, 66	5.29	0.0214
Impala	Distance to water	-0.0017 ± 0.0007	1, 42	7.07	0.0078
	Plant density	-0.0307 ± 0.0139	1, 42	4.63	0.0314
	Proportion of broken and uprooted plants	0.0912 ± 0.0488	1, 42	3.12	0.0774
	Proportion of coppiced trees	-0.1445 ± 0.0959	1, 42	0.21	0.6486
	Distance to water * proportion of coppiced trees	0.0002 ± 0.0001	1, 42	4.66	0.0309
Zebra	Distance to water	-0.0002 ± 0.0002	1, 55	6.20	0.0128
	Plant density	-0.0514 ± 0.0151	1, 55	19.77	<0.0001

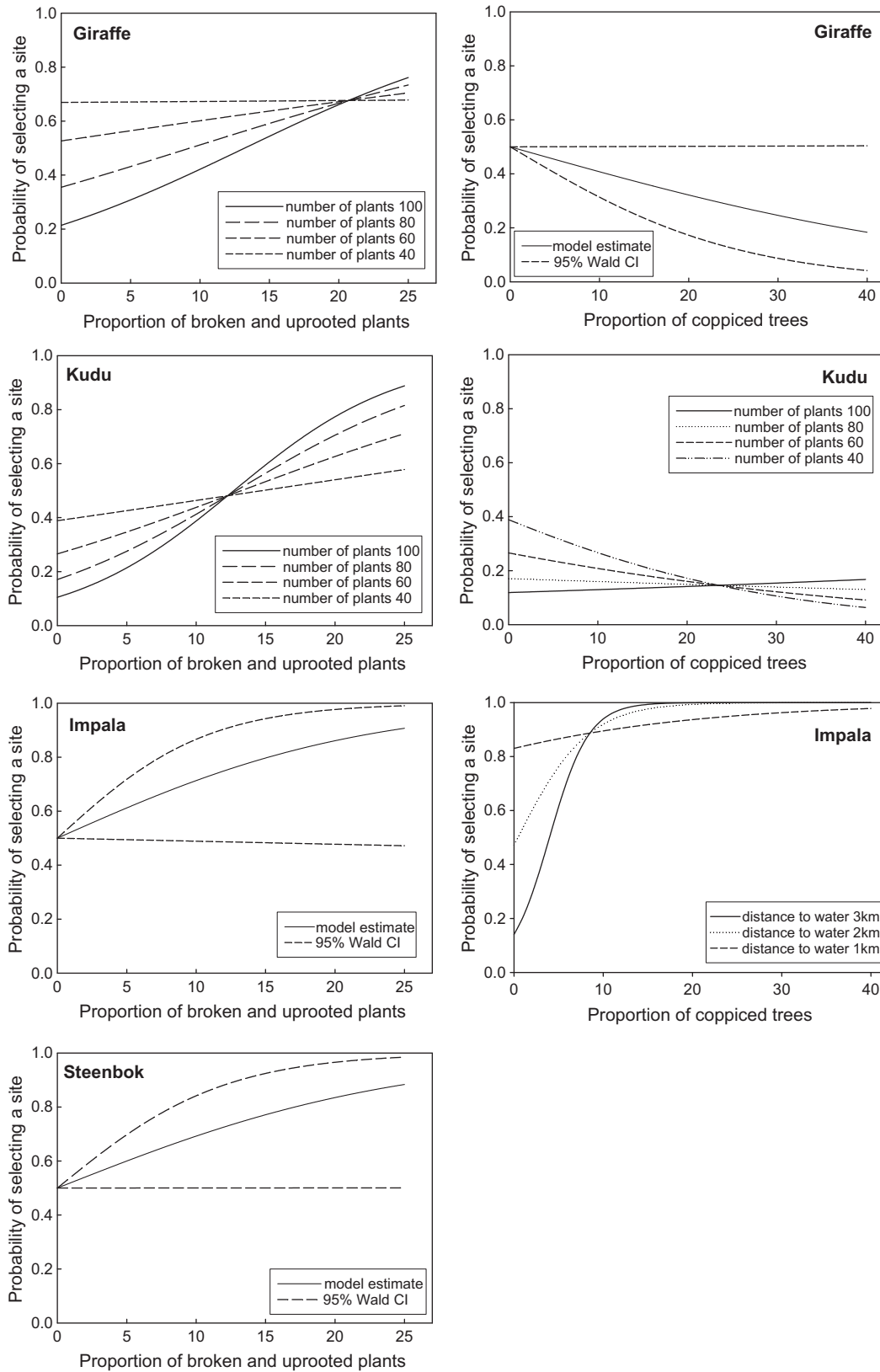


Fig. 3. Relationship between the proportion of the different types of vegetation impacts by elephants and the probability of selecting a site (results from logistic regressions). All relationships were significant at the p level of 0.10. Proportions are arcsine transformed.

recent intriguing question has been the role of ecosystem engineers in influencing the distribution and abundance of other species (Jones et al., 1997). Here, we show that elephants can be

considered ecosystem engineers in this ecosystem because they modify food availability as well as visibility, hence the predation risk, in the habitats of other herbivores. The results presented here

Table 3

Results of the linear regressions modelling the food-related indices and the visibility indices depending on the proportion of type of elephant impact. The number of plants was controlled for before testing for the effect of the three other variables. Proportions were arcsine transformed. Results are presented as slope estimates (\pm standard error) when significant at the level $p < 0.05$. NS is indicated when $p > 0.05$.

	Dependent variables			
	Plant density	Proportion of broken and uprooted plants	Proportion of plant stumps	Proportion of coppiced trees
Leaf abundance >3 m	0.038 \pm 0.011 $F_{1, 419} = 11.79$	-0.117 \pm 0.052 $F_{1, 419} = 8.19$	-0.065 \pm 0.035 $F_{1, 419} = 7.20$	-0.073 \pm 0.033 $F_{1, 419} = 4.98$
Leaf abundance <3 m and >1 m	0.142 \pm 0.017 $F_{1, 419} = 72.03$	-0.279 \pm 0.084 $F_{1, 419} = 11.39$	NS	0.146 \pm 0.054 $F_{1, 419} = 7.39$
Leaf abundance <1 m	0.103 \pm 0.017 $F_{1, 419} = 46.51$	NS	0.185 \pm 0.057 $F_{1, 419} = 13.83$	NS
Leaf greenness >3 m	0.043 \pm 0.014 $F_{1, 419} = 8.73$	-0.194 \pm 0.066 $F_{1, 419} = 12.66$	-0.086 \pm 0.044 $F_{1, 419} = 6.76$	NS
Leaf greenness <3 m and >1 m	0.174 \pm 0.025 $F_{1, 419} = 51.27$	-0.448 \pm 0.122 $F_{1, 419} = 14.37$	NS	0.216 \pm 0.078 $F_{1, 419} = 7.71$
Leaf greenness <1 m	0.117 \pm 0.022 $F_{1, 419} = 39.09$	NS	0.218 \pm 0.072 $F_{1, 419} = 13.42$	NS
Grass cover	-0.094 \pm 0.038 $F_{1, 419} = 6.42$	NS	NS	NS
Grass greenness	-0.108 \pm 0.060 $F_{1, 419} = 4.69$	-1.632 \pm 0.292 $F_{1, 419} = 38.85$	NS	NS
Grass height	NS	-0.221 \pm 0.130 $F_{1, 419} = 5.13$	NS	0.217 \pm 0.083 $F_{1, 419} = 6.90$
Mean visibility (>1 m)	-0.200 \pm 0.028 $F_{1, 419} = 50.29$	0.494 \pm 0.138 $F_{1, 419} = 15.88$	NS	-0.210 \pm 0.088 $F_{1, 419} = 5.70$
Minimum visibility (>1 m)	-0.059 \pm 0.021 $F_{1, 419} = 5.73$	0.196 \pm 0.104 $F_{1, 419} = 5.69$	NS	-0.144 \pm 0.067 $F_{1, 419} = 4.65$
Mean visibility (<1 m)	-0.135 \pm 0.021 $F_{1, 419} = 43.63$	0.335 \pm 0.103 $F_{1, 419} = 11.23$	NS	-0.188 \pm 0.066 $F_{1, 419} = 8.20$
Minimum visibility (<1 m)	-0.055 \pm 0.015 $F_{1, 419} = 15.16$	0.205 \pm 0.071 $F_{1, 419} = 8.68$	NS	-0.119 \pm 0.046 $F_{1, 419} = 6.82$

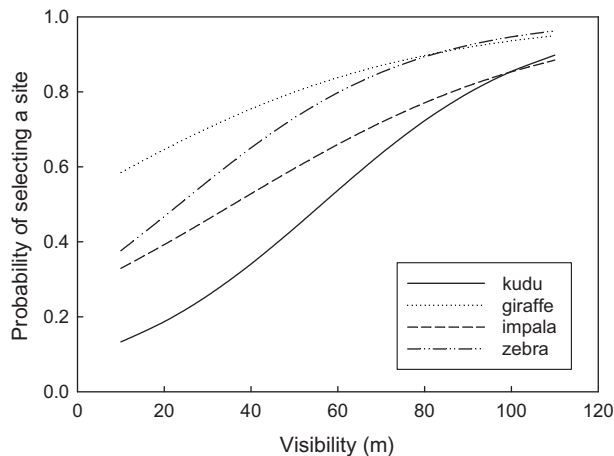


Fig. 4. Relationship between visibility and the probability of selecting a site (results from logistic regressions using distance to water = 1.5 km and the median plant abundance for each herbivore species). All relationships were significant at the p level of 0.05 (except for impala for which $p = 0.0611$).

highlight the complexity of the effects of elephants on their ecosystem by showing that different types of elephant-induced vegetation changes have opposite effects for food availability and visibility for other herbivores.

This study provides evidence that there is no clear single significant effect of elephant-induced vegetation changes on microhabitat selection by other herbivores in Hwange. However, it allowed us to detect more subtle possible effects. Elephant-induced vegetation changes appear to have some influence on browsers (giraffe, kudu and steenbok) and impala, but apparently not zebra. Small herbivores (steenbok and impala) appear to select sites characterized by vegetation impacted by elephants, regardless of the type of impact. The influence of elephant-induced vegetation changes on larger browsers (giraffe, kudu) is more complex: they appear to se-

lect sites characterized by plants uprooted and broken by elephants, but avoid sites characterized by coppiced trees. Thus, different vegetation changes induced by elephants may have opposite effects for microhabitat selection by other herbivores. There are significant variations in terms of leaf abundance, leaf greenness, grass cover, grass greenness and visibility between the wet and dry seasons in the study site. However, the very small number of animal observations in the wet season did not allow us to test for any seasonal effect. Our results are mainly valid for the dry season and further data collection in the wet season is needed to generalize the findings to the whole year, and to identify any seasonal differences.

The results for small species (impala and steenbok) show that they selected sites impacted by elephants. Interestingly, impala selected sites characterized by high proportion of tree stumps and shrub stumps, which were associated with higher leaf abundance (and greenness) in the intermediate height stratum (1–3 m), and steenbok selected sites characterized by high proportion of tree stumps and shrub stumps, which were associated with higher leaf abundance (and greenness) below 1 m. This corroborates findings from similar studies in Chobe National Park, Botswana, where small herbivores showed a positive correlation between their spatial distribution and the extent to which vegetation is modified by elephants (Skarpe et al., 2004). In this ecosystem, browsers (impala, kudu) feed preferentially on tree individuals with accumulated elephant impact because of an increased shoot abundance at low levels in the canopy (Makhabu et al., 2006). Hence, elephant-driven conversion of woodland to shrubland appears to have increased dry-season browse availability for browsers along the Chobe Riverfront and this has probably contributed to the observed population increase of such herbivores in the area (Rutina et al., 2005). Our results support the hypothesis of an increased food abundance and quality at low levels in trees/shrubs previously broken by elephants. Hence, the results for steenbok and impala are consistent with a medium-term browsing facilitation hypothesis. The modification of trees and shrubs to 'browsing lawns' (*sensu* Fornara and

du Toit, 2007) through the activity of elephants may be beneficial to smaller herbivores, but only if the rebrowsing by elephants is not so intense as to deplete all available new shoots. The results for steenbok may also be due to the existence of possible hiding places since steenbok is a species whose anti-predation behaviour is based on cryptic behaviour involving freezing and hiding (Fritz and Loison, 2006). Impala selected sites where the vegetation was impacted by elephants (mainly coppiced trees) particularly when they were not in the vicinity of a waterhole. This result suggests that the dependence of impalas on water is so strong that they use any vegetation type in the vicinity of water (regardless of the degree of elephant impact), but once further from water (~3 km) they become selective and mainly use elephant-modified microhabitats characterized by higher browse availability and palatability. Giraffe and kudu, however, avoided plots characterized by coppiced trees, often associated with higher leaf abundance. Hence, our results do not support the medium-term browsing facilitation hypothesis presented above for larger browsers. However, our study only focused on indices of resource abundance (index of leaf abundance, index of grass cover, index of grass height) and quality (index of leaf greenness, index of grass greenness): the plant species concerned, the extent to which leaves and grasses were made up of palatable vs. unpalatable species, may have also influenced microhabitat selection by herbivores. Consequently, our conclusions are limited by the lack of detailed data on palatable vs. unpalatable plants, which will need to be collected in future research.

This study has revealed consistent findings regarding the role of visibility: (i) all the browsers and the mixed-feeder selected sites with a high proportion of trees and shrubs uprooted and broken by elephants, (ii) these sites are often associated with higher visibility, and (iii) all study species selected sites characterized by high visibility. A recent study has already demonstrated that habitat preferences for many large herbivores were strongly correlated with visibility, but not tree density once visibility was held constant (Riginos and Grace, 2008; see also Matson et al. (2005) for impala). Their results suggest that most species prefer areas of low tree density because of greater visibility in these areas (even giraffe which is a strict browser), and not the plant characteristics associated with low tree density (Riginos and Grace, 2008). In African savannas, where many predators rely on stealth, visibility is crucial for early detection of an approaching predator (Lima and Dill, 1990). High visibility is often correlated with lower levels of vigilance in many taxa, and foraging animals frequently increase their vigilance in patches where the view is obstructed (e.g. Burger et al., 2000; Whittingham et al., 2004). Greater vigilance in low visibility patches might reduce the profitability of the patch because time spent being vigilant detracts from time spent feeding (Butler et al., 2005). However, in large mammalian herbivores, the costs of vigilance in terms of intake rate may not be that high (Fortin et al., 2004). If herbivores pay little cost in terms of intake by being vigilant, but still avoid areas characterized by a low visibility, then either the probability of being attacked is very high, or food resources may be very limiting so that the slight decline in intake makes these areas unprofitable compared to others areas in the landscape. One interesting result is that the larger browsers (giraffe and kudu) selected sites characterized by uprooted and broken plants (i.e. higher visibility) strongly in wooded areas only. This result suggests that in sites with fewer trees, visibility may be good enough to allow herbivores to forage 'safely', whereas in sites with many trees, where visibility is lower, herbivores forage in microhabitats where elephants have uprooted or broken some plants allowing for a better visibility. Our study suggests that perceived predation risk influences microhabitat selection by large herbivores, and that elephants, by modifying the visibility of habitats, may have strong indirect effects on predator–prey

relationships. This has never been considered and calls for further research.

Herbivores face trade-offs when selecting a foraging site, such as maximizing access to food while avoiding predators (Illius and Fitzgibbon, 1994; Fortin et al., 2004). However, the conditions affecting such behavioural trade-offs remain poorly understood (Lima, 1998). In Hwange where microhabitats have been modified by elephants, it is likely that other herbivores have the choice between: (i) foraging in coppiced tree areas where available leaf abundance is higher but where they need to dedicate a large amount of time to vigilance activities because of poor visibility, or (ii) foraging in sites where elephants have broken and uprooted several trees, and food availability is reduced (not in the short-term because more leaves are made available within reach of smaller herbivores, but decreased in the medium-term), but visibility is greater, allowing for lower levels of vigilance, so the profitability of the patch is increased. Hence, elephant-induced vegetation changes may indirectly influence the trade-offs that herbivores face between foraging and anti-predation behaviour. To date most studies of indirect effects have focused on trophic cascades initiated by predators (e.g. Ripple et al., 2001; Ripple and Beschta, 2008). The results presented here reinforce the idea that herbivores can also initiate powerful indirect effects on the structure and dynamics of ecosystems.

In addition to being of theoretical interest, the influence of elephant-induced vegetation changes on microhabitat selection by other herbivores is also of importance for conservation. Understanding the processes driving the selection of habitats by animals is fundamental in ecology as it can provide insights into the processes driving population dynamics and community structure and functioning (Morris, 2003). Habitat preferences are assumed to be adaptive, such that the use of preferred habitats increases fitness (Martin, 1998). The influence of elephant-induced vegetation changes on herbivore habitat selection might affect the dynamics of these herbivore populations. The densities of all the five species have declined in the study area since the mid 1980s during which period the elephant density has increased from 0.2 to 3 elephants/km² (Valeix et al., 2007). The study area is now characterized by a landscape where elephant-induced vegetation changes are widespread but heterogeneous. If elephant modified vegetation would be detrimental to other herbivores, we would expect these herbivores to avoid heavily impacted sites. In contrast, the work reported here shows that the five species did not strongly and consistently avoid sites where elephant-induced vegetation changes have occurred: zebra were indifferent, while giraffe and kudu selected microhabitats with uprooted and broken plants (though they avoided plots with coppiced trees), and impala and steenbok selected sites where the overall impact of elephants was greatest. Even though habitat engineering by elephants may lead to complex indirect effects that are likely to play a crucial role in the functioning of savanna ecosystems, our study does not provide support to the hypothesis that the declines in the populations of these five herbivores were caused by direct effects of elephants on the structure of vegetation in this ecosystem.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.10.029.

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