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Processes involved in the functioning of large mammal communities: the role of the African elephant in the ecology of predator-prey relationships

Nicolas Ferry

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Processes involved in the functioning of
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the role of the African elephant in the ecology of
predator-prey relationships

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Avant-Propos / Foreword

Cette thèse a été réalisée dans la Zone Atelier CNRS (Centre National de Recherche Scientifique) de Hwange, au Zimbabwe, qui s'appuie sur le programme historique de recherche HERD (Hwange Environmental Research Development), fruit de la collaboration à long-terme (depuis 1999) entre le CNRS, le CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement) et la ZPWMA (Zimbabwe Parks and Wildlife Management Authority). Cette thèse a bénéficié d'un financement de thèse du Ministère de la Recherche français via l'Ecole Doctorale E2M2 de l'Université Claude Bernard Lyon 1, du soutien financier du réseau des Zones Ateliers du CNRS et d'un PICS qui a facilité la collaboration avec la Wildlife Conservation Research Unit de l'Université d'Oxford. Cette thèse de doctorat est rédigée en anglais pour faciliter la restitution de ce travail aux partenaires zimbabwéens.

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Résumé / *Abstract*

Les communautés écologiques sont connues pour être des systèmes complexes composés de multiple espèces entrant en interaction les unes avec les autres. De nombreux modèles théoriques ont été développés pour étudier les communautés. Certains ont souligné l'importance des effets indirects que les espèces pouvaient avoir les unes sur les autres, tels que les chaînes d'interactions et les modifications d'interactions (par modification du trait d'une des espèces en interaction ou de l'environnement où se déroule l'interaction). Bien que la science expérimentale vienne confirmer le rôle fondamental que pourrait avoir ces effets indirects, peu d'études à l'échelle des communautés en milieu naturel ont été conduites, et encore moins chez les grands mammifères.

Le Parc National de Hwange, au Zimbabwe, est un écosystème de savane arborée semi-aride caractérisé par une quasi-absence d'eau de surface naturelle (point d'eau, rivière) pendant la saison sèche, et ce n'est qu'avec la création de points d'eau artificiels pompés que la richesse spécifique des communautés de grands mammifères et les fortes abondances animales sont maintenues. De plus, cet écosystème a la remarquable particularité à la fois d'abriter l'une des plus fortes densités d'éléphants, et d'être considéré comme l'un des bastions africains pour sa population de lions. Le lion est connu comme étant un chasseur à l'affût, utilisant les éléments de son habitat (fourrés, souches, hautes herbes, etc.) pour se rapprocher au maximum de sa proie et lui bondir dessus par surprise. De plus, cette espèce semble profiter de l'agrégation des herbivores aux points d'eau pendant la saison sèche pour chasser autour de ces points d'eau. L'éléphant d'Afrique quant à lui est capable d'aménager son milieu et est ainsi susceptible de favoriser l'accès à certaines ressources pour les autres espèces, telles que des abris ou au contraire une meilleure visibilité. En revanche, de par sa masse corporelle exceptionnelle et son régime alimentaire généraliste, il est possible qu'il soit un compétiteur clé pour les autres herbivores. Enfin, étant très nombreux dans l'écosystème étudié, nécessitant de grandes quantités d'eau, et devenant de plus en plus agressifs au fil de la saison sèche, les éléphants influencent l'utilisation des points d'eau par les autres herbivores.

Cette thèse porte donc sur le rôle que peuvent avoir les éléphants sur les interactions trophiques entre les lions et leurs proies, via des mécanismes d'effets indirects. Différents axes de recherche sont abordés. Le premier porte sur l'effet des éléphants sur la communauté de grands herbivores aux points d'eau, et plus particulièrement comment ils peuvent influencer leur distribution spatiale, et à terme leur vulnérabilité vis-à-vis des prédateurs. Un évitement spatial des éléphants par les autres herbivores en début de saison sèche suggère fortement que les éléphants sont de potentiels compétiteurs. Cependant, à la fin de la saison sèche, le phénomène s'inverse et certaines espèces d'herbivores se rapprochent fortement des éléphants. Deux scénarios portant sur les mécanismes pouvant expliquer ce patron ont été

explorés, sans succès : une nécessité croissante d'accéder à de l'eau de meilleure qualité au niveau des pompes des points d'eau, et une augmentation du risque de prédation qui pourrait rendre les éléphants « attractifs » aux yeux des herbivores, les éléphants adultes étant invulnérables à la prédation et capables de les faire fuir par des comportements de harcèlement. Le deuxième axe de recherche porte sur l'effet des éléphants sur la distribution spatiale des herbivores à l'échelle du paysage et de l'habitat, et sur les conséquences possibles que cela peut avoir sur l'écologie spatiale des prédateurs. L'absence de ségrégation entre éléphants et herbivores ne supporte pas l'hypothèse d'un effet de compétition par exploitation, et l'investigation quant à l'effet sur les prédateurs n'a pas été poussée plus avant. Le rôle facilitateur des éléphants, permettant l'accès à une ressource plus abondante et de meilleure qualité en cassant les branches et les troncs, semble en revanche être plausible pour les impalas qui sélectionnent les habitats utilisés par les éléphants. Le troisième axe de recherche s'intéresse à l'effet des éléphants sur la végétation et aux implications de ces changements pour la localisation des sites de chasses réussies des lions. Pendant une longue période (15 ans) de forte densité de la population d'éléphants, la composition de la végétation n'a pas changé pas (composition spécifique, traits fonctionnels) excepté en ce qui concerne les espèces rares. De plus, la structure globale de la végétation n'a pas été profondément affectée par une forte pression d'herbivorie des éléphants, à part dans la strate de hauteur de 50-200 cm où une réduction importante de la taille de la couronne des arbres (un proxy du volume occupé) est observée. Ces impacts des éléphants se traduisent par une augmentation légère de la visibilité et de la distance à un site potentiel d'affût (ex. souche, fourré). Les lions, qui tuent leur proie à une petite distance de l'endroit où ils étaient à l'affût, devraient donc contre-sélectionner ces habitats impactés par les éléphants et aller dans les habitats où la visibilité et la distance à un site d'affût sont plus faibles. Cependant, l'inverse est observé à large échelle, ce qui pourrait être expliqué par la présence plus abondante de proies dans les habitats impactés par les éléphants. A fine échelle, les sites de chasses réussies sont néanmoins caractérisés par des habitats avec une plus faible distance à un site d'affût comparé aux habitats qui sont disponibles aux alentours. Les éléphants semblent bien avoir un effet sur la localisation des sites de chasses réussies, et donc sur leurs interactions trophiques, via la modification de l'environnement mais cet effet dépend de l'échelle considérée. Cette étude suggère que les effets indirects peuvent agir à l'échelle des communautés en milieu naturel. De plus, elle renforce l'idée qu'il est important de prendre en compte ces effets indirects pour avoir une compréhension approfondie et une meilleure capacité de prédiction quant aux conséquences que peuvent avoir des perturbations sur la structure et le fonctionnement des communautés.

Species can indirectly affect other species and their interactions. The trophic interaction between a predator and its prey can be modified by the presence of a third species either through chain interactions (e.g. successive predation link) or through interaction modification. However, these indirect effects have received little attention in theoretical modelling of food web, and very few studies have tried to explore this phenomenon at the scale of natural complex communities of large mammals. The role of elephants as modifiers of lion's trophic interaction is explored in the semi-arid woodland savanna ecosystem of Hwange National Park, Zimbabwe. African elephants, as keystone-competitors (male body mass ~ 4000 kg with aggressive behaviour) can shape the behaviour of herbivores at waterholes, and adult elephants, being invulnerable to predation and able to deter predators such as lion, could represent safety for other herbivores. However, spatial and behavioural pattern observed do not allow to state on the elephant mediation of lion trophic interaction at waterholes. Further, elephants can compete for food resources with other herbivores, or on the contrary by enhancing regrowth of new shoots on trees they impact, elephants can facilitate other species. We observed that impalas selected habitats more intensively used by elephants, suggesting that elephants may facilitate the availability of food resources for impalas. However, no effect of facilitation or competition was observed for the other herbivores, which leads to think that elephants do not influence lion trophic interaction in that way. Finally, by altering the physical environment (i.e. ecosystem engineering), elephants affect the visibility and the availability of ambush sites for lions in the woody vegetation and ultimately seem to influence lion kill site selection. This study suggests that indirect effects may act at the community level even if their observation and quantification are difficult in natural communities. Moreover, it supports the observation that it is important to take into account these indirect effects in order to have a thorough understanding and a better ability to predict the consequences that disturbances may have on the structure and functioning of communities.

Mots - clés : Fonctionnement des communautés, savane semi-aride africaine, grands mammifères, éléphant d'Afrique, lion d'Afrique, interactions trophiques, effets indirects, chaînes d'interactions, modification d'interactions, ingénieur des écosystèmes, compétiteur clé.

Keywords: Community functioning, semi-arid African savanna, large mammals, African elephant, African lion, trophic interactions, indirect effects, interaction chain, interaction modification, ecosystem engineer, keystone-competitor.

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Ferry N., Cordonnier M., Hulot F. D., Dakwa F., Lovelater S., Dray S., Fritz H., & Valeix M. Heterogeneity of water quality in artificial waterholes: do African herbivores show preferences and does it lead to interference competition? *In prep. for submission in Journal of Arid Environments*

Ferry N., Maissonette E., Dutour M., Cordonnier M., Léna J.P., Sebele L., Dray S., Fritz H., & Valeix M. Does the presence of African elephants *Loxodonta africana* reduce the predation risk perceived by plains zebra *Equus quagga* at waterholes? *In prep. for submission in Animal Behaviour*

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General Introduction



« Alors la trompe du vieil éléphant se redressa, se recourba et un barrissement plus sonore, plus aigu, plus effrayant que l'éclat de cent trompettes de guerre retentit dans la sérénité de la brousse »

Le Lion (1958) de Joseph Kessel

1- Community functioning and structure

"Ecological communities are among the most complex systems that natural scientists attempt to understand, and ecologists continue to search for a conceptualization of communities that will enable this understanding." Werner & Peacor (2003).

In the first quarter of the twentieth century, there was considerable debate about the nature of an ecological community (Begon *et al.* 1986, McIntosh 1998). Clements (1916) conceived the community as a sort of superorganism whose member species were tightly bound together both at a given time and in their common evolutionary history. Thus, individuals, populations and communities were intertwined in a way similar to that between cells, tissues and organisms. By contrast, the individualistic concept devised by Gleason (1926) and others saw the relationships of coexisting species as the result of similarities in their requirements and tolerances. The current view considers an ecological community as an assemblage of species populations, which co-occur in space and time. Community ecology therefore focus on the manner in which assemblages of species are distributed in nature and how these assemblages can be influenced, or caused, by the physical forces of their environment and by interactions between species (Begon *et al.* 1986).

2- Interspecific interactions between two species

Understanding the dynamics of ecological communities depends therefore on a thorough knowledge of its member species and their interdependence. This interdependence suggests that changes in the abundance of a species in a community will affect the species with which it interacts (Wootton 1994). Collectively, these interactions determine how effects are transmitted from one species to another and underlie community functioning and structure (Dambacher and Ramos-Jiliberto 2007). Interactions between at least two individuals from two different species can be placed on a continuum of interactions ranging from mutualism to competition according to the effects of this interaction on the fitness of the protagonists. Here, we will focus on three common interspecific interactions: predation, competition and facilitation.

2.1- Trophic interactions

2.1.1- Predation

In a food web, energy flows via trophic links (Odum 1968), which are mainly represented by predation (carnivory and herbivory). Predation refers to the interaction in which individuals of one species kill and are capable of consuming a significant fraction of the biomass of individuals of another species (Abrams 2000). A predator's aim is to feed on its prey, whereas the prey's goal is to avoid being eaten by a predator. Predators and prey are therefore caught in arms races and their traits (e.g., behaviour) co-evolved in consequence. Predator-prey relationships have been extensively studied, although most existing research was done from a prey's point of view to understand decision-making processes (Lima 2002). This body of literature has documented a variety of anti-predator behaviours such as increase of vigilance (Caro 1992), grouping (Hamilton 1971), habitat shift (Pyare and Berger 2003), temporal niche shift (Valeix *et al.* 2009a), activity adjustment (Berger 2005), etc. Even though studies from a predator's point of view are scarcer (Lima 2002), recent works have addressed this issue in both theoretical (Lima 2002) and empirical studies (e.g. Kaufmann *et al.* 2007, Valeix *et al.* 2011a). It is also noteworthy that the characteristics of the habitats where predators and prey live may strongly influence predator-prey relationships (e.g. for landscape heterogeneity see Kauffman *et al.* 2007 and Laundré *et al.* 2014, for moon-light and habitat cover see Prugh and Golden 2014).

2.2- Non-trophic interactions

2.2.1- Competition

Interspecific competition can occur when two or more species share the same resource (food, light, space, time, breeding site, etc.). Species can compete through either exploitative or interference competition. Exploitative competition (Park 1954) occurs where a species diminishes the availability of a limited resource for another species by depleting it. Interference competition occurs where a species inhibits the accessibility to a resource for another species (Schoener 1983). Whereas these two different forms of competition are easy to apprehend conceptually, they can be difficult to detect and

quantify in natural ecosystems, as they can occur through different mechanisms: consumptive, preemptive, overgrowth, chemical, territorial, and encounter (Schoener 1983). Indeed, evidence of interference competition can be difficult to reveal, for instance when the outcome is an avoidance without any directly observable signs of agonistic behaviour from the interfering species (a process known as cryptic interference competition, Gyimesi, Stillman and Nolet 2010). Ultimately, competition is considered as one strong driver of community structure and functioning (Case and Gilpin 1974, Tilman 1982, Begon *et al.* 1996).

2.2.2- Facilitation

This interaction is analogous to the commensalism in the sense that one species will benefit from the presence of another species, without positive or negative effects on the latter. An example is the feeding facilitation between herbivores where the utilization of a resource by a species will enhance the access and/or quality of this resource for other species (Hempson *et al.* 2014). Facilitation through increased access to resources was first described by Vesey-Fitzgerald (1960). He revealed a grazing succession in tall floodplain grasslands in the Rukwa Valley in Tanzania, where trampling and feeding by African elephants (*Loxodonta africana*) exposed medium-height grasses to buffalo (*Syncerus caffer*), which in turn generated shorter grass exploited by topi (*Damaliscus lunatus*). Another example of facilitation through increased quality of the resources is from Gordon (1988) who found that red deer (*Cervus elaphus*) in spring preferred to feed in areas that had been grazed previously by cattle (*Bos taurus*) during the preceding winter. Although several facilitation mechanisms have been described (McNaughton 1985), the implications of this interaction in community functioning are still largely unknown (Arsenault and Owen-Smith 2002) and there were calls for considering its role in ecological communities (Stachowicz 2001).

3- From a species pair to the community: the indirect effects of species interactions

The interspecific interactions described above were considered for an association of two species only. However, natural communities are complex systems regrouping multiple species. Interspecific interactions are not isolated and can have indirect effects

throughout the community, affecting other species and their interactions. A species can therefore affect other species along direct and indirect paths, and it is not uncommon for indirect effects to oppose direct effects (Dambacher and Ramos-Jiliberto 2007). For instance, a population abundance may increase despite a change in circumstances that favors its enemy or diminishes its food (Sih *et al.* 1985). Two main types of indirect effects are distinguished.

3.1- Interaction chains

Figure 1A represents indirect effects that result from a series of direct interactions between species pairs (Wootton 1993). Thus, one species directly alters the abundance of a second species, the change in the second species abundance affects a third species, and so on. In mathematical terms, the functions describing the direct interactions between species pairs do not change; only the abundances of the species change. This is typically the case of trophic cascades whereby a predator indirectly affects the abundance of producers by modifying herbivore density (Estes *et al.* 2011, Ripple *et al.* 2014). Another example known as “mesopredator release” (e.g. Prugh *et al.* 2009, Ritchie and Johnson 2009) occurs when the removal of an apex predator leads to the demographic increase of smaller predator populations (e.g. with foxes killing weasels Latham 1952), which in turn conducts to a decline of the mesopredator prey (e.g. rabbits killed by mongooses killed by lynx Palomares *et al.* 1995). In the literature, such indirect effects have been referred to as trophic linkage indirect effects (Miller and Kerfoot 1987), interaction chains (Wootton 1993), numerical indirect interactions (Janssen *et al.* 1998), or density-mediated indirect interactions (Werner and Peacor 2003). In this thesis, we will refer to these indirect effects as interaction chains.

Box 1 – Competition as an indirect interaction?

Previously, we considered exploitative competition as a direct non-trophic interaction between two species. However, in most cases, this interaction can be considered as a trophic interaction chain, where the shared resource is considered as a species and not as an abiotic consumed resource (e.g. water for plants). One species C can reduce the abundance of its prey B, thereby reducing the food base of the other consumer A of the prey (Fig. 1A). What about interference competition? Interference can cover various forms from the aggressive encounter (direct effect) to the disturbance of a species (indirect effect) and the distinction between direct and indirect effect could be discussed depending on the form taken by the interference. However, regarding the nature of interference competition in this thesis, we will consider it as a direct effect between two species.

3.2- Interaction modification

Figure 1B represents indirect effects whereby a change in the density of one species alters the nature of a direct interaction between two other species (Wootton 1993). In mathematical terms, it changes the function describing the direct interaction between a species pair. Therefore, a species that indirectly influences another species in this manner directly affects the interaction between two species rather than the abundance of another species (Wootton 1993). There is a growing body of ecological literature (Wootton 1993, 1994, 2002; Werner and Peacor 2003, Arditi *et al.* 2005, Lin and Sutherland 2014) that demonstrates that per capita effects shared between two species are not fixed, but rather vary as a function of a third species (as in Figure 1B, where species C modifies the intensity of A and B's interaction). In the literature, these indirect effects have been referred to as higher-order interactions (Billick and Case 1994), interaction modifications (Wootton 1993), functional indirect interactions (Janssen *et al.* 1998), or rheagogies (Arditi *et al.* 2005). In this thesis, we will refer to such indirect effects as interaction modifications.

Interaction modifications can arise from two scenarios (Wootton 2002, Dambacher and Ramos-Jiliberto 2007). The first scenario is the trait-mediated interaction modification scenario whereby species C influences a phenotypically plastic trait of species A or B. For instance, competitive interactions between two ant species appear to be reversed in the presence of a phorid fly, a parasitoid of the soldier caste of one of the species (Feener 1981). The dominant species in the absence of the fly wins 63% of the confrontations at baits. However, in the presence of the fly it wins only 13% of the confrontations. When the fly is present, the soldier class of the dominant species hides in the leaf litter or returns to the nest instead of engaging the competing ants. The second scenario is environment-mediated interaction modifications whereby species C leads to a change in some factor, environmental agent, or context involved in the interaction between A and B. Ecosystem engineer species typically fall in this last category; Arditi *et al.* (2005) even designated them as "interaction modifiers". This term designates organisms that "directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials" (*sensu* Jones *et al.* 1994). For instance, shell production by mollusks leads to shell aggregation and create refuges for other species (Gutierrez *et al.* 2003).

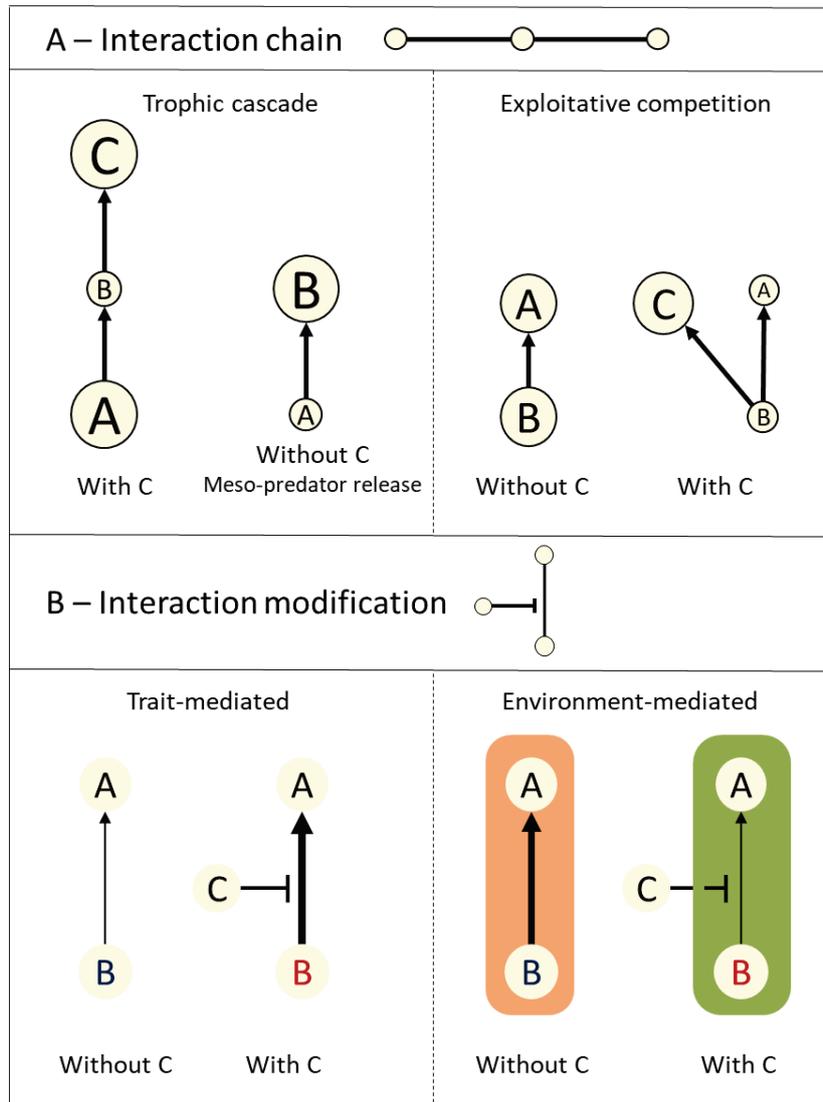


Figure 1: Diagram depicting the difference between A) interaction chains and B) interaction modifications as indirect effects. In this diagram, only trophic interactions (solid-line links with an arrow) are considered as direct interactions between species, with size representing the strength of the interaction. Trophic interaction modifications are represented either by broken horizontal solid-line (environment-mediated) either by entire horizontal solid-line (trait-mediated). Circle sizes represent population abundances which are subject to changes in interaction chain but not in interaction modifications. Orange and green shapes represent the environments where A, B and C inhabit. In the interaction chain example, species C indirectly affects species A through a chain of direct interactions (e.g. trophic cascade, exploitative competition). In the case of trophic cascade, if C is a large predator, B a meso-predator and A a prey, this interaction chain can lead to the “meso-predator release” without species C. In the interaction modification example, species C affects the interaction between A and B (e.g. altering the rate at which species A feeds on species B) either by modifying a species trait (e.g. vigilance behaviour) represented here by the modified colour of letter B, or by modifying the environment (e.g. creation of refuges) represented here by the modified colour of the habitat.

3.3- Importance of interaction modifications in ecological communities

The prevalence of interaction modifications in natural communities has been recognized in recent years. Werner and Peacor (2003) reviewed the mechanistic basis and empirical evidence for the presence of interaction modifications in both aquatic and terrestrial ecosystems and found that interaction modifications were widespread in ecosystems and often as strong as, or stronger than interaction chains. A meta-analysis revealed that the effects of anti-predator behaviour (trait-mediated interaction modification) might be as large as the effects from direct consumption by predators on prey species (Preisser *et al.* 2005). Abrams (1995), however, highlighted that comparisons of relative magnitudes of direct and indirect interactions should always be interpreted with caution, given that trait dynamics (translating to changes in interaction modification strength over time) can affect the latter but have rarely been accounted for in empirical studies (see also Lin and Sutherland 2014). Empirical and theoretical studies showed that both interaction chains and interaction modifications vary widely in their impacts on the stability and relative species abundances of ecological communities, depending on the relative strengths of direct and indirect effects and the quantitative balance between positive and negative feedback loops in ecological networks (Ulanowicz and Puccia 1990, Wootton 1994). The importance of embracing interaction modifications in understanding the response of real-world communities to global change has recently been highlighted (O'Connor and Donohue 2013).

3.4- Trophic interaction modification

Trophic interaction modifications are defined as the modification of a consumer-resource interaction (Wootton 1993) and are therefore a subset of interaction modifications. Trophic interaction modification can link a wide range of important ecological phenomena as modification of functional responses (Terry *et al.* 2017). They are now considered as widespread and most documented examples on interaction modifications are actually about trophic interaction modifications. Again, we find the distinction between trait-mediated and environment-mediated trophic interaction modifications. Examples of trait-mediated trophic interaction modification include a predator causing a behavioural shift in its prey that makes the prey more or less vulnerable

to another predator (Dayton 1973), or unpalatable prey species reducing predation intensity on palatable prey by reducing foraging profitability in a patch (Pfister and Hay 1988). Other examples include alternative prey that increases predator handling times, and dangerous higher-level predators that inhibit foraging (Golubski and Abrams 2011). Examples of environment-mediated trophic interaction modification include a species altering the physical environment in which a predator searches for prey, changing the predator's foraging efficiency (e.g. light-colored limpet *Lottia digitalis* appeared more cryptic on light-colored goose barnacles *Pollicipes polymerus* and is less predated by American Black Oystercatchers *Haematopus bachmani* - Wootton 1992). Ecosystem engineers are important trophic interaction modifiers by modifying their environment. For instance, leaf mines of *Eriocrania* spp. on *Betula pendula* when overlapping with the central leaf vein decrease the ability of aphids to attack those leaves (Johnson *et al.* 2002).

Box 2 – Facilitation as trophic interaction modification

As for exploitative competition, we previously considered facilitation interaction as a direct interaction between two species. In the framework of this thesis, this interaction can actually be considered as an environment-mediated trophic interaction modification as saw with the Vesey-Fitzgerald study (1960) where trampling and feeding by elephants exposed medium-height grasses to buffalo. Further, facilitation can also be considered as a trait-mediated trophic interaction modification, for instance if the facilitation passes through an increase of the resource quality (e.g. Gordon 1988, Part 2.2.2 Facilitation).

Studies with small numbers of species have repeatedly demonstrated that trophic interaction modifications have the capacity to drive population dynamics (e.g. Werner and Peacor 2003; reviewed in Preisser *et al.* 2005) and to have large quantitative effects on the dynamics of simple communities, evidence accumulating from studies (Preisser and Bolnick 2008; Beckerman *et al.* 2010), reviews (e.g. Wootton 2002; Abrams 2010) and meta-analyses (Preisser *et al.* 2005; Preisser *et al.* 2007). There is growing impetus from other recent works to address the challenges of detecting, measuring and testing the potential role of trophic interaction modifications in more complex systems such as natural communities (e.g. Wootton 1994, Peacor & Werner 2004, Okuyama & Bolker 2007). A greater understanding of how they influence population dynamics will be a key part of improving our ability to forecast how ecosystems will respond to global changes (Kéfi *et al.* 2012) as trophic interaction modifications are often identified as the cause of unexpected responses to perturbation (Terry *et al.* 2017 and references therein).

4- African savannas: open-air laboratories to assess trophic interactions in large mammal communities

4.1- An ecosystem with very rich large mammal communities

African savannas cover about half of sub-Saharan Africa (du Toit and Cumming 1999), and host high densities and diversities of large (>5 kg) mammalian herbivores (Fritz & Loison 2006) and carnivores (Keast 1969). The herbivore biomass density in some protected savanna ecosystems accounts for some of the highest levels of herbivory ever quantified in terrestrial ecosystems (McNaughton and Georgiadis 1986). African herbivores are characterized by a variety of body sizes (see examples in Table 1, Fig. 2) ranging from steenbok *Raphicerus campestris* (♀ et ♂: 11 kg) to megaherbivores, i.e. herbivores weighting more than 1000 kg (Owen-Smith 1988) such as African elephants *Loxodonta africana* (♀: 2 800 kg / ♂: 4 000 kg). There are also characterized by a variety of diets with browsers (feeding on leaves, soft shoots or fruits) such as giraffes (*Giraffa camelopardalis*) and greater kudu (*Tragelaphus strepsiceros*), grazers (feeding on grasses) and more precisely woodland grazers such as sable (*Hippotragus niger*) and roans (*Hippotragus equinus*), grassland grazers such as wildebeests (*Connochaetes taurinus*) and zebras (*Equus quagga*) and finally mixed-feeders (feed on both) such as elephants (*Loxodonta Africana*) and impalas (*Aepyceros melampus*, Lamprey 1963, Jarman 1974). All carnivores (small, meso- and large carnivores) present in Africa (with the exception of the fennec (*Fennecus zerda*) and the sand cat (*Felis margarita*)) occur in savanna ecosystems (Turpie 1994). This is particularly true for “top-order predators”, term defining predators with a range of body sizes that occur at the upper end of the food chains, which by their nature are relatively rare in natural ecosystems (Hayward and Somers 2009), such as the African lion (*Panthera leo*) or the spotted hyaena (*Crocuta crocuta*). Large mammal communities in these ecosystems are therefore very rich with diversified and widespread interspecific interactions, leading to a complex network where indirect effects are certainly playing a major role in the functioning of these communities and ecosystems.

African savanna ecosystems are the last terrestrial places where the Pleistocene megafauna is still largely intact (Martin 1984), where intact guilds of large carnivores have been preserved (IUCN, Ripple *et al.* 2014), and thus where natural interactions can be observed among animals from the top of the trophic web (Sinclair *et al.* 2010). Top-order predators have been extensively studied because they are iconic species (Ripple *et al.* 2014), key to understand human-carnivore conflicts (Woodroffe *et al.* 2005) and because of their important role in ecosystem functioning (e.g. Terborgh *et al.* 1999, Sinclair *et al.* 2003, Dalerum *et al.* 2008, Owen-Smith and Mill 2008,). Therefore, we now have a good understanding of the behavioural and evolutionary ecology of top-order predators (Somers and Gusset in Hayward and Somers 2009), of their lethal (predation) and non-lethal effects on prey (Brown *et al.* 1999) and evidence is accumulating on their effects through trophic cascades (Estes *et al.* 2011, Ripple *et al.* 2014, Sinclair *et al.* 2010). Megaherbivores too have been the focus of ecological research as they can be keystone competitors (Fritz *et al.* 2002) affecting herbivore community abundance and composition and they are ecosystem engineers (*sensu* Jones *et al.* 1994) affecting their physical habitat favouring or inhibiting other species. However, extremely little is known about the effects of each of these two guilds on the other, and we know virtually nothing on the extent to which one of these two guilds influence the relationships between the other guild and the remaining species of the community (i.e. interaction modification). Direct effect of top-order predators on megaherbivores has been studied but megaherbivores suffer little or no predation (Owen-Smith 1990; Owen-Smith and Ogutu 2003, Sinclair *et al.* 2010) except when environmental constraints (e.g. forage availability) affect their body condition and strength (Owen-Smith *et al.* 2005, Loveridge *et al.* 2006, Owen-Smith and Mills 2008). To our knowledge, nothing is known about the effect of top-order predators on megaherbivore trophic interaction (i.e. herbivory) as they do with smaller herbivore species (e.g. landscape of fear – *sensu* Laundré *et al.* 2001), or if megaherbivores affect competition interactions between top-order predators. Today, only a few recent studies have started to investigate if megaherbivores can modify the trophic interaction between top-order predators and their prey via trait-mediated (Schmitt *et al.* 2014), and environment-mediated trophic interaction modification (Tambling *et al.* 2013).

Table 1: Species description of the main herbivores species studied in this PhD. From Wilson & Mittermier (2011).

Common name	Latin name	Body mass (♀/♂) en kg	Diet	Home range (km ²)	Social organization / Group size
African savannah elephant	<i>Loxodonta Africana</i>	2800 / 6000	Mixed-feeder	50 - 30 000	Herds female/young, male-male bond, solitary male
Cape buffalo	<i>Syncerus caffer</i>	350-620 / 500-900	Grazer	126 - >1000	Herds female/young, bachelor, solitary male
Giraffe	<i>Giraffa Camelopardalis</i>	450-1180 / 1800-1930	Browser	25 - 160	Dynamic groups of female/young
Wildebeest	<i>Connochaetes taurinus</i>	164-216 / 232-295	Grazer	2 - 5	Female herds: 13-34, bachelor, territorial males
Greater kudu	<i>Tragelaphus strepsiceros</i>	170 / 257	Browser	3.6 - 11	Female group: 2-4, male group: up to 10
Sable antelope	<i>Hippotragus niger</i>	215-280 / 235-300	Grazer	40 - 120	Herds female/young: 6-20, bachelor, territorial males
Roan antelope	<i>Hippotragus equinus</i>	160-180 / 180-230	Grazer	12 - 25 up to 320	Herds female/young: 15-25, hierarchycal territorial bulls
Impala	<i>Aepyceros melampus</i>	43-47 / 57-64	Mixed-feeder	0.4 – 2.7	Kin groups of female, bachelor, territorial male.
Warthog	<i>Phacochoerus africanus</i>	50-75 / 60-150	Omnivorous	64-374 (ha)	Herds female/young, bachelor, solitary male.
Steenbok	<i>Raphicerus campestris</i>	9-13 / 9-13	Browser	4-5 ha up to 1 km ²	Territorial monogamous pair
Plains zebra	<i>Equus quagga</i>	175-320 / 175-320	Grazer	Restricted by water	Harem, bachelor.

Figure 2: Species photography.



African savannah elephant



Cape buffalo



Giraffe



Zebra



Sable antelope



Wildebeest



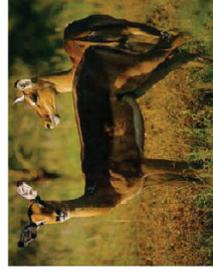
Greater kudu



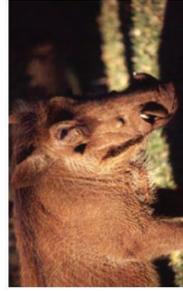
Steenbok



Roan antelope



Impala



Warthog

4.2-Ecosystems under global changes and human practices

4.2.1- Climate changes

Climate is a major determinant of the natural distribution of species, with evidence both from fossil records (Escarguel *et al.* 2011) and from recently observed trends (Parmesan & Yohe 2003). Climate changes, i.e. changes in the trend of a climate variable, such as temperature or rainfall, or in the frequency of climatic events, such as floods and droughts over time (Okali 2011), therefore may pose a serious threat to species persistence (Parmesan 2006, Bellard *et al.* 2012). Southern Africa is particularly vulnerable to aridification (Kusangaya *et al.* 2014) and warming (Okali *et al.* 2011). For example, in Zimbabwe, extreme weather events, namely droughts, have increased in intensity (Chamaillé-Jammes *et al.* 2007). Such climate changes can affect negatively animal populations through effects on demographic rates, such as survival and fecundity (Okali *et al.* 2011), but also through spatial and temporal shift and where animal adapt to the new conditions (Bellard *et al.* 2012). In African savannas, extreme climatic events may have dramatic effects such as alteration of birds and mammals' abundance and diversity, especially in semi-arid zones (Okali *et al.* 2011). However, the main effects induced by climate changes on species are indirect. Particularly, through alterations of species interactions (Griffith *et al.* 2017, White *et al.* 2017), climate change can modify community structure and ecosystem functions (Bellard *et al.* 2012). For instance, changes in growth rates can alter body sizes, and influence the outcome of species interactions, Gilman *et al.* 2010). In many wooded and bushed savannas in East and southern Africa, Okali *et al.* (2011) exposed that climate warming is likely to reduce the production of woody plant fruits/seeds with negative consequences on the abundance of browser herbivores. In order to limit the ecological and economic impacts of such climate changes in African ecosystems, Okali *et al.* (2011) preconized to provide artificial sources of water, to expand protected areas to include migration corridors and seasonal feeding areas and to improve connectivity of habitats to facilitate dispersal to appropriate habitats.

4.2.2- Land use changes and human practices

While African savanna ecosystems are vulnerable to climate changes, it is not the only factor threatening biodiversity in these ecosystems. Rapid human population growth, land development and the spread of firearms since colonial times have exterminated much of the megafauna in West, South and central Africa (Simon 1962), and will continue to be a major threat in the coming years. Protected African savanna areas are becoming increasingly isolated as land use changes impinge against their boundaries, increasingly restricting the area available for wildlife movements, especially for large wide-ranging mammals (Ogutu *et al.* 2012). Péron & Altwegg (2015) showed for example that land use change and ecological succession appear as faster, more direct drivers of passerine distribution changes than climate variables themselves in grasslands and savannas. Western *et al.* (2009) considered that current and upcoming sedentarization of populations is likely to become the biggest threat to wildlife in the East African savannas through the direct displacement of wildlife and the reduction in grass production due to permanent grazing. Hunting can also have negative consequences for species living in African savannas (Ripple *et al.* 2016), and particularly for the megafauna. Top-order predators are threatened directly by human persecution (Hayward and Somers 2009), trophy hunting (Packer *et al.* 2010), retaliatory killing as a response to livestock depredation (Treves & Karanth 2003) and indirectly, as a decline in wild prey will invariably lead to a decline in predator abundance through bottom-up limitation (Karanth *et al.* 2004; Hayward *et al.* 2007d). Megaherbivores are also under threat, particularly elephants, black (*Diceros bicornis*) and white rhinoceroses (*Ceratotherium simum*) because of poaching for ivory and rhinoceros horns, which has led to preoccupying population declines (Milliken *et al.* 2009, Maisels *et al.* 2013, Wittemyer *et al.* 2014).

4.3- Effects of human disturbances and global changes on indirect effects

Species abundances and species richness are often proxies used to evaluate the state of communities. However, there is a need to take into consideration the interdependence between species as they can help us to forecast how ecosystems will respond to global changes (Kéfi *et al.* 2012). Interspecific interactions are more difficult to identify and quantify, and yet it was proposed and demonstrated they can be impacted by

climate changes (Van der Putten *et al.* 2010, Gilman *et al.*, 2010) and human practices (e.g. predator-prey relationships in Valeix *et al.* 2012). However, as we saw above, ecological communities are complex, and interaction modifications are often identified as the cause of unexpected responses to perturbation (Terry *et al.* 2017 and references therein). In addition, indirect effects can lead to surprising responses to perturbations, but they can also be modified themselves by the perturbations, leading to feedback loops limiting our ability to predict community's trends and changes in ecosystem functioning facing these global changes. That is why it is of importance to study (both theoretically and empirically) these indirect effects in natural and complex communities.

5- Hwange National Park: the ideal open-air laboratory to assess the role of megaherbivores on trophic interactions

5.1- A semi-arid woodland savanna ecosystem modified by water management

Hwange National Park covers ~15 000 km² of savanna in north-western Zimbabwe (Figure 3). As a semi-arid savanna, this park is characterized by a wet season when most rains fall (between November and April) and by a dry season (from May to October). The long-term mean annual rainfall is 600 mm but is highly variable (CV = 25%, Chamaillé-Jammes *et al.* 2007). During the dry season, availability of natural surface water is very limited as no permanent river, and only a few pans retain water in an average year (Figure 3). Indeed, until its creation, almost no surface water was available at the driest period of the year in the park (Davison 1967). Since its creation, several artificial waterholes were created thanks to the pumping of underground water and animal communities began to change with water-dependent wildlife coming into the park (Davidson 1967). These artificial waterholes represent therefore key places in the landscape for large mammal species (herbivores, Valeix *et al.* 2009c, Valeix 2011, and predators Valeix *et al.* 2010, Davidson *et al.* 2012), were interspecific interactions, and ultimately interaction modifications, could be enhanced as encounters with other species are more frequent there. In the future, the key role of artificial waterholes in the functioning of the large mammal community of the park could be exacerbated as droughts are expected to become drier (Chamaillé-Jammes *et al.* 2007).

Box 4: The elephants and the water in Hwange National Park (from Valls Fox 2015).

- **19th Century:** Intensive hunting by European hunters throughout Southern Africa progressively shifted northward following the decimation of South African populations by the early 1800's. In the mid-19th century, 2000-3000 were killed annually in the neighboring areas corresponding to present day Botswana. By the turn of the 20th century elephants had been exterminated from most of the region, small numbers remained in isolated pockets such as the area covered by present-day Hwange National park (Vandewalle & Alexander 2014).
- **1928:** Proclamation of the Wankie Game Reserve, less than a thousand elephants in the Reserve (Davison 1967).
- **1936:** First windmills erected to supply water and effective protection enforced. However elephants do not stay during the dry season due to lack of water. (ibid.)
- **1940's:** First diesel pumps provide reliable water supply throughout the dry season. The number of pumped pans increases gradually up to about 60 pumped pans in the 1980's. (Chamaillé-Jammes *et al.* 2014)
- **1930-1966** Elephant population increases exponentially (5%/ year) (Cumming 1981)
- **1966:** Start culling program. A threshold of 13000 elephants was only defined in 1974 (ibid.)
- **1970's:** Population estimated at 14 000 elephants. (ibid.)
- **1983:** It is estimated there are more than 20 000 elephants. The major culls of 1984, 1985 and 1986 brought the population down to 13 000 (Cumming 1981).
- **1986:** End of culling operations. Elephant population doubled from 15 000 to 30 000 in a few years probably due to immigration from an unknown location (ibid.). However, elephant bulls are still shot in surrounding Safari Areas by trophy hunters or in Communal lands by competent authorities as Problem Animal Control (Guerbois 2012).
- **1992-present:** Elephant populations fluctuates around 35 000-45 000 individuals (Chamaillé-Jammes *et al.* 2008; Dunham 2015)
- **2000-2008:** Collapse of tourism and Hwange National Park revenues, the economic crisis results in an unquantified reduction of game water supply.
- **2008-2015:** Revival of the tourism industry. New waterholes are opened in private concessions. The occurrence of poaching events increases (particularly at the end of the dry season) but the number of animals lost remains low in comparison with the total estimated population.
- **2014:** Aerial population census of 45 846 ± 6 300 individuals (Dunham 2015)

Two-third of the park lies on the eastern fringes of Kalahari sands that cover most of Botswana. The vegetation is characteristic of the wider region with its semi-arid climate and dystrophic soils, being a mix of bushland and patches of *Baikiaea plurijuga* woodland. Monospecific stands of mopane trees *Colophospermum mopane* cover much of the north of the park interspersed with grassland vleis, where the rich-nutrient soils are derived from basalt and the climate is more arid (Rogers, 1993). The park is therefore dominated by woodland savanna (64%, Rogers 1993, Figure 3), at the opposite of other African open grassland savannas such as the very well-studied Seregenti-Masai Mara ecosystem (Tanzania-Kenya).

Hwange National Park is a semi-arid woodland savanna ecosystem superficially similar in habitats to other large national parks such as Kruger National Park (South Africa) and Chobe National Park (Botswana), but it differs in the way surface water is distributed and changes during the season, because in these other parks animals can also access one or several permanent rivers.

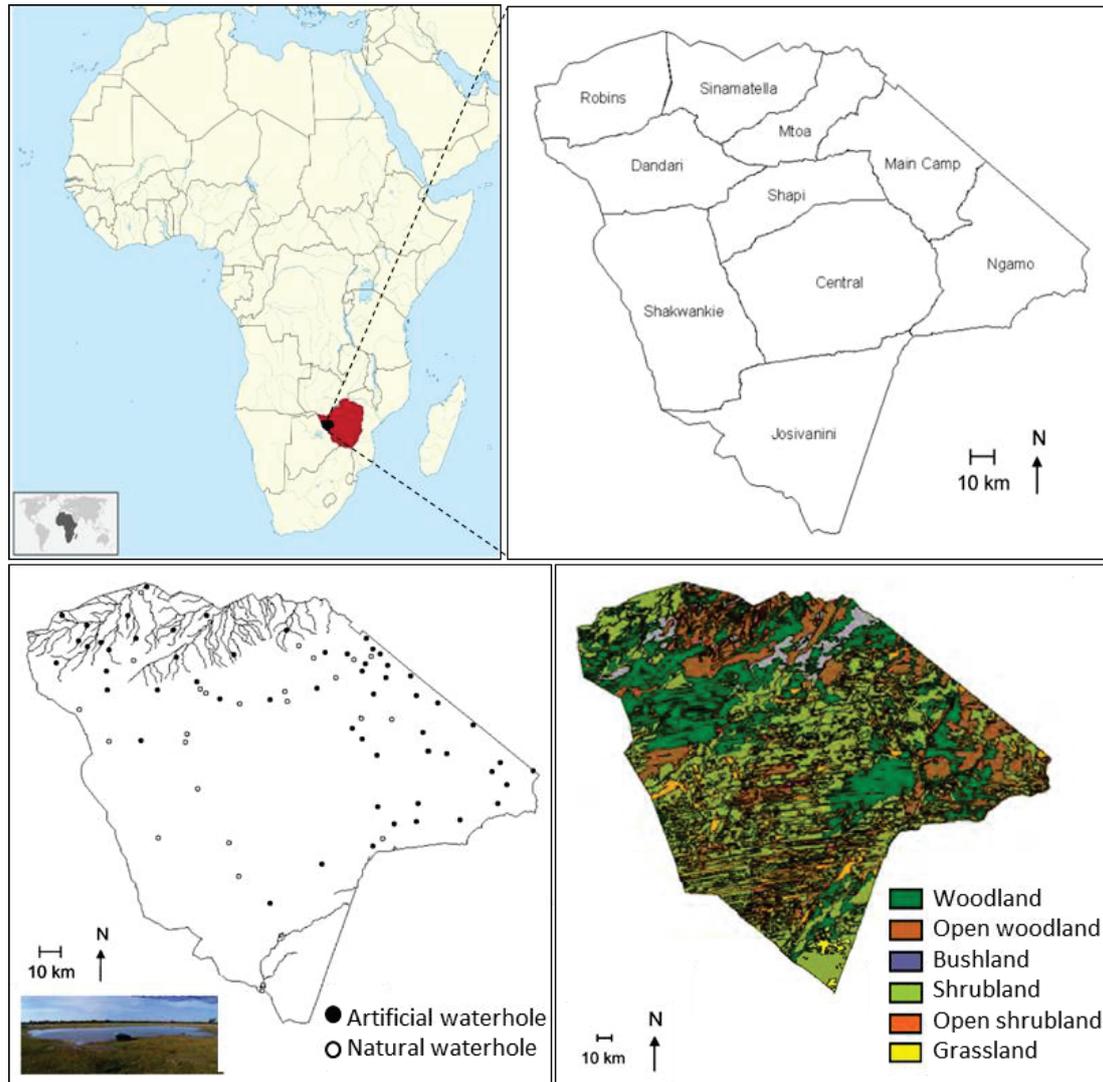


Figure 3: Location of the Hwange National Park, Zimbabwe, with the different administrative zones. The main areas studied in this thesis were Ngamo, Main Camp, Sinamatella and Robin. Distribution of the surface water in the park (the natural waterholes represented are those keeping water during the dry season). Distribution of the main vegetation profiles in the park (Rogers 1993).

5.2- An elephant and lion stronghold

Following moratorium on lion trophy hunting, where adult males were primarily targeted, imposed by the Zimbabwe Parks and Wildlife Management Authority between 2005 and 2008, a 62% increase in the total population and a 200% increase in adult male density was observed in the lion population of Hwange National Park (Loveridge *et al.* 2016). The lion population density is now estimated around 4.3 lions/100 km² in the park

(Loveridge *et al.* 2016), which is now considered as one of the lion stronghold (Riggio *et al.* 2013). In addition, the park is characterized by the overwhelming presence of the biggest terrestrial megaherbivore, the African elephant (Blanc *et al.* 2003, Fritz *et al.* 2002). Thanks to the creation of the artificial waterholes, the elephant population increased from one thousand at the creation of the park (Davison 1967) to 8000 in the 60's (Williamson). Concerns about high elephant densities then arose and a culling program was initiated (Cumming 1981) until 1986. Since the stop of the culling, the elephant population increased once more to attain one of the highest elephant population density of the world. Indeed, the north-western part of the park attains densities of more than 4 elephants.km⁻² in dry periods (Chamaillé-Jammes *et al.* 2009) and it is possible to see hundreds of elephants coming at waterholes at the end of the day during the dry season (pers. obs.).

As both elephant and lion populations are at high density in the park, the potential indirect effects of these two species on each other should be maximized and easier to observe than in any other ecosystem where these two species are less abundant.

6- Thesis aims and structure

6.1- Aims

This thesis focuses on trophic interaction modifications in large mammal communities. More precisely, the aim of this work is to investigate the role of megaherbivores (here the African elephant) as modifiers of the trophic interactions between a top-order predator (here the African lion) and its prey herbivore species. This work was carried out in Hwange National Park, whose large mammal community is characterized by one of the most abundant elephant population and a large lion population (Fritz *et al.* 2002).

On the one hand, the African lion is a stalk and ambush predator that relies on features of the habitat providing concealment (e.g. rocks, termite mounds or dense vegetation) to approach and attack their prey (Hopcraft *et al.* 2005, Loarie *et al.* 2013,

Davies *et al.* 2016). In addition, they are particularly attracted by waterholes, which condition their movements (Valeix *et al.* 2010, Davidson *et al.* 2012) and their hunting behaviour (Valeix *et al.* 2009b, Valeix *et al.* 2011a, Davidson *et al.* 2012). More than the necessity to drink (lions are known to be independent from surface-water; Eloff 1973), this is the predictable presence of high prey density around waterholes that explains this waterhole-driven spatial behaviour (Valeix *et al.* 2010).

On the other hand, the African elephant is a particular terrestrial species mainly due to its exceptional body mass (Owen-Smith 1988) and is considered as a keystone-competitor (Fritz *et al.* 2002) and an ecosystem engineer (Coverdale *et al.* 2016). Owen-Smith (1988) pointed out that though elephants may compete with other species (because they remove large quantities of resources, or cover, see Jachman and Bell 1985), it is possible that feeding and trampling by elephants induces regrowth of new shoots of higher quality in both the herb- and the shrub-layer, thus facilitating smaller and more selective species (see also the “browsing lawn hypothesis”, Makhabu *et al.* 2007) with consequences for habitat selection by other species (Valeix *et al.* 2011b). In addition, elephants can have profound effect on the vegetation, and its structure, with repercussion for the whole ecosystem functioning (e.g. grass-tree coexistence Sankaran *et al.* 2005, fire dynamics van Langevelde *et al.* 2003, animal biodiversity Pringle 2008). In this thesis, we will particularly assess their possible role for predator-prey relationships (see also for herbivores Coverdale *et al.* 2016, and carnivores Loarie *et al.* 2013, Tambling *et al.* 2013). Due to their body size and their high abundance in the study ecosystem, elephants are also expected to dominate all interactions with other herbivores (Owen-Smith 1988). At the scale of the waterhole, they are considered as one of the drivers of the waterhole use by other herbivores, as they can lead to temporal shift and modification of the behaviour of other herbivores at the waterholes (e.g. Valeix *et al.* 2007, Valeix *et al.* 2009a). In addition, adult elephants are considered invulnerable to predation (Sinclair *et al.* 2003) and are able to deter predators, even lions, by mobbing behaviour (McComb *et al.* 2011, pers. obs.). Elephants could therefore affect lions, their prey or both and have consequences for lion trophic interactions, particularly around waterholes.

6.2- Thesis structure

This thesis was built around three research axes to assess if elephants can alter lion predator-prey relationships.

The **first research axis** evaluates the effects of elephants on other herbivore species, i.e. prey for lions, at the **scale of the waterhole**, and ultimately investigates the implications for lion trophic interactions at waterholes. This first research axis assesses a prey **trait-mediated trophic interaction modification** (Figure 4.1). In *Chapter 1*, I explored the dynamics of interference competition between elephants and other herbivores for the access to water in the dry season (Figure 5-*Chapter 1*). I used data collected on the fine-scale spatial distribution of large herbivores and elephants at waterholes and studied their spatial aggregation/segregation patterns. I discussed the dynamic trade-off herbivores seem to face over the dry season between costs associated to interference competition with elephants and other costs associated either with access to water of sufficient quality (“water quality hypothesis”) or with perceived predation risk (“bodyguard hypothesis”). To understand the results from *Chapter 1*, the two different hypotheses suggested were investigated in *Chapter 2* and *Chapter 3* respectively. In *Chapter 2*, to explore the “water quality hypothesis”, I considered that waterholes are not homogeneous patches of resource but show a gradient of water quality. I therefore assessed if interference competition with elephants occurs for the access to water of high quality, not for the access of water in general (Figure 5-*Chapter 2*). I collected observational data on the drinking position of large herbivores and sampled water quality in different areas of the waterholes. *Chapter 3* represents the first part of the trait-mediated trophic interaction modification process, whereby elephants could modify the anti-predator behaviour of lion’s prey. The rationale of the “bodyguard hypothesis” is that elephants, thanks to their body size and their mobbing behaviour, may represent safety for smaller herbivores against predation by lions. Thanks to a behavioural experiment, I assessed if after an increase of the perceived risk of predation by lions at the waterholes zebras benefit from the elephant presence (i.e. aggregating to these lasts and reducing their vigilance behaviour, Figure 5-*Chapter 3*).

The **second research axis**, constituted by *Chapter 4*, considers elephants either as exploitative competitors for food resources (i.e. **interaction chain**, Figure 4.2A) or as an engineer species facilitating availability of resources of higher quality (i.e. **trait-mediated trophic interaction modification**, Figure 4.2B), at the **scale of the landscape and of the habitat**. For some herbivore species, elephants by depleting food resource could lead herbivore local abundances to decrease in areas highly used by elephants, which could ultimately have consequences for lion local abundance in these habitats (Figure 5 – *Chapter 4*). On the contrary, by breaking twigs and trunks, elephants are likely to enhance the growth of many shoots on impacted trees, which may be preferred by other herbivores, leading to an increase of herbivore local abundances in the habitats used by elephants with subsequent consequences for lion local abundance (Figure 5 – *Chapter 4*). Road count data collected between 2004 and 2014 were analyzed to assess segregation/aggregation pattern between elephants and other herbivores at the landscape scale to test these hypotheses.

In the **third research axis**, I studied the effects of elephants on lion foraging behaviour through changes in the vegetation structure (**environment-mediated trophic interaction modification**, Figure 4.3). In *Chapter 5*, I focused on the effects of the long-term exposure to high elephant densities on woodland structure, species composition and functional traits. I first described the dynamics of elephant impacts in 2001, 2008 and 2015, then assessed if these impacts were linked to species community changes leading to functional trait community changes. Finally, I analysed the dynamics of the vegetation structure in the 50-200 cm height layer, which is the height zone important for predator-prey relationships. Data on all woody plant (species, height, crown diameter, and stem girth) present in 12 vegetation plots, recorded in 2001, 2008 and 2015, and functional trait gathered from plant databases were used for this chapter. In **Chapter 6**, I finally assessed if the habitats impacted by elephants are characterized by a higher visibility and a higher distance to a potential ambush site (item behind which lions could hide, e.g. shrub), and the role of the presence of elephant impacts, the visibility and the distance to a potential

ambush site on the kill site selection by lions. Lion kill site locations were identified thanks to GPS radio-collared lions monitored in the framework of Moreangels Mbizah's DPhil work (WildCRU, University of Oxford) between 2014 and 2015. Elephant-induced vegetation changes, visibility and distance to a potential ambush site were recorded at each kill site, and these data were used for the analyses of this chapter.

The last part of the manuscript discusses the results about the role of elephants in some features of the predator-prey relationships of lions, with the limits and the perspectives associated to each research axis. A synthesis of the role of elephants in the lion trophic interaction, and more generally in the large mammal community is provided. Finally, I underline the necessity to consider indirect effects in food webs for the study of community structure and functioning.

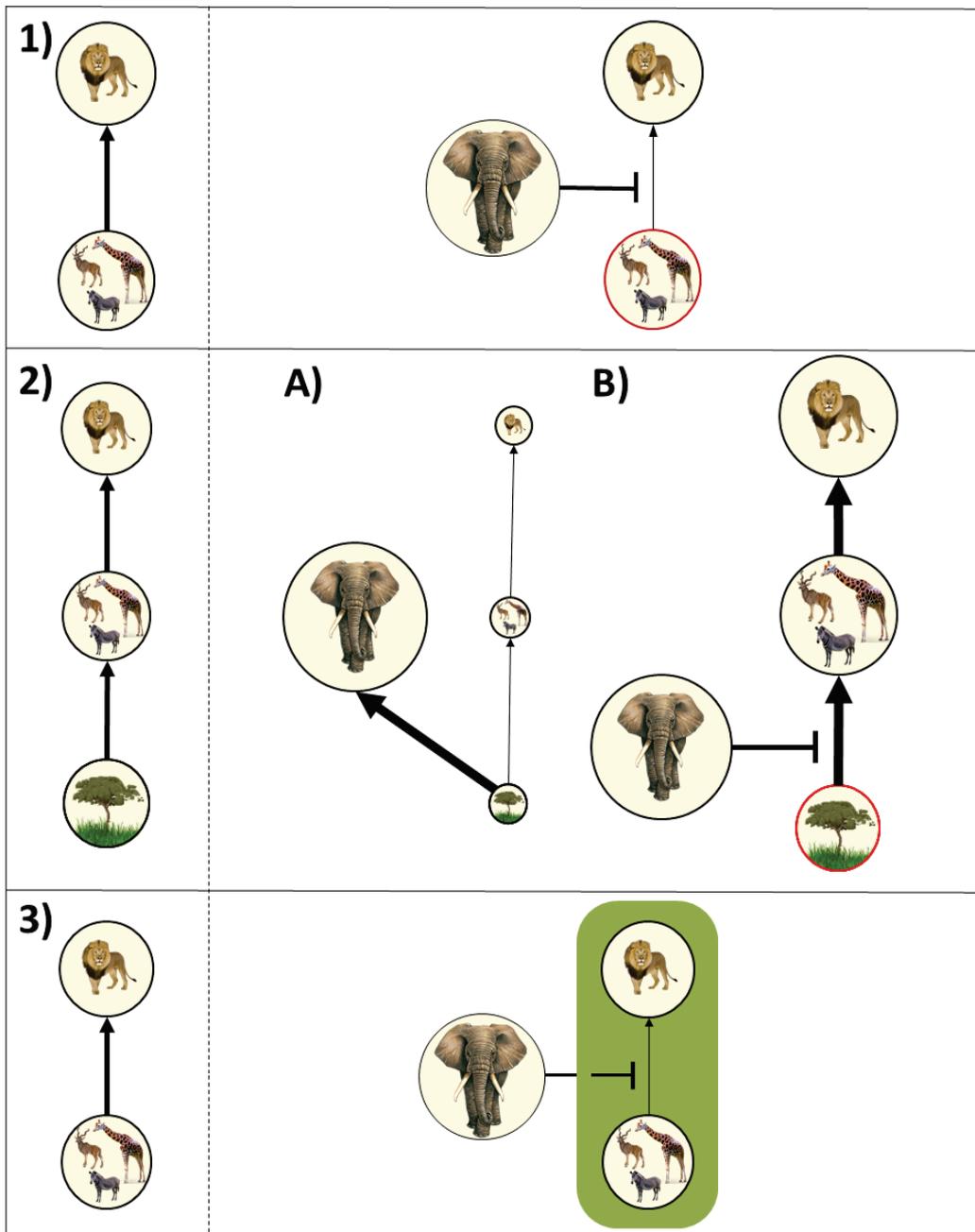


Figure 4: Diagram depicting the different types of indirect effects envisaged to assess the role of elephants as modifiers of lion trophic interactions in the three research axes of the thesis. 1) Trait-mediated trophic interaction modification, with elephants modifying a behavioural trait of the prey. 2) A) Exploitative competition (interaction chain) between elephants and other herbivores, leading to a decrease of herbivores abundances (and thus predators) in areas with high density of elephants. B) Facilitation interaction (represented here as a trait-mediated trophic interaction modification) increasing trophic interaction between herbivores and plants affected by elephants, followed by an increase of the herbivore abundances (and thus predators) in areas with high elephant density. 3) Environment-mediated trophic interaction modification, with elephants modifying the vegetation structure, which in turn modifies the strength of the predation by lion in habitats modified by elephants.

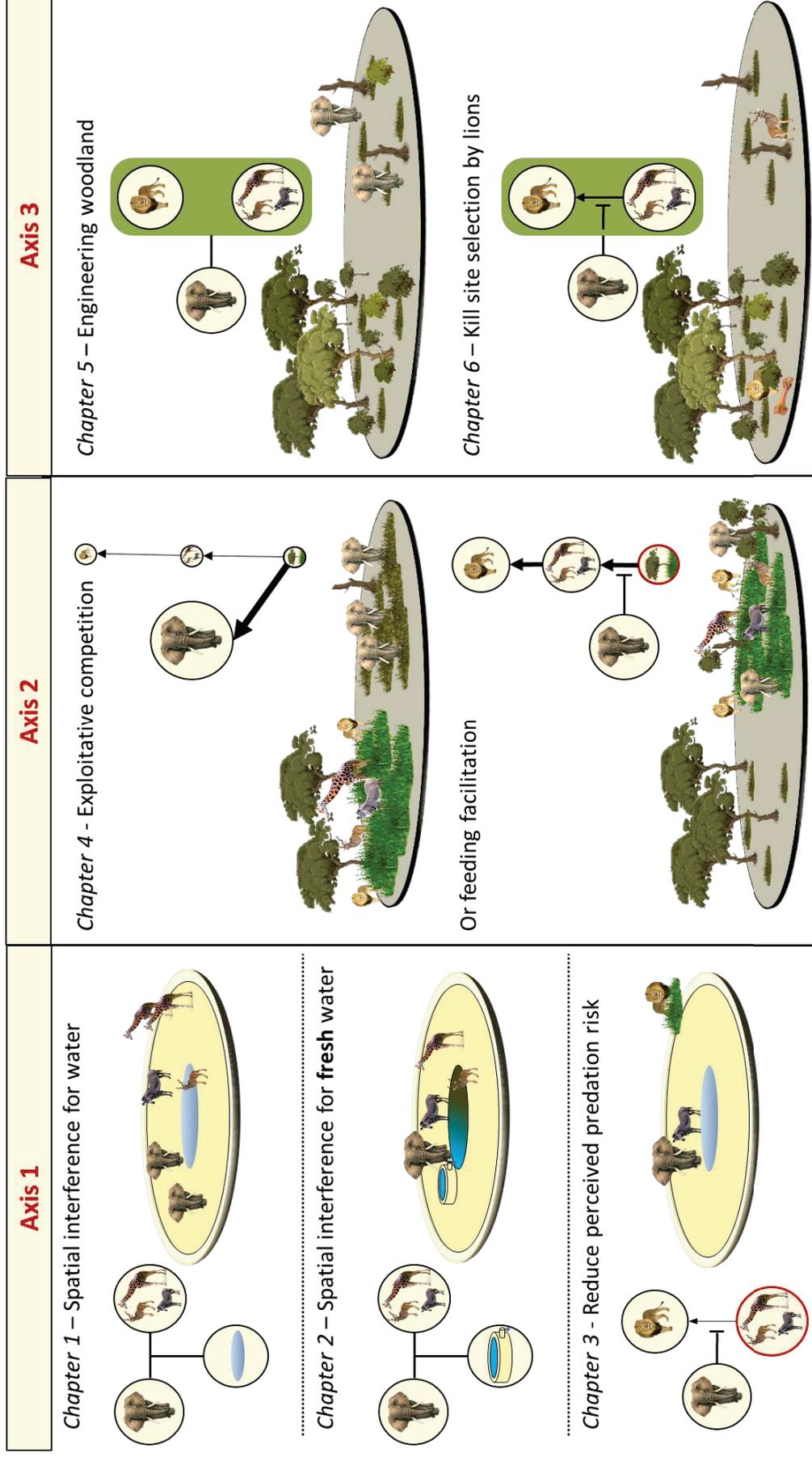


Figure 5: Representation of the different chapters of the thesis, with the direct and indirect effects investigated in each chapter.

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AXIS 1.

Effect of elephants on herbivore's
behaviour at waterholes



« Le coassement des grenouilles n'empêche pas l'éléphant de boire. »

Chapter 1: Interspecific interference competition at the resource patch scale: do large herbivores spatially avoid elephants while accessing water?

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Abstract

1. Animals may anticipate and try to avoid, at some costs, physical encounters with other competitors. This may ultimately impact their foraging distribution and intake rates. Such cryptic interference competition is difficult to measure in the field, and extremely little is known at the interspecific level.
2. We tested the hypothesis that smaller species avoid larger ones because of potential costs of interference competition and hence expected them to segregate from larger competitors at the scale of a resource patch. We assessed fine-scale spatial segregation patterns between three African herbivore species (zebra *Equus quagga*, kudu *Tragelaphus strepsiceros* and giraffe *Giraffa camelopardalis*) and a megaherbivore, the African elephant *Loxodonta africana*, at the scale of water resource patches in the semi-arid ecosystem of Hwange National Park, Zimbabwe.
3. Nine waterholes were monitored every two weeks during the dry season of a drought year, and observational scans of the spatial distribution of all herbivores were performed every 15 min. We developed a methodological approach to analyse such fine-scale spatial data.
4. Elephants increasingly used waterholes as the dry season progressed, as did the probability of co-occurrence and agonistic interaction with elephants for the three studied species. All three species segregated from elephants at the beginning of the dry season, suggesting a spatial avoidance of elephants and the existence of costs of being close to them. However, contrarily to our expectations, herbivores did not segregate from elephants the rest of the dry season but tended to increasingly aggregate with elephants as the dry season progressed.
5. We discuss these surprising results and the existence of a trade-off between avoidance of interspecific interference competition and other potential factors such as access to quality water, which may have relative associated costs that change with the time of the year.

Keywords: *Loxodonta africana*; asymmetric interaction; contest competition; distance analysis; megaherbivore; savanna; spatial-constrained null model; waterhole use

Introduction

Interspecific interference competition, that is when a species reduces the ability of other species to make use of a shared resource through its presence or agonistic interactions, is ubiquitous in nature (Amarasekare 2002). It has been documented in a wide range of taxa (e.g. Ziv *et al.* (1993) for rodents, Caro & Stoner (2003) for large mammalian carnivores, Elliott (2003) for insects, Razgour, Korine & Saltz (2011) for bats, Colman *et al.* (2012) for large mammalian herbivores) and can impact individual behaviour (e.g. spatial distribution – Berger & Gese 2007; Broekhuis *et al.* 2013), individual fitness (e.g. Eccard & Ylönen 2002), species coexistence (e.g. Case & Gilpin 1974; Amarasekare 2002) and character displacement (e.g. Grether *et al.* 2009, 2013). In addition to the risk of injury or death during agonistic interactions (e.g. Palomares & Caro 1999; Berger-Tal, Mukherjee & Kotler 2009), interference competition can carry costs that are extremely difficult to evaluate in the field. This is the case when interference competition leads to reduced intake rates (Abramsky, Rosenzweig & Subach 2001) due to apprehension (i.e. attention redirected from foraging to predator/competitor detection in a manner that lowers both risk and feeding rate, Kotler, Brown & Dall 2002) or to a reduced access to resources resulting from avoidance behaviour (a process known as cryptic interference competition as such responses are often difficult to observe in the field, Gyimesi, Stillman & Nolet 2010). The need to account for the possibility that animals anticipate and try to avoid, at some costs, physical encounters with other competitors when studying intake rates and foraging distributions has recently been highlighted (Bijleveld, Folmer & Piersma 2012). This may indeed underlie the spatial distribution of animals and their foraging tactics at the community level, and while this has started to be studied at the landscape scale (Vanak & Gompper 2010), and at the inter-patches scale (Razgour, Korine & Saltz 2011), extremely little is known at the finer scale of the resource patch.

Interspecific interactions are often asymmetrical, and smaller species often lose aggressive contests for resources with larger species that are often characterized by stronger traits (e.g. strength, weapons (Peters 1983), see also Durant (2000) for large mammalian carnivores, Cioni & Gherardi (2004) for decapods, Grangier & Lester (2011) for ants and wasps). Therefore, smaller subordinate species are expected to adjust their behaviour to decrease the risk of interference competition with dominant species. Avoidance of dominant competing species can occur at both spatial (Durant 2000; Tannerfeldt, Elmhagen & Angerbjörn 2002) and temporal scales (Ziv *et al.* 1993; Valeix, Chamaillé-Jammes & Fritz 2007). However, overall

spatial and temporal avoidance of interference competitors may prevent animals from using very valuable patches of resources. Thus, fine spatio-temporal scale responses should play a crucial role in adjusting the trade-off between avoidance of competitors and access to high-quality resources. This fine-scale spatio-temporal avoidance of interference competition has yet rarely been explored in the field at the interspecific level.

Here, we assessed fine-scale spatial segregation patterns between three African herbivore species and a megaherbivore, the African elephant *Loxodonta africana*, which is expected to dominate all interactions with other herbivores (Owen-Smith 1988), at the scale of a water resource patch. To our knowledge, this intra-patch scale has never been investigated. In arid and semi-arid savannas, surface water resources become scarcer as the dry season progresses and are vital resource patches for water-dependent species survival. This leads to a high level of herbivore aggregation around the remaining water sources at the end of the dry season (Valeix 2011), which can lead to interference behaviour. Behavioural interactions between elephants and other species sometimes lead to other herbivores being chased away from the waterhole area (Valeix, Chamaillé-Jammes & Fritz 2007), and other more extreme interactions can even be the cause of injuries or fatalities, but these are extremely rare (M. Valeix, pers. obs., see also Slotow & van Dyck 2001). Hence, herbivores may anticipate and try to avoid being close to elephants. Understanding the impact of elephant presence and abundance on other herbivore species at key resource patches, such as waterholes, is crucial in a context where elephant populations have reached high densities in several southern African ecosystems causing concern about their influence on other forms of biodiversity and questioning adequate management options (e.g. Van Aarde & Jackson 2007; Kerley *et al.* 2008). Manipulating surface water distribution has been suggested as an efficient tool to manage high elephant population densities (Chamaillé-Jammes, Valeix & Fritz 2007; Hilbers *et al.* 2015). In this study, we assessed the extent to which cryptic interspecific interference competition between elephants and other herbivores contributes to animal spatial distribution at waterholes and consequently may influence access to water when this resource becomes crucial. The study took place in Hwange National Park, Zimbabwe, an ecosystem characterized by scarce water sources in the dry season (Chamaillé-Jammes, Fritz & Murindagomo 2007a) and one of the largest African elephant populations (Chamaillé-Jammes *et al.* 2008). To assess the fine-scale segregation spatial patterns between elephants and other herbivores, we recorded the distribution of elephants and other herbivores around waterholes, and without previous reference studies, we also

developed a methodological approach to analyse such fine-scale spatial data on aggregation/segregation patterns with short term dynamics as well as seasonal changes. We tested the hypothesis that interference competition with elephants is a key driver of herbivore spatial distribution at waterholes and herbivores avoid elephants once at waterholes. We predicted that as the dry season progresses and surface water becomes scarcer, (i) elephants should increasingly use waterholes, (ii) the co-occurrence between elephants and other herbivores at waterholes as well as the frequency of agonistic interactions between them should increase, and (iii) other herbivores should spatially segregate from elephants around waterholes and this pattern should increase throughout the dry season.

Materials and methods

Study site

The study was carried out in Hwange National Park in the north-western part of Zimbabwe. This ecosystem covers ~15 000 km² of semi-arid dystrophic savanna, mostly on nutrient-poor Kalahari sands. Most rain falls between November and April. The long-term mean annual rainfall is 600 mm but is highly variable (CV ≈ 25%). The study took place during the dry season (i.e. from May until the first rains in October) of a drought year (2003) which received only 474 mm of annual rainfall and followed below average rainfall in 2002 with 363 mm. Hence, the study was carried out under extremely dry conditions. During the dry season, water is only available at artificial waterholes as natural waterholes dry up and appears to be a limiting resource as the increase in the number of artificially pumped waterholes has led to the increase of almost all herbivore populations (Davison 1967). Animals gather at high densities near waterholes in the dry season (Valeix 2011), and elephants represent 80–90% of the herbivore biomass (Fritz *et al.* 2011). Water depletion at the scale of a waterhole is reduced in the dry season when ground water is actively pumped into water troughs that then fill the artificial waterholes (Appendix S1a, Supporting Information). Thanks to this quasi-permanent renewal of surface water at the end of the dry season, which is the critical period for herbivores in terms of water acquisition, Hwange National Park is an ideal site to study interference mechanisms.

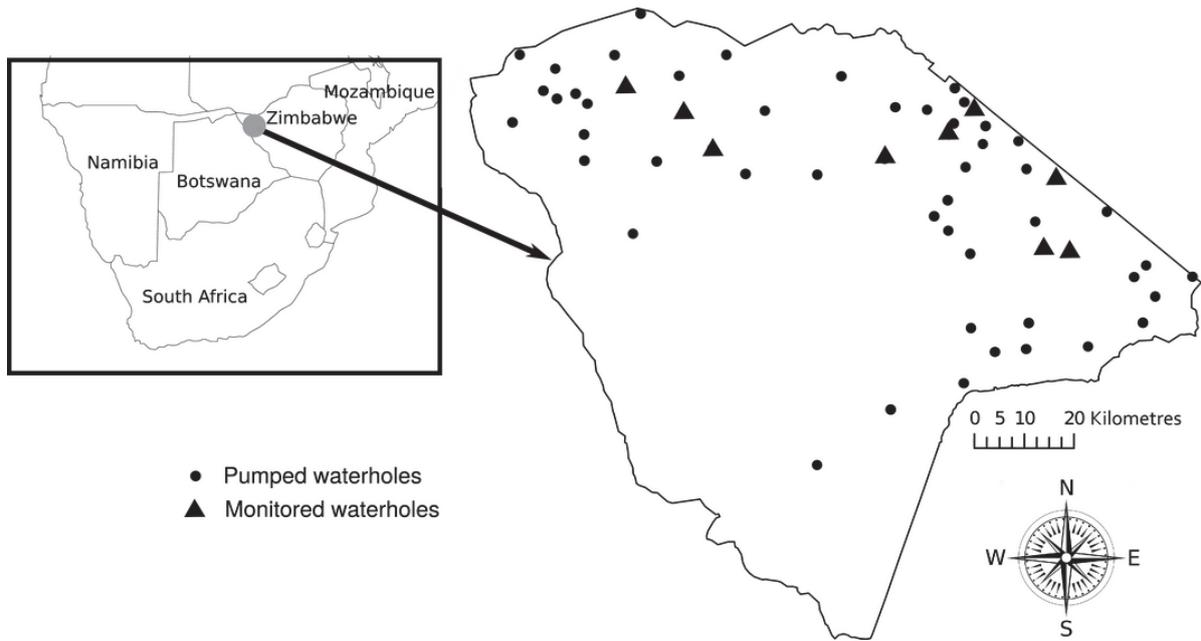


Figure 1. Map of the distribution of artificial waterholes (dots) in Hwange National Park, Zimbabwe, showing the location of the monitored artificial waterholes (triangles) for this study.

Data

From May to October 2003, we monitored every two weeks nine artificial waterholes (average diameter of a waterhole: 100 m) during the daytime (from 6 h until 18 h), in the northern part of Hwange National Park (Fig. 1). This represents 1296 h of observation. There were few herbivore observations at these artificial waterholes at the beginning of the dry season, that is in May and June. We pooled data from these 2 months as they were characterized by similar climatic conditions and natural water was still available in the landscape. We thus have five periods (one-2-month and four-1-month) with similar number of observations for the subsequent analyses.

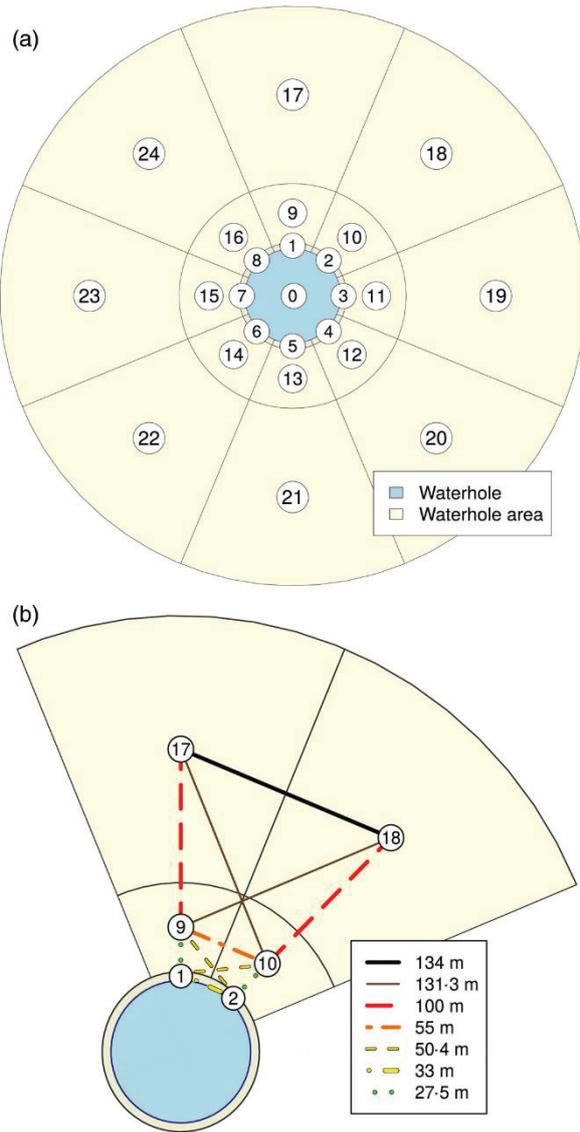


Figure 2. Spatial sampling design. (a) Representation of the waterhole area divided into four concentric circles: (i) the waterhole itself (cell 0 in pale blue at the centre) where there was most of the time no herbivore except elephants that regularly bath, (ii) the water-access area (cells 1–8, between 0 and 5 m from the waterhole edge) which represents the area where herbivores come into contact with water and can drink, (iii) the intermediate area (cells 9–16, between 5 and 55 m from the waterhole edge) and (iv) the area further away from the waterhole (cells 17–24, between 55 and 205 m from the waterhole edge). For the third and fourth circle, distances were preliminary measured in the field for all study waterholes and specific items in the landscape were used to assess the limits between the different circles of the grid (e.g. a bush, a big hole, a termite mound). (b) Representation of a portion of the weighted spatial graph. Weights were assigned as the distances computed using the average size of the study waterholes.

During the waterhole monitoring, each herbivore group entering the waterhole area (defined as a ~200-m-radius circle around the waterhole) was recorded (species and group size) as well as all agonistic interactions between elephants and other herbivores (ranging from intimidation with trumpeting to an aggressive chase). Observational scans of the spatial distribution of all herbivores in the waterhole area (scans hereafter) were performed every 15 min in order to describe the spatial distribution of herbivores and ultimately assess the potential for cryptic interference competition. At each scan, the location of animals was recorded on a grid composed of 24 cells representing the waterhole area (Fig. 2 a). For each waterhole, the cells where the water trough was located were recorded. Observations were done from a reasonable distance from the waterhole not to disturb the animals (either from a viewing platform, a tree platform or a vehicle parked at a distance) but not further than 200 m to respect of good visibility condition for observers. The statistical unit considered was the group of individuals of the same species in the same cell (group hereafter). The study focused on the spatial response of three herbivore species to the presence and abundance of elephants: giraffe (*Giraffa camelopardalis* – average body mass = 750 kg), greater kudu (*Tragelaphus*

strepsiceros – average body mass = 135 kg) and plains zebra (*Equus quagga* – average body mass = 200 kg). We restricted our analyses to these three species because they were the three only species for which the sample size in co-occurrence with elephants was reasonable for each month and overall allowed for a statistical test of their spatial pattern related to elephant location throughout the dry season. In the dry season, zebra, which is a grazer, is more water dependent than the two other species, which are browsers (Western 1973).

Temporal and spatial dynamics of waterhole use by elephants

Three variables were used to assess the seasonal dynamics of waterhole use by elephants: (i) the number of elephants that visited a waterhole per day, (ii) the percentage of scans with elephants, indicating the amount of time that elephants were present, and (iii) the number of elephants present for each scan, indicating the level of elephant local abundance. We then studied the seasonal dynamics of three other variables describing the spatial use of waterholes by elephants: (i) the number of elephants in the cells 0–8 for each scan, indicating the abundance of elephants potentially drinking or bathing, (ii) the proportion of the cells 0–24 occupied by elephants, indicating the level of homogeneity in the spatial use of the waterhole area by elephants, and (iii) the proportion of the cells 0–8 occupied by elephants, indicating the level of homogeneity in the spatial use of the water-access area by elephants.

Temporal dynamics of co-occurrence and interactions between elephants and herbivores

We investigated the co-occurrence of elephants and other herbivores at waterholes by performing for each study species a logistic regression (dependent variable was 1 for situations of co-occurrence and 0 for situations with no elephant) to test for the increased probability of co-occurrence with elephants at waterholes as the dry season progresses, assuming independence between scans. We then assessed the seasonal dynamics of agonistic behaviours of elephants towards other herbivores by calculating the number of aggressive interactions per month standardized by the number of scans with co-occurrences.

Spatial response of herbivores to waterhole use by elephants

A least-cost path approach

We considered the distance between a herbivore and an elephant as an inversed proxy of the interaction risk with elephants: the closer the herbivore to an elephant, the riskier the situation in terms of a costly interaction. We modelled the waterhole area using a weighted

spatial graph (Dale & Fortin 2010) where each cell corresponds to a node (Fig. 2a). Edges were defined using a queen specification (i.e. polygons that shared common boundaries and vertices) and weighted by the associated Euclidean distances between the centres of cells (Fig. 2b). We then computed distances among nodes (i.e. cells) as the least-cost path on the weighted spatial graph using the Dijkstra's algorithm ('igraph' package for R statistical software 3.3.0, The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). We thus obtained a spatial distance matrix containing the length of least-cost paths for all pairs of cells. For each scan, this distance matrix was used to compute distances between herbivores and elephants. The observed distance of interest in this study and noted D_{obs} is, for scans with one group of the study herbivore species, the distance connecting herbivores to the nearest group of elephants. For scans with several groups of the study herbivore species, we calculated the mean minimum observed distance (D_{obs}) as the average of all groups' minimum observed distance weighted by the number of individuals of each group of herbivores (Fig. 3a). For each scan with co-occurrence between elephants and the other study herbivores, we thus obtained only one value of observed distance (D_{obs}), whatever the number of groups on the scan. This value represented the average behaviour of the study herbivore species in the context of the considered scan.

Spatially constrained null model

The observed intensity of spatial aggregation/segregation for a given scan was evaluated by comparing the statistics D_{obs} to values obtained under the null hypothesis of random distribution of herbivores. We developed a spatially constrained procedure that randomizes the position of the herbivores relative to the elephants but preserves both the locations of elephant groups and the spatial configuration of herbivores (hence the potential for intraspecific interactions) (Fig. 3b). Hence, instead of complete randomization of cells, we rotated and translated the cells occupied by the study herbivore groups but did not modify the spatial distribution of elephants (see Fig. 3c–e for a detailed description of the procedure). Depending on the observed spatial configuration of herbivores, this randomization procedure can provide up to 24 random values (eight rotations and two translations) and allows to compute the mean ($D_{random-MEAN}$), maximum ($D_{random-MAX}$) and minimum ($D_{random-MIN}$) possible values that could be obtained if herbivores distribute randomly. We repeated this procedure for all scans.

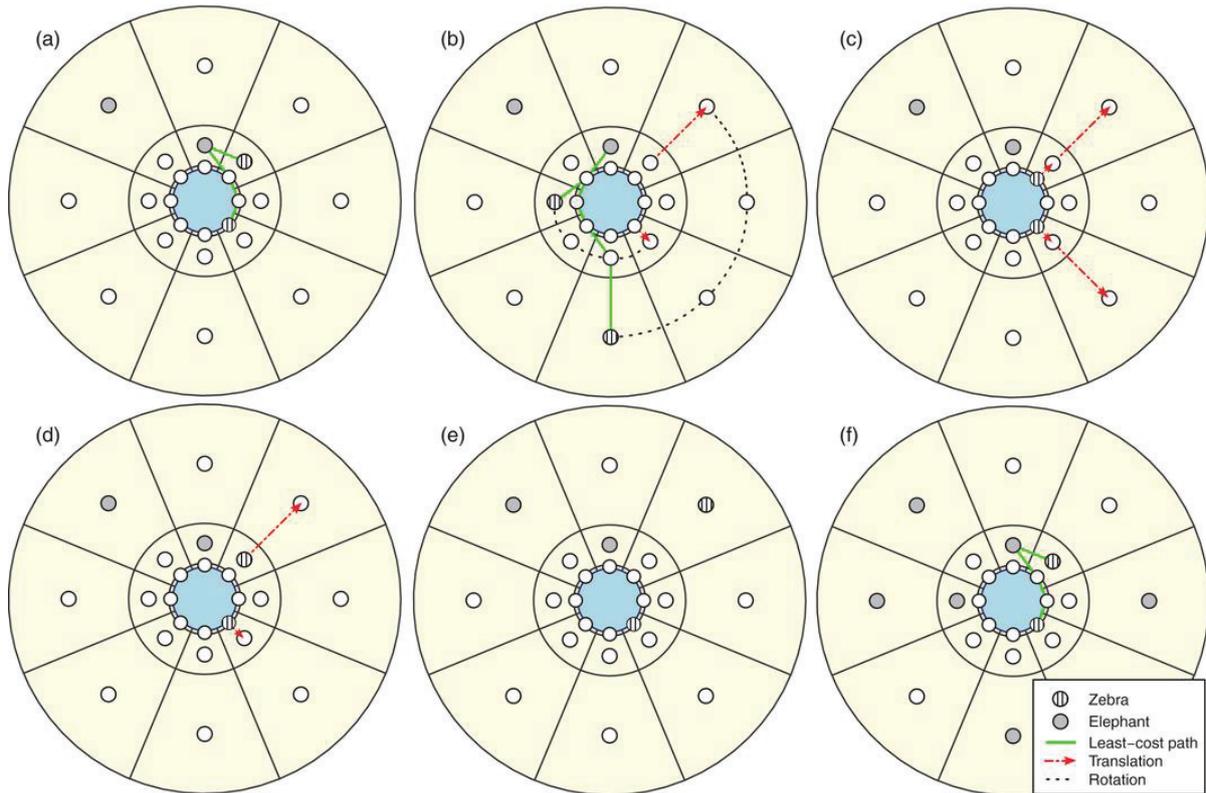


Figure 3. Illustration of the different steps to calculate the spatial aggregation–segregation index. The occupation of cells is represented as follows : empty cells are white, cells with elephants are grey and cells with zebra are black striped. (a) For each group of the study herbivore species (here zebra), the least-cost path to the closest group of elephants is calculated with the Dijkstra's algorithm (green lines), and the mean of these paths corresponds to the observed distance (D_{obs}) for this scan. (b) For the randomization procedure, we applied a combination of rotations (black arrows) and translations (red arrows) when possible. Green lines represent the new least-cost paths calculated under this randomized scenario. Translations are not always performed in order to preserve the spatial configuration between groups (hence the potential intraspecific interactions). In (c), zebras occupy only one circle, two translations (red arrow) are thus possible without breaking the spatial configuration, whereas in (d), they occupy two circles and only one translation is allowed. If we perform another translation, the spatial configuration of the zebra groups is not respected. Finally, in situation (e) where zebras occupy the two extreme circles, no translation is possible and only eight rotations were then performed. (f) There was a need to take into account the spatial availability in our approach. While in (a) and (f), zebras are at the same distance from a group of elephants, the context is different: in (a), zebras are close to the elephants but have the possibility to occupy a large portion of the waterhole area remaining far enough from the elephants, whereas in (f) they have no other choice than being close to an elephant group, leading to different biological interpretations.

Analysis of spatial aggregation/segregation patterns between herbivores and elephants

To assess variations in aggregation/segregation patterns over the dry season, results were compiled per month (but detailed results for each scan characterized by co-occurrence are provided in Appendix S2). As the range of possible values (defined by math formula and math formula) varies between scans, a value of D_{obs} has no meaning per se (compare Fig. 3a and f for an illustration). We thus developed a spatial aggregation/segregation index (hereafter distance index) that rescales the statistics D_{obs} according to the range of possible values so that it was possible to compare and compile results among scans.

Hence, for each scan, we computed:

$$I_{\text{obs}} = \frac{|D_{\text{obs}} - D_{\text{random}_{\text{max}}}| - |D_{\text{obs}} - D_{\text{random}_{\text{min}}}|}{|D_{\text{random}_{\text{max}}} - D_{\text{random}_{\text{min}}}|},$$

$$I_{\text{random}} = \frac{|D_{\text{random}_{\text{mean}}} - D_{\text{random}_{\text{max}}}| - |D_{\text{random}_{\text{mean}}} - D_{\text{random}_{\text{min}}}|}{|D_{\text{random}_{\text{max}}} - D_{\text{random}_{\text{min}}}|}$$

I_{obs} is the observed distance index whereas I_{random} is the expected value under the null hypothesis for a given scan. The index ranges from -1 (when $D_{\text{obs}} = D_{\text{random}_{\text{MAX}}}$; i.e. maximal segregation) to 1 (when $D_{\text{obs}} = D_{\text{random}_{\text{MIN}}}$; i.e. maximal aggregation). Changes in this index over the course of the dry season would indicate a modification of the aggregation / segregation behaviour. For instance, an increased avoidance of elephants by herbivores as the dry season progresses would imply I_{obs} to decrease and tend to -1 in a more pronounced way than I_{random} . As the response of herbivores can be elephant-density-dependent, we also developed an approach to take into account the average density of elephants around the herbivore group rather than the distance to the closest elephant group (Appendix S3 for details). Results provided by both approaches were similar and thus only results on distance are presented hereafter (Appendix S3 for the results on the impact of the local density of elephants).

Ranks and probability combination test of Stouffer

The statistical significance of the observed segregation/aggregation patterns was evaluated for each month and for each of the three species. For each scan, we determined the rank of the observed distance (D_{obs}) among all random distances (from $D_{\text{random}_{\text{MIN}}}$ to $D_{\text{random}_{\text{MAX}}}$) computed for the scan. We then calculated a P -value as the probability among these random distances to be equal or superior to the observed distance. Finally, we used the unweighted Z-transform test (Stouffer *et al.* 1949; Whitlock 2005) to combine the P -values obtained in a given month for a given species. As the Fisher's combined probability test, this test allows combining the P -values from k independent tests of the same null hypothesis to calculate a new statistic test that provides 'the significance of the aggregate' of the k independent tests.

Results

Temporal and spatial dynamics of waterhole use by elephants

We observed two phases in the dynamics of elephant use of waterholes. The first phase of the dry season corresponded to a strong increase in the use of waterholes by elephants with the daily number of elephants per waterhole more than tripling between May–June and August, with, respectively (mean \pm SE), 126.3 ± 34.6 elephants and 439.6 ± 137.7 elephants (Fig. 4a). The second phase of the dry season (between August and October) corresponded to a plateau with a mean of 350 ± 56 elephants per day at a waterhole, which is significantly higher than during the first phase (KS test = 0.239, $P < 0.05$). Similar patterns were observed for the dynamics of the percentage of scans with elephants with nearly 50% of the scans with elephants between August and October (Fig. 4b, $\chi^2 = 148.85$, $P < 0.001$). Regarding the number of elephants per scan, it started with 17.5 ± 1.3 elephants per scan in May–June, peaked in August with 31.5 ± 2.0 elephants per scan and decreased after until 22.4 ± 1.4 elephants per scan in October (Fig. 4c). Once again the second phase is significantly higher than the first phase concerning the number of elephants per scan (KS test = 0.117, $P < 0.001$). Although there were more elephants per scan as the dry season progressed, the elephant number in the water-access area of waterholes (cells 0–8) did not increase (Fig. 4d). In addition, the proportion of cells occupied, and therefore, the surface area used by elephants, did not increase neither in the entire waterhole area (cells 0–24) nor in the water-access area (cells 0–8) (Fig. 4e,f).

Temporal dynamics of co-occurrence and interactions between elephants and herbivores

The probability of co-occurrence with elephants significantly increased over the dry season for the three study species (zebra: $\beta = 0.437$, $P < 0.001$; kudu: $\beta = 0.397$, $P < 0.001$; giraffe: $\beta = 0.278$, $P < 0.001$; see also Fig. 5a–c, respectively). In addition, there was an increase in the percentage of agonistic interactions between elephants and other herbivores reaching almost one-fifth of the scans characterized by co-occurrence between elephants and other herbivores at the end of the dry season (Fig. 5d).

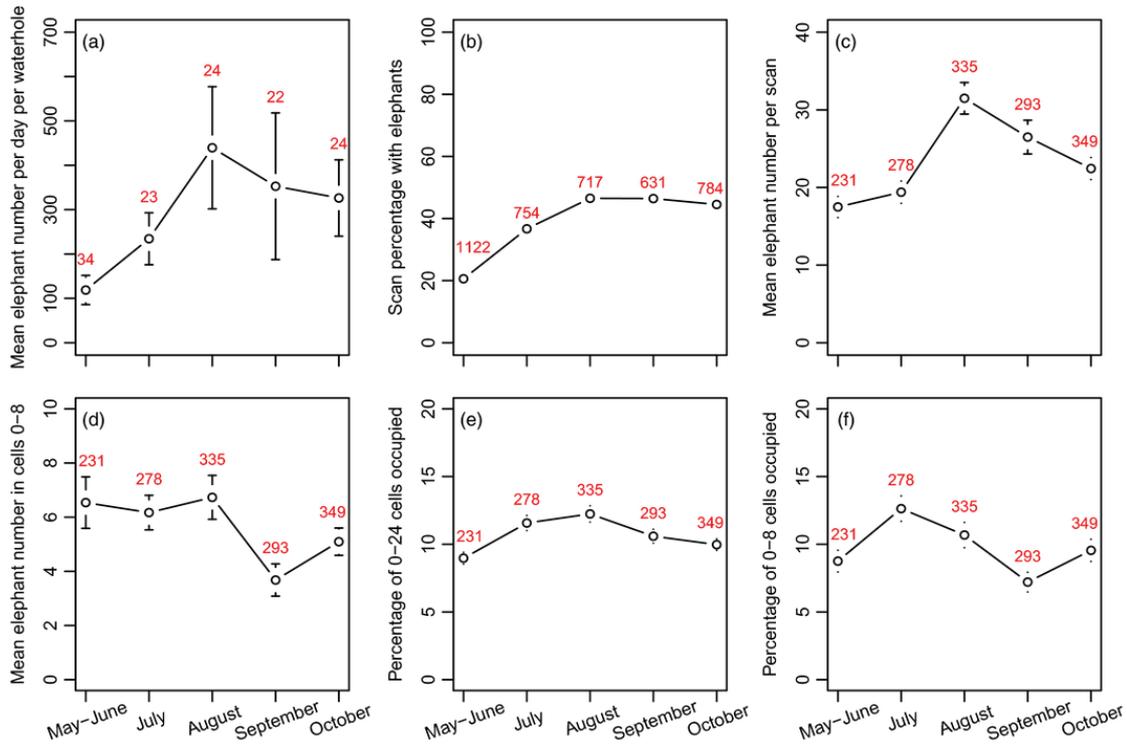


Figure 4. Dry season dynamics of waterhole use by elephants in Hwange National Park, Zimbabwe, with (a) the mean elephant number (\pm SE) per day per waterhole, (b) the percentage of scans with elephants, (c) the mean elephant number (\pm SE) in the waterhole area per scan, (d) the mean elephant number (\pm SE) in the water-access area (cells 0–8) per scan, (e) the percentage (\pm SE) of all cells (0–24) occupied by elephants, (f) the percentage (\pm SE) of cells in the water-access area (0–8) occupied by elephants. Red numbers indicate the number of surveys for (a), the total numbers of scans for (b) and the number of scans with elephants for (c–f).

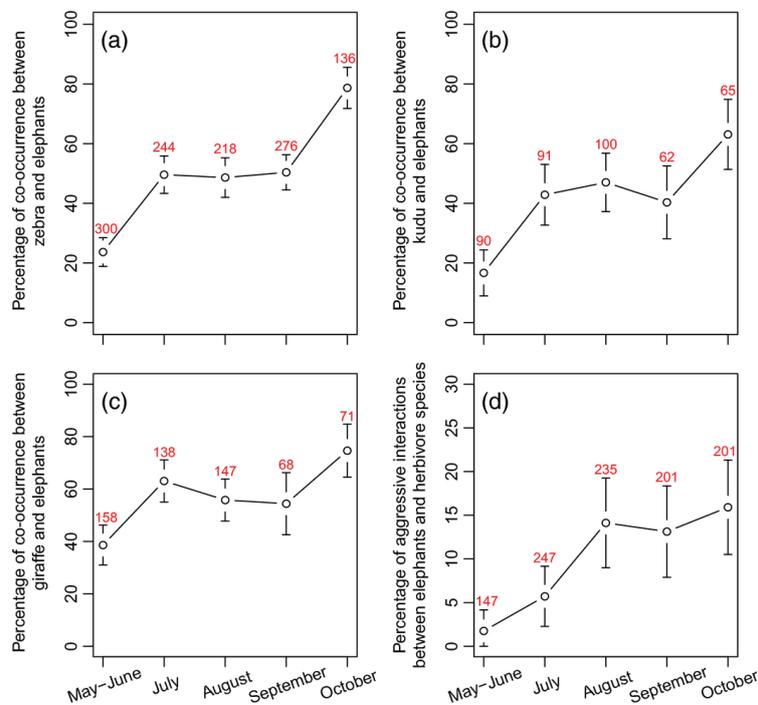


Figure 5. Dry season dynamics of the percentage of scans with co-occurrence between elephant and (a) zebra, (b) kudu and (c) giraffe at waterholes in Hwange National Park, Zimbabwe. Red numbers for (a), (b) and (c) indicate the total number of scans. (d) Dry season dynamics of the percentage of scans during which there was an aggressive interaction (charge, intimidation, etc.) from elephants against the other herbivores. Red numbers for (d) indicate the number of scans with co-occurrence.

Spatial response of herbivores to waterhole use by elephants

All three study species tended to segregate from elephants at the beginning of the dry season (see comparison of the median of I_{obs} with the median of I_{random} in Fig. 6), and this pattern was significant for zebras in May–June only (Stouffer test $S = 2.95$; $P = 0.002$; Fig. 6a). Contrarily to our expectations, herbivores did not segregate from elephants the rest of the dry season but tended to increasingly aggregate with elephants as the dry season progressed (see changes in the median of I_{obs} and changes in the statistics of Stouffer test). This was particularly the case for zebra and kudu for which the median of the observed distance index increased from $I_{obs} = -0.31$ for zebras and -0.41 for kudus in May–June to 0.62 for zebras and 0.60 for kudus in October (Fig. 6a,b). The distribution of all the observed distance indices with their associated expected value under the null hypothesis of random distribution of herbivores are provided for each month and each study species in Appendix S2. Information on the geographic distance between herbivores and elephants are also provided in Appendix S4.

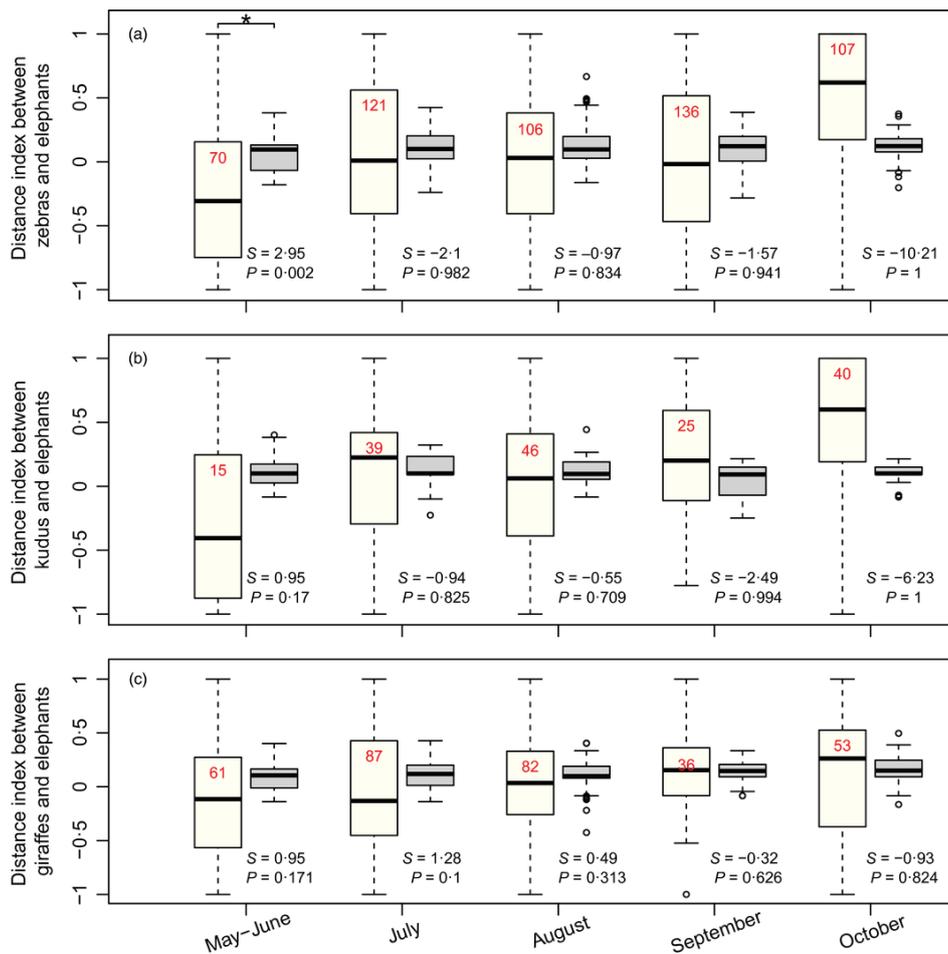


Figure 6. Dry season dynamics of the spatial aggregation/segregation patterns between herbivores and elephants at waterholes in Hwange National Park, Zimbabwe. White boxplots represent the distribution of the observed distance index I_{obs} . Grey boxplots represent the distribution of the random distance index I_{random} from the null models. Red numbers indicate the number of scans with co-occurrence. S and P -values are the statistics of Stouffer tests for segregation patterns, and stars indicate results which are significant at the P -value of 0.05.

Discussion

Use of waterholes by elephants: a heterogeneous spatial use of the waterhole area

In our study, which was during a drought, elephants increasingly used waterholes as the dry season progressed. Not only were elephants more numerous at a given time (higher elephant abundance per scan), but they also used a larger time window (more scans with elephants). The fact that elephants exhibited a larger temporal niche at the end of the dry season corroborates previous findings at the inter-annual scale (Valeix, Chamaillé-Jammes & Fritz 2007), and suggests that elephants, by widening their temporal niche at waterholes, may attempt to avoid intraspecific competition when dry conditions lead to increased elephant abundance. Interestingly, our results revealed that this growing number of elephants at waterholes is associated neither with an increase in their use of the entire waterhole area (cells 1–24), nor with an increase in their use of the waterhole access area (cells 1–8), which indicates that elephants aggregate in some specific sectors of the waterhole area. Because animals are expected to be choosier if there is a strong heterogeneity in the resource quality (Sih & Del Giudice 2012), we believe our results could be explained by a strong heterogeneity in the quality of the drinking water between water troughs (where ground water is actively pumped) and the waterhole, and within the waterhole depending on how far animals drink from the area where the pumped water flows from the water troughs to the waterhole. Elephants are indeed known to be sensitive to the quality of the water they drink and, for example, seem to be actively looking for sodium-rich water (Weir 1972). Additionally, because of the growing concentration of animals at waterholes, there are significant quantities of faeces, urine and evacuated toxins that accumulate in waterholes as the dry season progresses, leading to higher concentrations of ammonium and a deterioration of the drinking water (F. Hulot, unpublished data). Hence, it is likely that, at the peak of the dry season, elephants are attracted by the good-quality water available in the water troughs, where clear water is pumped from underground water-table. Alternatively, they would use areas of the waterhole close to where the pumped clear water flows. These preferences would easily explain their aggregation in some sectors of the waterhole area and the fact that they do not use the entire waterhole perimeter (Appendix S1). Some additional results showed that elephants stayed throughout the dry season closer to water troughs than expected under the hypothesis of a random distribution of elephants in the waterhole area (Appendix S5). Consequently, a density-dependent competition phenomenon is likely to occur around water troughs and not at the scale of entire waterhole areas.

Signs of cryptic interference competition: herbivores segregate from elephants at the beginning of the dry season

As expected, co-occurrence between elephants and other herbivores, as well as agonistic interactions between them, increased over the course of the dry season, confirming the increased potential for interspecific interference competition between elephants and other herbivores. Our prediction regarding the segregation between other herbivores and elephants during the whole dry season was surprisingly not confirmed as the only significant segregation pattern was in May–June for zebras. However, it is interesting to note that all three study species showed a tendency to segregate from elephants at the beginning of the dry season and that the low sample size for kudus in May–June may have reduced our ability to detect a significant pattern. Hence, herbivores seem to globally segregate from elephants at the beginning of the dry season, suggesting a spatial avoidance of elephants, but not the rest of the dry season. This result does not support a scenario whereby there would be no cost at all of being close to elephants, and provides support for the existence of a moderate cryptic interference competition between elephants and other herbivores. Some potential costs of interference competition with elephants have already been revealed through herbivore temporal niche shifts in dry years to reduce temporal overlap with elephants at waterholes (Valeix, Chamaillé-Jammes & Fritz 2007). Spatial responses to the risk of interference competition with larger competitors have already been revealed at the inter-patch scale (see Razgour, Korine & Saltz (2011) for an example on desert bat communities at waterholes), and our study provides useful insights into how similar mechanisms may occur at the intra-patch scale.

Aggregation at the end of the dry season: a trade-off between interspecific interference competition avoidance and access to quality water?

Unexpectedly, herbivores got closer to elephants as the dry season progressed despite the increased level of potential aggressive interactions from elephants. This was particularly the case for zebras and kudus for which there was a clear tendency to aggregate with elephants in the very dry months. These surprising results are rather counter-intuitive, but we can suggest two possible hypotheses to explain the emergence of these aggregation patterns. First, predation risk is high around water sources in semi-arid savanna ecosystems (Valeix *et al.* 2009a,b; De Boer *et al.* 2010) and is known to strongly influence herbivore behaviour (Lima 1998; Périquet *et al.* 2010). The aggregation of prey whether at the intraspecific level (Lima 1995) or at the interspecific level (Pays, Ekori & Fritz 2014; Schmitt *et al.* 2014) is a

widespread anti-predator response to increase detection of predators and a dilution effect. We cannot rule out a scenario whereby herbivores would actively get close to elephants to feel less vulnerable from predators as elephants are rarely attacked by predators and can often chase them away. Unfortunately, this hypothesis could not be explored in this work. Secondly, it is possible that the decrease in water quality in most of the waterhole at the end of the dry season led herbivores to seek the good-quality water found in water troughs and in the waterhole access area where the pumped water arrives. Under this scenario, which is similar for elephants, the herbivores would end up being close to elephants just because both are attracted by the sector around the water troughs, and the observed aggregation patterns would then be a mechanism of passive aggregation. Some additional results are consistent with this hypothesis since we observed an increasing spatial aggregation of herbivores around the water trough over the dry season (Appendix S6). Altogether, our results could suggest the existence of a trade-off between the costs associated with interspecific interference competition highlighted by the avoidance of elephants by herbivores (which seems to be the most important constraint at the beginning of the dry season and explains the segregation patterns) and the costs associated with the access to good-quality water (which seems to be the most important constraint at the end of the dry season). Further, there might be costs associated with waiting for elephants to move away from the clear water since (i) this ultimately decrease the time dedicated to foraging, (ii) there are thermoregulatory costs associated with staying in open areas (see also Valeix, Chamaillé-Jammes & Fritz 2007), and (iii) it is likely that increased time at waterholes increase herbivore vulnerability to predation as lions are known to ambush their prey around waterholes (Valeix *et al.* 2009b), and further work will be needed to assess their importance.

Conclusions

The aggregation patterns observed at the end of the dry season could then be explained by the decrease in water quality over the course of dry season leading to higher costs associated with good-quality water deprivation, which would ultimately exceed those associated to interference competition with elephants. While herbivores can afford to avoid elephants at the beginning of the dry season, which clearly indicates that there are some potential costs associated to interspecific interference competition with elephants, they have no choice than being close to them at the end of the dry season to access some good-quality

drinking water. This study illustrates the importance of studying interference phenomena over large temporal windows as the shift in segregation/aggregation patterns over the course of the dry season allowed us to identify this possible trade-off. To our knowledge, our work is one of the first studies to highlight such trade-off in the field. The logical next step to this study is to determine the impact of both avoidance of interference and good-quality water deficiency in terms of physiological/energetic costs in order to quantify the costs of interference competition (e.g. Abramsky, Rosenzweig & Subach (2001) in laboratory). Our results also encourage for further studies on the heterogeneity of water quality in water sources and on the associated implications in terms of attractiveness for wildlife. It paves the way for a reflection on the impact of water trough design on wildlife (see also Machado Filho *et al.* (2004) for livestock).

This study also seems to suggest that different ecological constraints lead to different trade-offs between avoidance of interference competition and access to good-quality water. Indeed, giraffe is the only species that did not get close to elephants and appeared to maintain a minimum distance from elephants. Our results also revealed that they tended to avoid areas of the waterhole characterized by high surrounding elephant abundances. This is consistent with the fact that giraffe is the only of the three study species to react negatively to the abundance of elephants for the probability of drinking once at a waterhole (Valeix *et al.* 2007). This may be explained by the fact that giraffes are known to be less water dependent than the two other species (Western 1975) and could thus afford to wait for longer periods before accessing water. Moreover, drinking is the only activity when giraffes are vulnerable to costly interactions such as predation or interference competition because of their splay-legged posture. Our results further revealed a high variability in the fine-scale spatial responses at the population level for the three studied species, illustrating high group variability (Appendix S2). Some individuals are more risk-prone than others depending on their body condition (Mikolajewski, Johansson & Brodin 2004), physiology (Leary *et al.* 2004) or personality (Quinn *et al.* 2012), and this may influence group decision. This also constitutes an important field of investigation for future research.

Ultimately, our work provides useful information into the impact of high elephant population densities on other herbivores, particularly in the context of increasing frequency and magnitude of droughts (Holmgren *et al.* 2006; Chamaillé-Jammes, Fritz & Murindagomo 2007b) as the frequency and strength of interspecific interactions at water

sources are expected to increase. Understanding the impact of these interactions on the functioning of animal communities is important to improve conservation and management policies (Van der Putten, Macel & Visser 2010). This is especially true in Hwange National Park, which has been characterized by a strong increase in elephant densities (Chamaillé-Jammes *et al.* 2008) and where most of the other herbivore species have shown declines in their populations (Valeix *et al.* 2008) rising concerns about the impact of elephants on other herbivore species. Our work shows that while there seem to be some costs associated to cryptic interference competition with elephants, these costs are not high enough to prevent other herbivores from accessing high-quality resources at the peak of the dry season when water requirements are crucial. Our work provides an original contribution by pointing out the potential importance of water troughs and water quality provisioning. We hope this will be useful for a better understanding of the role of the interaction between elephants and water in the functioning of herbivore communities and savanna ecosystems and ultimately a better designing of surface water management plans in arid and semi-arid ecosystems (Smit, Grant & Devereux 2007; Hilbers *et al.* 2015).

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Supporting information

Appendix S1: (a) Elephants drinking at a water-trough. The pumped water is then directed to the waterhole. (b) Elephant aggregation around a water-trough area.

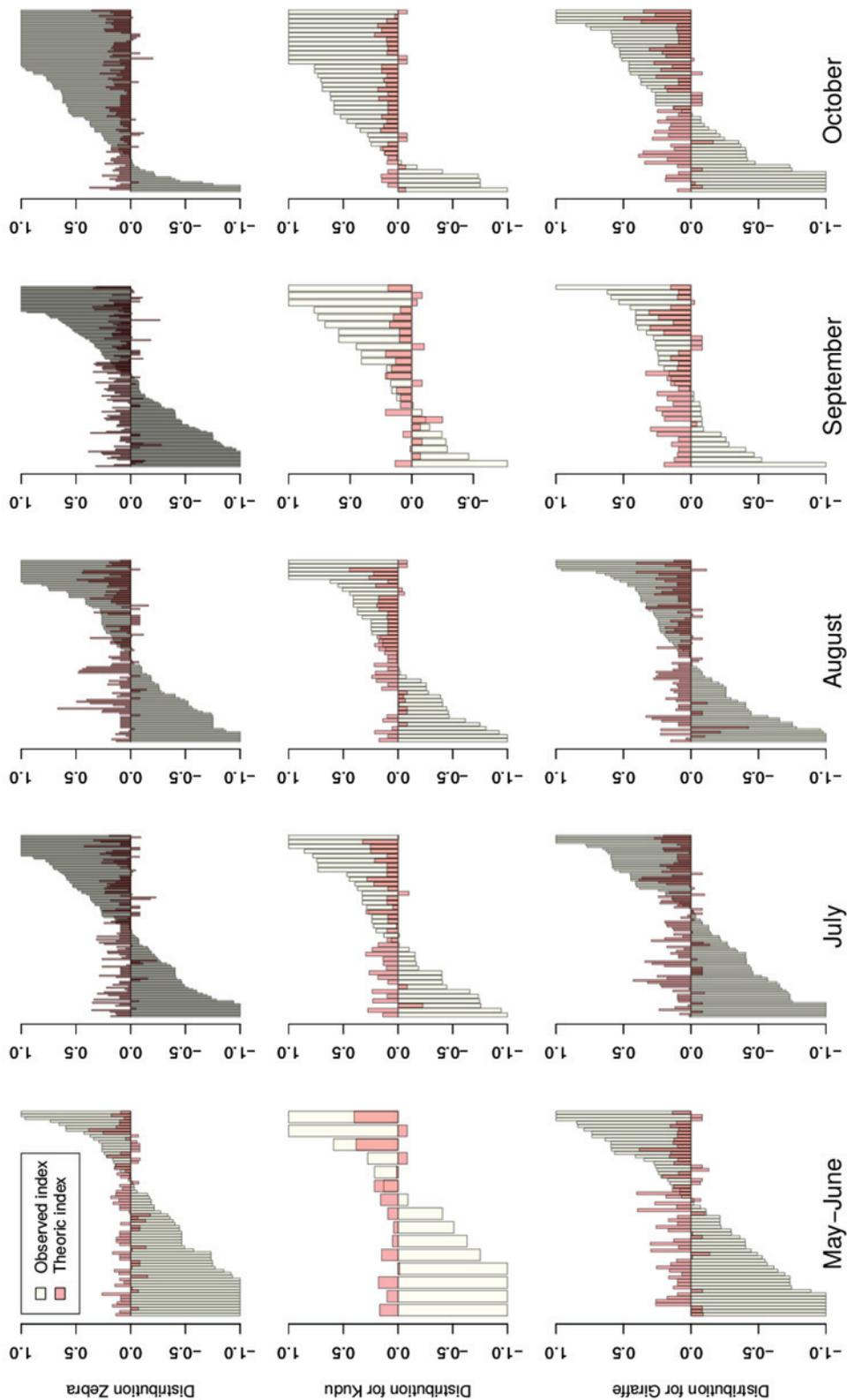
(a)



(b)



Appendix S2: Distribution of the observed distance index with their associated expected value under the null hypothesis of random distribution of herbivores for each month and each study species. Note the shift for kudu and particularly zebras in the distribution of the observed distance index from negative towards positive values as the dry season progresses.



Appendix S3: Analysis of the spatial response of herbivores to the surrounding elephant local abundance.

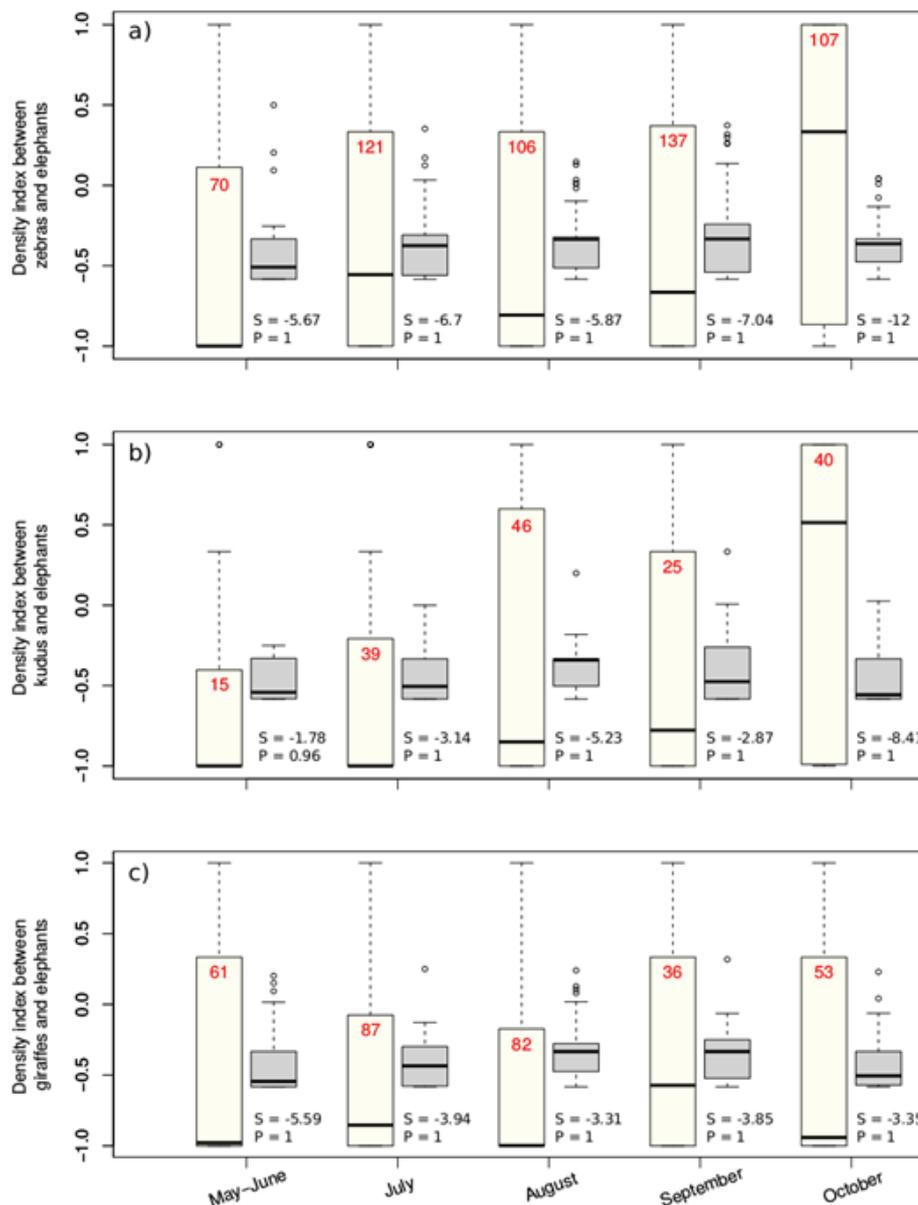
To calculate the density indices, two adjustments were made to the method used to calculate the distance indices. First, we used the mean density of elephants around the study herbivores, i.e. we calculated the mean of the densities in all cells adjacent to the cell occupied by the group of the study herbivores. Second, the index was slightly modified as follows to keep the same logic as the distance index (i.e. ranging from -1 to +1 with negative values indicating avoidance of high elephant local densities and positive values indicating preference for high elephant local densities).

$$I_{obs} = \frac{|D_{obs} - D_{random_min}| - |D_{obs} - D_{random_max}|}{|D_{random_min} - D_{random_max}|}$$

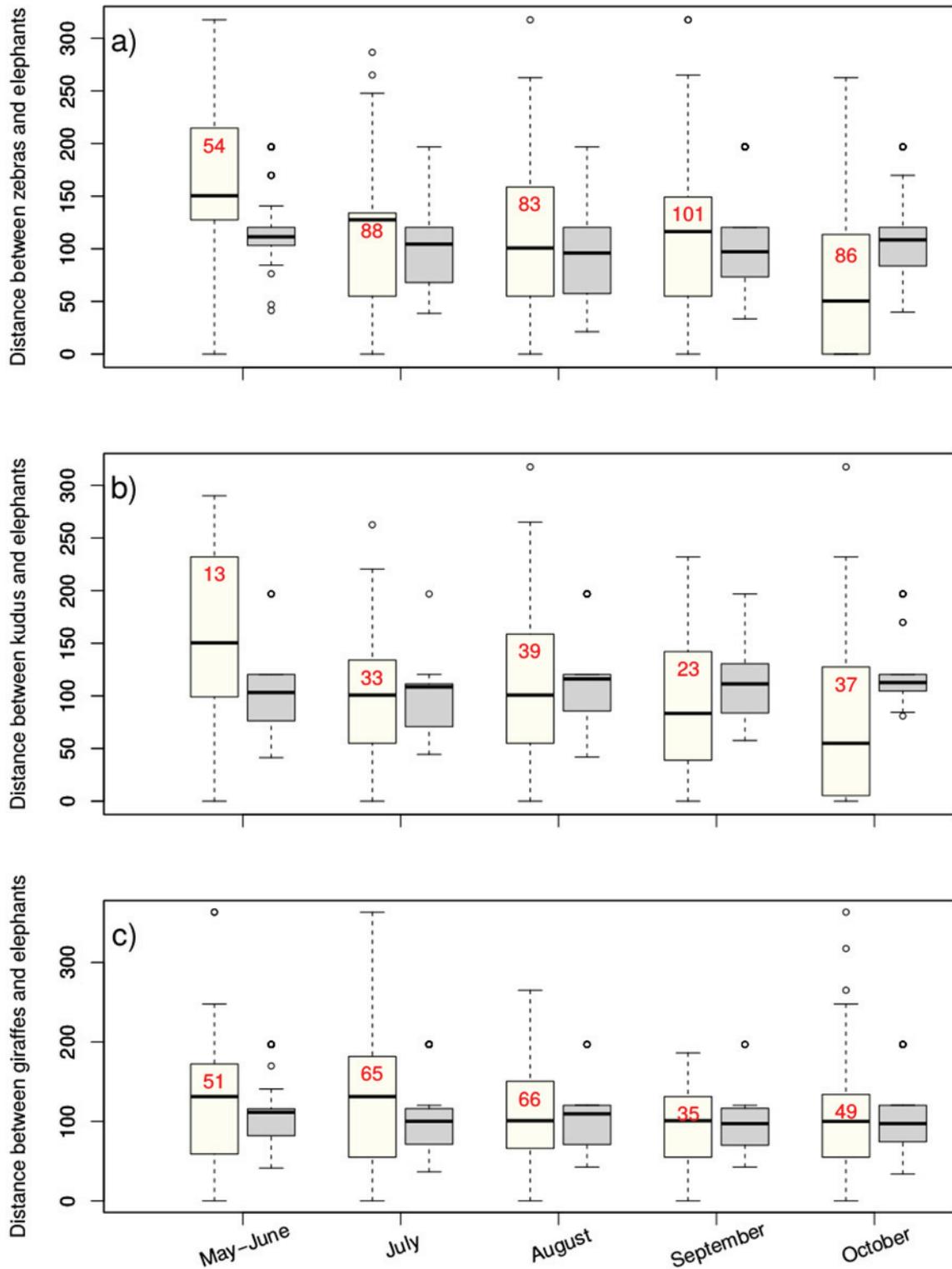
$$I_{random} = \frac{|D_{random_mean} - D_{random_min}| - |D_{random_mean} - D_{random_max}|}{|D_{random_min} - D_{random_max}|}$$

Ranks and probability combination test of Stouffer were also performed.

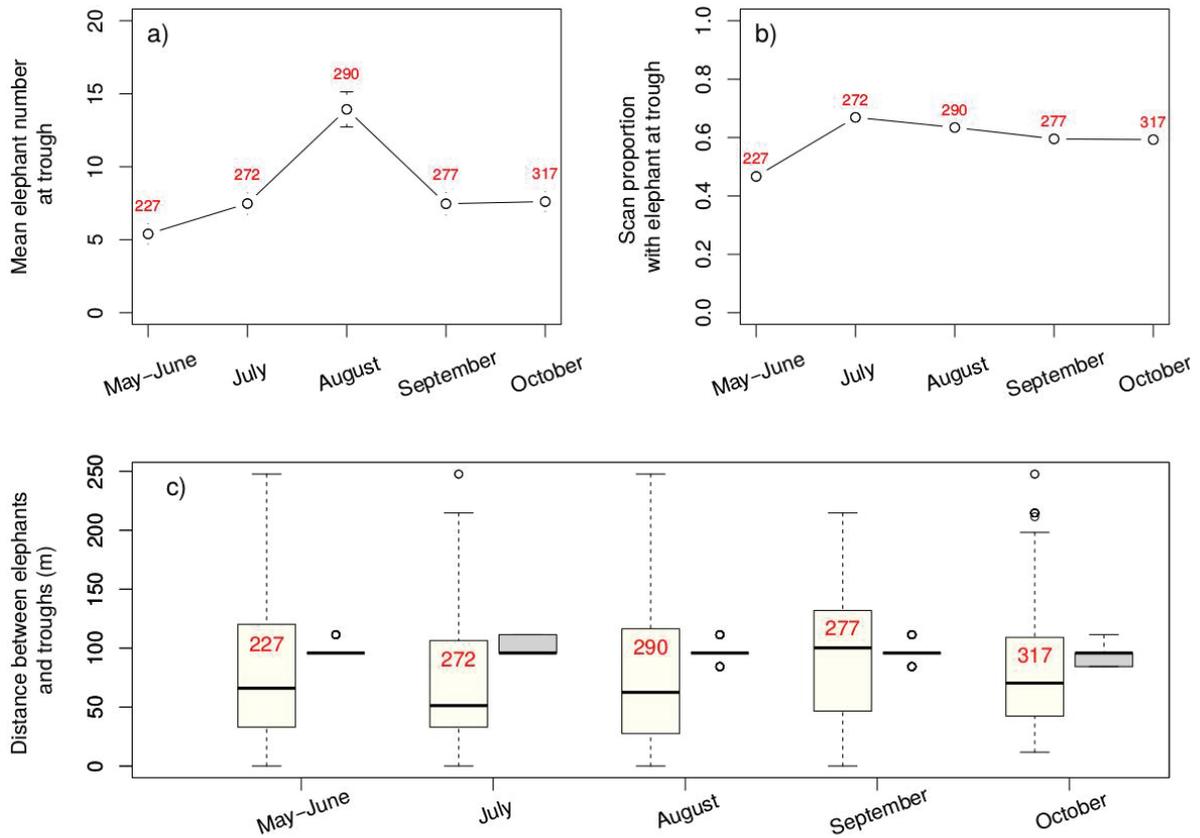
In the figure below, white boxplots represent the distribution of the observed density index I_{obs} . Grey boxplots represent the distribution of the random density index I_{random} from the null models. Red numbers indicate the number of scans with co-occurrence. S and P values are the statistics of Stouffer tests for segregation patterns



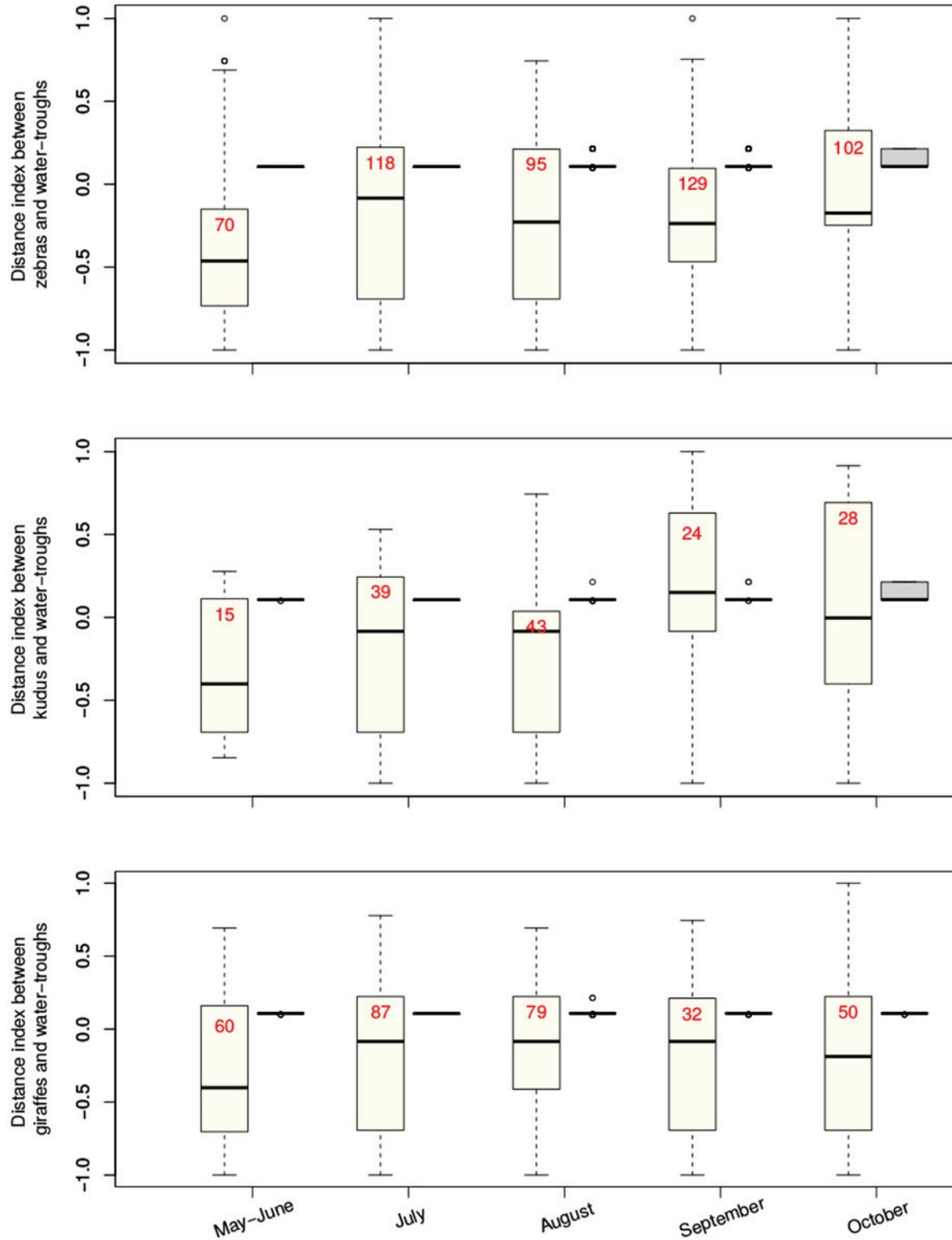
Appendix S4: Distances (in m) between elephants and other herbivores throughout the dry season. White boxplots represent the distribution of the observed distances, and grey boxplots represent the distribution of distances under random distribution of herbivores. Red numbers indicate the number of scans with co-occurrence.



Appendix S5: Analyses of the spatial relationship between elephants and water-troughs in Hwange National Park, Zimbabwe. (a) Dry season dynamics of the mean elephant number (+/- se) at the water-trough. (b) Dry season dynamics of the proportion of scans with elephants present at the water-trough. (c) Dry season dynamics of the distance between elephant groups and water-troughs. White box plots represent the distribution of the observed distances and grey boxplots represent the distribution of the distances under the null hypothesis of random distribution of elephants. Red numbers indicate the number of scans with elephants.



Appendix S6: Dry season dynamics of the distance between herbivore groups and water-troughs. White box plots represent the distribution of the observed distances for herbivore groups and grey boxplots represent the distribution of the distances under the null hypothesis of random distribution of herbivores. Red numbers indicate the number of scans with herbivores.



Chapter 2: Heterogeneity of water quality in artificial waterholes: do African herbivores show preferences and does it lead to interference competition?

Article *in prep.* for submission in *Journal of Arid Environments*

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Abstract

In many semi-arid savanna ecosystems, surface water provided in artificial pumped waterholes represent the only source of surface water available to animals at the end of the dry season. This scarcity of water generates aggregation of a wide range of herbivores around artificial waterholes, inducing interspecific competition between species simultaneously exploiting water resources. Evaporation and accumulation of herbivore faeces and urine in waterholes as the dry season progresses gradually decrease the overall quality of the water. In artificial waterholes, this could lead herbivores to seek for good-quality water where the clear pumped water arrives, conducting elephants and other herbivores to aggregate near the trough. Studies about impacts of the quality of water resources for wild animals are rare and virtually nothing is known on the role of the heterogeneity of water quality in waterholes. Here, we studied the positioning of different herbivore species when they drink and the quality of the water in different areas of artificial waterholes in the semi-arid savanna of Hwange National Park, Zimbabwe. We identified a gradient of water quality in the waterhole at the end of the dry season. We did not detect interference competition between elephant and zebras or kudus for the access to water of better quality, but we showed that elephants, and to a lesser extent roans and sables, drank the water that flowed from the trough whereas other species drank farther in the waterhole. We conclude that this species-dependent drinking position certainly have with implications for African mammal's health should be an issue for wildlife management and conservation.

Keywords: Water quality, resource quality heterogeneity, waterholes, interference competition, large African herbivores, spatial aggregation, semi-arid savannah

Introduction

Species distribution patterns depend on the spatial distribution of resources (O'Neill *et al.* 1988, Pearson 1993). Patches of resources represent attractive areas in the landscape, around which animals are likely to aggregate and may temporarily form mixed-species groups (Waser 1982, Stenland *et al.* 2003). The co-occurrence of different species can lead to interspecific competition (exploitative or interference, Schoener 1983), forcing some species to avoid more competitive ones at both spatial (Durant 2000, Tannerfeldt *et al.* 2002) and temporal scales (Ziv *et al.* 1993, Valeix *et al.* 2007). The intensity of these competition processes increases as resource quantity or accessibility decreases. This is typically the case of surface water resources in arid and semi-arid ecosystems, as they dry up as the dry season progresses. In many arid and semi-arid savanna ecosystems, surface water during the dry season is mainly provided through artificial pumping of underground water. These artificial waterholes often represent the only source of surface water available to animals at the end of the dry season. This scarcity of water leads to the aggregation of a wide range of large mammal species around artificial waterholes, sometimes at very high levels of abundance (Weir & Davison 1965, Valeix 2011).

While several studies have focused on the use of artificial waterholes by large wild mammal species (Western 1975, Redfern *et al.* 2003, Hayward & Hayward 2012), our understanding of the underlying processes of the setting up of co-occurrence patterns of different species is still incomplete. Interspecific competition is likely to be a major process taking place between species simultaneously exploiting water resources. For example, Valeix *et al.* (2007) showed a temporal avoidance of African elephants *Loxodonta africana* by several other herbivores species. However, a recent study revealed that when zebras *Equus quagga*, and to a lesser extent kudu *Tragelaphus strepsiceros*, co-occur with elephants around artificial waterholes at the end of the dry season, they tend to all aggregate in the same specific sections of the waterhole area (Ferry *et al.* 2016). One hypothesis suggested to explain this unexpected result is that it is not only the presence or the quantity of the resource that matters but its quality. The documented patterns may result from a passive species aggregation; all these species are attracted by the same characteristics of the water, e.g. quality, in particular areas of the waterholes. Numerous studies have reported that animals

select patches with food of higher quality (e.g., Langvatn & Hanley 1993; Wilmshurst *et al.* 1995, Van der Wal *et al.* 2000, Hochman & Kotler 2006). However, studies on the influence of the quality of water resources on wild animals drinking behaviour are rare (but see Wanke & Wanke 2006, Chamailé-Jammes *et al.* 2007). At a fine scale, nothing is really known about the role of the spatial heterogeneity of water quality in waterholes on drinking choices and surface water use. Herbivores are active carriers of nutrients when they urinate and defecate in water (Naiman & Rogers, 1997, Masese *et al.* 2015, Subalusky *et al.* 2015, Hulot *et al. in prep*). It is therefore possible that the combined effect of evaporation and accumulation of herbivore faeces and urine in waterholes as the dry season progresses leads to a decrease in overall quality of the water in most waterholes (e.g. Gereta & Wolanski 1998, Strauch 2013, Msiteli-Shumba *et al. in press*) and to a spatial gradient of water quality in artificial waterholes. In these artificially pumped waterholes, the presence of an area where the clean pumped water arrives could lead herbivores to actively seek for good-quality water (Wanke & Wanke 2006). Under this water quality hypothesis, elephants and most other herbivores are expected to end up being aggregated as the dry season progresses just because the water coming from the trough attracts them all.

Here, we studied the quality of the water in different areas of artificial waterholes in the semi-arid savanna of Hwange National Park, Zimbabwe, where we also monitored the positioning of different herbivore species when they drink at these waterholes. We tested the hypothesis that the heterogeneity of the quality of water in a waterhole explains aggregation patterns at attractive areas of the waterhole, and ultimately may lead to interference competition between elephants and other herbivore species. We predicted (i) the existence of a water quality gradient at the waterhole scale at the end of the dry season, (ii) the attraction of trough where pumped underground water emerges, represented by a low distance between drinking herbivores and the trough, and (iii) an interference competition between elephants (the largest and a potentially aggressive species – Valeix *et al.* 2007) and other herbivore species for the access to water of better quality, resulting in a higher distance to the trough when drinking in the presence of elephants compared to situations without elephant.

Materials and methods

Study site

The study area (~7 000km²) is located in the northern region of Hwange National Park which covers ~15 000 km² of semi-arid dystrophic (low nutrient soil) savanna in northwestern Zimbabwe (19°00' S, 26°30' E; Fig. 1). The vegetation is primarily woodland and bushland savanna. The long-term mean annual rainfall is ~ 600 mm, which falls primarily between November and April, and the dry season stretches from May to October. Waterholes are depressions that are fed by rainwater runoff during the rainy season and, for artificial waterholes, by pumped groundwater pumping during the dry season. The surface water available to animals is found in natural as well as artificial waterholes. However natural water bodies dry up during the dry season and only artificial waterholes offer drinking water all over the year. This study focused on four artificial waterholes and addressed eight herbivore species: two browsers (giraffe *Giraffa Camelopardalis* and greater kudu), two mixed-feeders (African elephant and impala *Aepyceros melampus*) two woodland grazers (roan antelope *Hippotragus equinus*, and sable antelope *Hippotragus niger*) and two grassland grazers (warthog *Phacochoerus africanus* and Burchell's zebra).

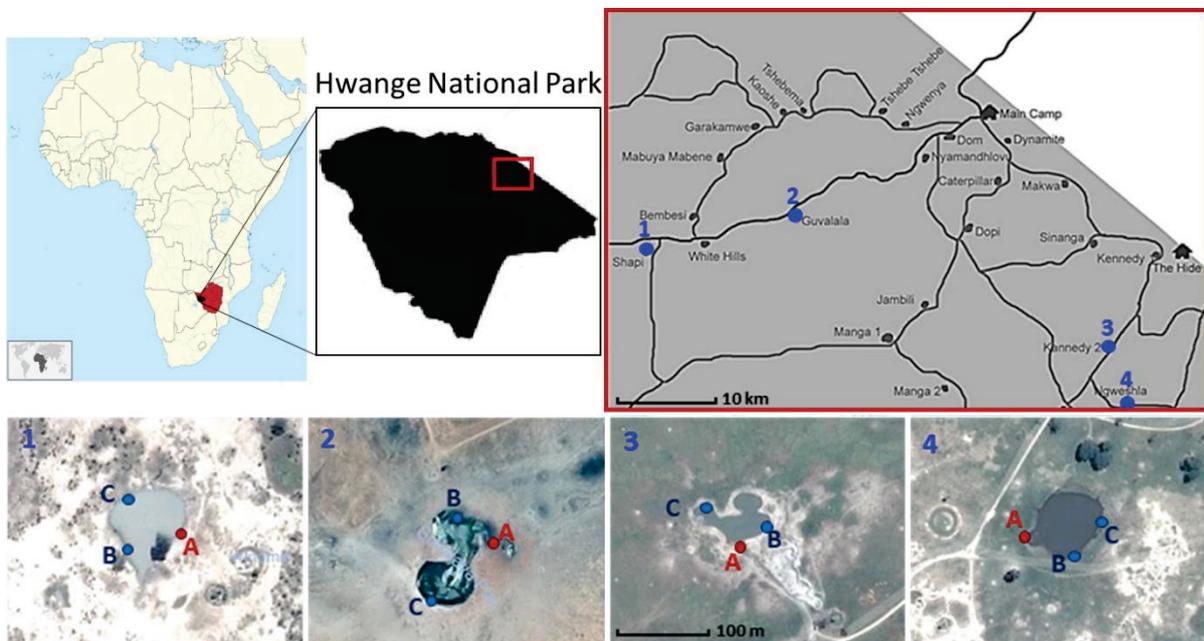


Figure 1: Map of the four monitored artificial waterholes in Hwange National Park, Zimbabwe. Locations B and C (in blue) and A (in red, corresponding to the trough) for each waterhole. Aerial photos of the waterholes were taken from Google Map.

Data

Water quality – The quality of the water has been sampled in four monitored artificial waterholes (Fig. 1) in October 2017, i.e. at the end of the dry season. A water sample was collected in three different areas for each waterhole. The first sample was taken in the water near the trough (A), the second at the furthest location from the trough (C), and the third at an intermediate distance (B) (Fig. 1). For the four waterholes, the mean distance between A and C is 73.2 m (ranging from 61m at Shapi to 87 m at Guvalala) and represented the maximal distance to the trough when animals are drinking. Water samples were taken before 12 a.m. to minimize variability in the time of the day. We measured near the shoreline temperature, dissolved oxygen concentration, pH, turbidity and chlorophyll a concentration with a YSI 6600 VZ Multiparameter water quality probe. Conductivity was measured with a Hanna HI 98312 portable conductivity meter. Water samples for laboratory analyses were collected on site at the deepest point with a bottle fastened to a 3 m pole. Water was stored on ice in one-litre polyethene bottles. Water was filtered with GF/F 47 mm filters. Total nitrogen and total organic carbon concentrations and water hardness were determined from unfiltered water samples. Ammonium, nitrite, nitrate and orthophosphate concentrations were determined from filtered water samples. Chemical analyses were realized with a Hach DR 3900 portable data logging spectrophotometer and reagents in accordance with the manufacturer's procedure.

Drinking position – Observations of drinking herbivores were made at the same four monitored artificial waterholes (Fig. 1) between August and November 2016, i.e. at the end of the dry season. Every day, observations were done from 6 a.m. until 6 p.m at one of the artificial waterhole. Observers were inside a car parked at approximately 100m from the waterhole as a compromise between disturbance and quality of the observation. Each time a herbivore or a group of herbivores drank at the waterhole, the position of the closest individual to the trough (focal individual) was recorded. In order to calculate the distance between the drinking focal individual and the trough, we recorded the angle to the north (with a compass) and the distance from the car (with a range finder) of the focal individual and the trough. For all drinking observations of the herbivores, we recorded if elephants were present at waterholes or not.

Drinking position and water quality were not studied the same year, but 2016 and 2017 were characterized by similar annual rainfall (438.3 and 477 mm respectively). Water availability depends on rainfall during the rainy season and evaporation and pumping during the dry season. Morphological characteristics (depth, shape) of the waterholes and trough position did not change between 2016 and 2017, we therefore assume that water had a comparable quality and quality gradient between these two years.

Analyses

Analyses were conducted using R v. 3.3 software (R Development Core Team, 2004).

Water quality

In order to assess the existence of a gradient of water quality inside waterholes, we performed multivariate analyses. First, a Principal Component Analysis (PCA, package *ade4*, Dray & Dufour 2007) was performed on the thirteen variables. We then removed the effect of the heterogeneity between waterholes with a within-class analysis and performed a between-class analysis to estimate the percentage of the remaining variability explained by the differences between the three locations A, B and C.

Drinking position

We first assessed the difference of position where animals drank at the waterhole between each study herbivore species by performing a mixed-model (package *lmer*, Bates 2008) on the distance to the trough when drinking. The species was considered as a fixed effect and the waterhole monitored as a random effect. A pairwise post-hoc comparison was then performed on the mixed-model between each pair of species (package *lsmeans*, Lenth 2016). The p-values were adjusted with the Tukey method. We then assessed the influence of elephant presence on the drinking position of other herbivores species. We performed a mixed-model with the distance to the trough when drinking as the dependant variable. The interaction between the presence of elephants when drinking and the herbivore species was introduced as an explanatory term in the fixed part of the model. This analysis could be carried out for kudu and zebras only as these two species were the only ones recorded both in the absence of elephants and with elephants at the study waterholes. The waterhole monitored was considered as a random effect.

Results

Water quality

After the within-class analysis removed the variability due to differences between waterholes, the between-class analysis revealed that 31% of the remaining variability was explained by differences of water quality between the locations A, B and C. As the distance to the trough increases (from A to C), the concentration of total organic carbon, dissolved oxygen, total nitrogen and ammonium, and the conductivity increased whereas the temperature, the turbidity and the nitrate concentration decreased (Fig. 2).

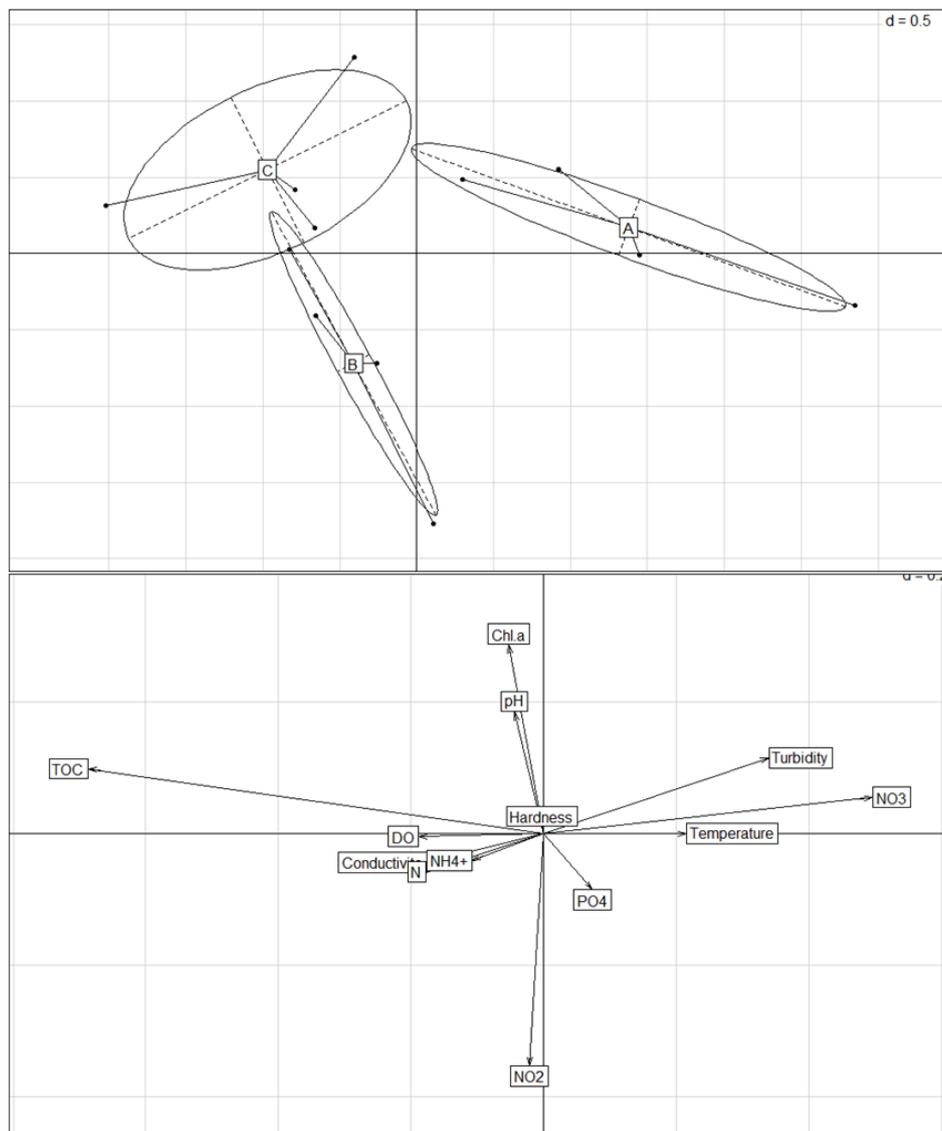


Figure 2: Graphical results of the between-class principal component analysis. Left: position of the four waterholes (black dots) with confidence ellipses around the categories defined by the distance to the trough (A, B and C). Right: position of the thirteen variable: dissolved oxygen (DO), total organic carbon (TOC), total nitrogen (N), ammonium (NH₄⁺), nitrite (NO₂), nitrate (NO₃), orthophosphate (PO₄) and chlorophyll a (Chl.a) concentration and conductivity (Conductivity), hardness (Hardness), turbidity (Turbidity) and temperature (Temperature).

Drinking position

The mixed model allowed to estimate the mean (\pm SE) drinking distance to the trough for the eight study species, which ranged from 15.5 m to 58.5 m (Fig. 3). Post-hoc tests revealed three different groups: (i) elephants, which drank the closest to the trough, (ii) roans and sables, which drank at intermediate distances from the trough, and (iii) all other study herbivore species (zebras, kudus, impalas, giraffes and warthogs), which drank the furthest from the trough (Fig. 3). No effect of the presence of elephants on the drinking distance from the trough was observed neither for zebras ($\beta \pm$ SE = 0.77 ± 6.56 , $t = 0.118$, $p = 0.9$), nor for kudus ($\beta \pm$ SE = -1.11 ± 8.23 , $t = -0.13$, $p = 0.9$).

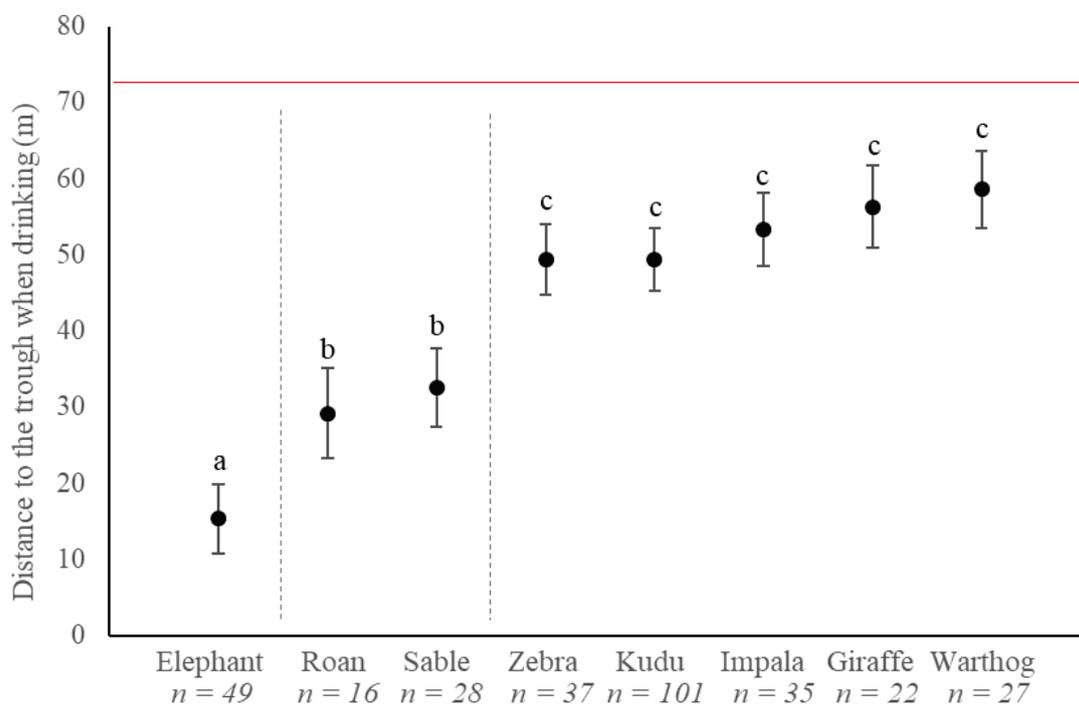


Figure 3: Estimated mean (\pm SE) of the distance to the trough for drinking individuals of the nine study herbivore species that visited the 4 study artificial waterholes in Hwange National Park, Zimbabwe. The number of observations (n) for each species is provided. Different letters (a, b, c) indicate significant differences obtained by pairwise post-hoc comparison on the mixed-model between each pair of species. Red line indicates maximum distance averaged between the four waterholes.

Discussion

In this study, we successfully identified a gradient of water quality at the scale of the waterhole at the end of the dry season. We then showed that elephants, and to a lesser extent roans and sables, drank the water that flowed from the trough but that a large number of species drank farther in the waterhole. Finally, we did not detect any spatial patterns indicative of interference competition for the access to water of better quality between elephant and zebras or kudus.

Our results revealed the existence of a gradient of water quality in artificial waterholes at the end of the dry season. Indeed, troughs are set up between the outlet of the pump and the waterhole and provide water of the same quality as the underground water to the animals because the trough is continually flushed (Wanke & Wanke, 2007). This water is generally less salty and conductive than free water. Given that there is no input of rainwater in the dry season, evaporation and changes due to fauna activity lead to variations of the physico-chemical characteristics of the water in the waterhole (Wanke & Wanke 2007, Msiteli-Shumba *et al. in press*) in particular concentration of ions which lead to an increase in conductivity and salinity.

Far from the trough, the water is enriched in organic matter (high concentration of total organic carbon, total nitrogen) and degradation product (ammonium). This organic matter may be inherent to microorganisms in the pan such as phytoplankton and zooplankton (Strauch 2013) which communities change in relation to physico-chemical characteristics discussed above (Msiteli-Shumba *et al.* 2017), and bacteria and protists (Strauch 2013). Organic matter may be also free in the water or stored in sediments and resuspended by wind or water movements created by the fauna (Gereta & Wolanski 1998), but also related to faeces of the numerous animals drinking in the waterhole. This last source of contamination is indeed frequently mentioned in the literature (e.g. Gereta & Wolanski 1998, Strauch 2013). The study site host one of the world's largest elephant population (Chamaillé-Jammes *et al.* 2008), that generate a high density of faeces deposition around waterholes (mean density of elephant dungs of 18.89 (\pm 26.04) g/m²/day in October 2014; Hulot *et al. in prep*). These organic matter inputs may lead to the water eutrophication observed in Hwange National Park (Msiteli-Shumba *et al. in press*) and can intensify heterogeneity of water quality between trough and remaining waterhole.

At the trough outlet, the pumped water has been in the ground aquifer for a long time after infiltration into the soil where the oxygen is quickly consumed (Strauch 2013). Water at the other side of the waterhole, thanks to its longer residence time in contact with the air, is newly oxygenate and concentrates the mineral salts thanks to evaporation (Wanke & Wanke 2007, Msiteli-Shumba *et al. in press*). The higher turbidity found at the trough outlet may be due to the water flushing that splashes around and induces sediment resuspension. This

constant flushing also repulses from the outlet suspended matter and associated micro-organisms that break down this matter. Flushing might impact water quality and create a gradient in the vicinity of the outlet. For instance, it is hypothesized that constant flushing might prevent the development of cyanobacteria in waterholes (Msiteli-Shumba *et al.* 2017).

Unfortunately, the influence on animals of most of the parameters studied here has not been investigated in the literature, but some parameters not studied here have been studied more extensively. For example, Auer (1997) showed that an increase of the water salinity led herbivores to sniff and taste the water extensively, try many positions at the waterhole, and sometimes leave the waterhole without drinking. Wolanski & Gereta (2001) further showed that surface water with high salinity may initiate the migration of zebras in the Serengeti National Park, Tanzania. Ramey *et al.* (2013) investigated total coliform bacteria and showed that elephants dig to access less contaminated drinking water. Stommel *et al.* (2016) studied the response of some African mammals to total aerobic bacterial load and suggested that digging is an adaptation to avoid poor quality water and potentially pathogenic microbes.

Our results showed that three species, roans, sables and particularly elephants, drank the water from the outlet of the trough, whereas other species drank farther in the waterholes. This species-dependent preference did not seem to be related to water dependency. Species considered as more water-dependent are elephants, warthogs and zebras (Hayward & Hayward 2012), because of the short time between successive waterhole visits (1-2 days; see Cain *et al.* 2012 for zebras, Chamaillé-Jammes *et al.* 2014 for elephants, frequency unknown for warthogs but see Estes 1991). Species considered as less water-dependent are impala (2-3, days; Young 1970 in Gaylard *et al.* 2003) and sable (2-4 days; Cain *et al.* 2012). No information is available for kudu, giraffe and roans. In each of these groups, occurred species preferring or neglecting fresh water coming from the trough. The water consumption per waterhole visit of elephant (35 and 77 liters for female and male respectively; Young 1970 in Gaylard *et al.* 2003) could explain its preference for the water close to the trough, in order to avoid the too high bacterial load (Epaphras *et al.* 2008, Ramey *et al.* 2013) that could be associated to the high volume of water consumed in other areas of waterholes. In addition, elephants' ability to drink directly into the trough (Young 1970 in Gaylard *et al.* 2003) prevents

them from having to dig (Ramsey *et al.* 2013, Stommel *et al.* 2016). However, other large-bodied species did not show a water-trough preference associated to the water consumption. Giraffe, kudu, zebra and impala (mean volume drunk per visit of resp. 10.6, 5, 4.7 and 0.9 litres; Young 1970 in Gaylard *et al.* 2013) neglected water-trough, whereas sable (4.6 litters; Young 1970 in Gaylard *et al.* 2013) selected water-trough (no information available for roans and warthog). Cain *et al.* (2012) suggested that the digestive system could explain differences of water-dependency between zebra and sable. It would be interesting to assess if the digestive system differences (e.g. stomach microbiota tolerances to bacterial loads) could also explain the species-dependent preferences for water of better quality. Auer (1997) have indeed shown that zebra was the most tolerant species to increased salinities. Such result could explain that some species better tolerate drinking low-quality water and therefore do not drink nearby the trough.

A previous study revealed that elephants do not prevent other herbivores from drinking at waterholes (Valeix *et al.* 2009). Here, we show that they do not prevent zebras and kudus from drinking close to trough as these two species did not drink closer to the trough when elephants were absent. The water-quality hypothesis seems unlikely to explain the spatial aggregation patterns observed by Ferry *et al.* (2016). Regarding the other herbivore species, we did not highlight any interference competition for the access of quality water as they almost always drank when elephants were absent and yet they did not drink at the trough. Only sables and roans are likely to face interference competition with elephants as they are the only ones drinking relatively close to the trough. Sables and roans almost never drank at waterholes when elephants were present, which would confirm that they temporally avoid elephants (Valeix *et al.* 2007).

At the end of the dry season, waterholes are characterized by a heterogeneous quality of the water, with a gradient from the trough to the opposite side of the waterhole. It would be interesting in future research to evaluate the temporal dynamics of the heterogeneity in water quality both at within- and between-year scales and assess the link between water quality and African mammal's health. The species-dependent preference for higher-quality water only starts to be unravelled and should be a major issue for wildlife management.

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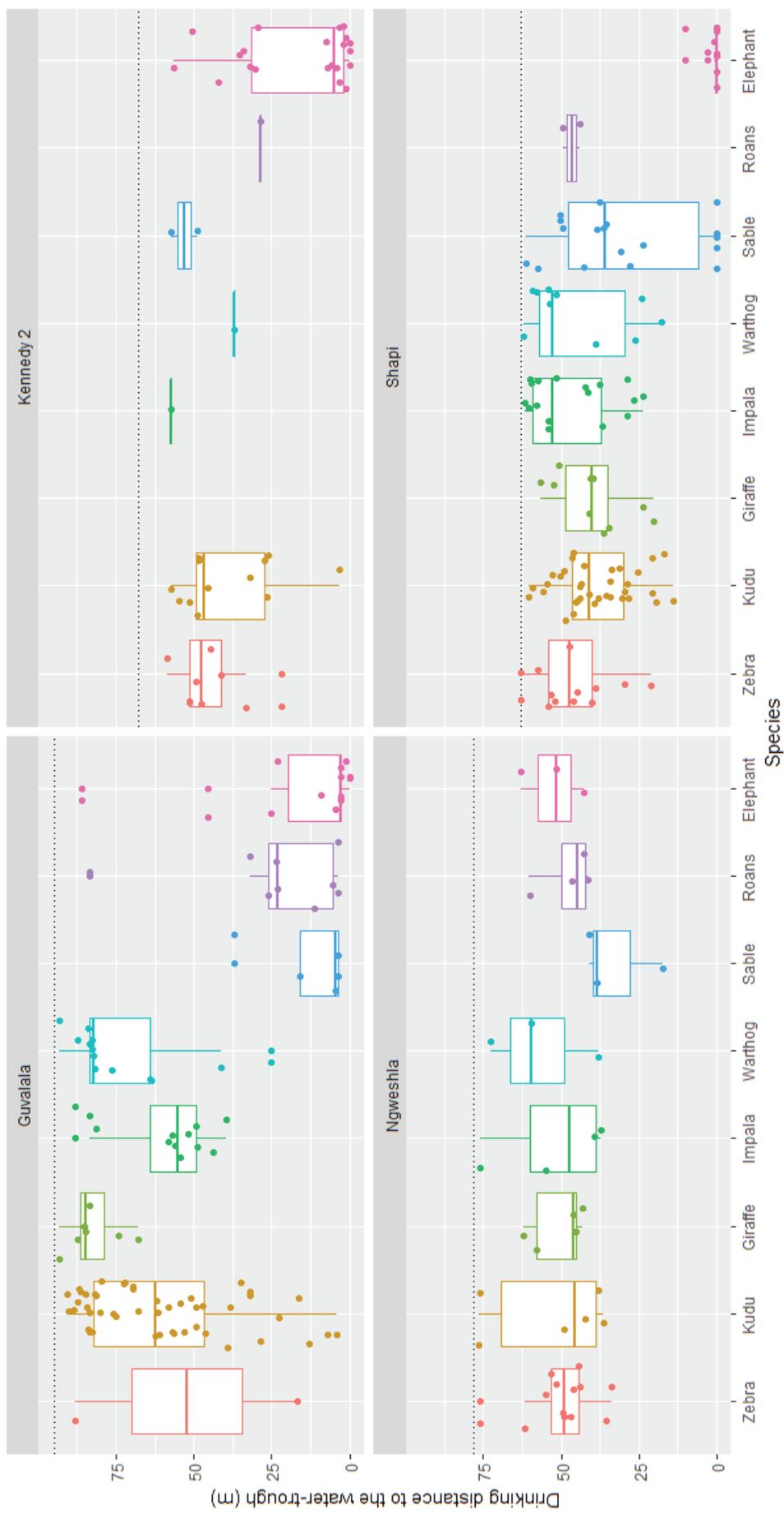
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Supporting information

Appendix 1: Distance to the trough for drinking individuals of the nine study herbivore species that visited the 4 study artificial waterholes in Hwange National Park, Zimbabwe. Dotted lines represent maximum drinking distance in the considered waterhole.



Chapter 3: Does the presence of African elephants *Loxodonta africana* reduce the predation risk perceived by plains zebra *Equus quagga* at waterholes?

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Abstract

Mixed-species groups can result from voluntary associations with other specific species for anti-predator advantages, for example with species able to deter predators. In arid and semi-arid African savanna ecosystems, limited surface water lead to the aggregation of a wide range of large mammal species around water sources, forming prey hotspots for large carnivores. Previous studies revealed an increasing aggregation pattern of zebras and African elephants *Loxodonta africana* at waterholes as the dry season progressed and suggested that a possible underlying mechanism could be a protective effect of elephants, called here the “bodyguard hypothesis”. Here, we designed a field playback experiment to test this hypothesis in evaluating zebra behaviour in response to playback of lion roaring in presence and in absence of elephant. We therefore investigated the effects of elephant’s presence on the aggregative, vigilance and drinking behaviours of zebras. We showed that zebras vigilance increased with perceived predation risk, with the presence or the absence of elephants. We also showed that zebras responded to the presence of elephants by increasing their vigilance after the control treatment. Contrary to our expectations, after the playback of lion, the presence of elephant did not result in a decrease of the vigilance response level of zebras. In addition, zebras never aggregated to elephants after lion roaring. The “bodyguard hypothesis”, under which thanks to their mobbing behaviour elephants are considered as pledge of security against predators at the waterhole, is not supported by our results. On the contrary the presence of elephants would be a source of increased vigilance for zebras.

Keywords: Predation risk, Predator deterrence, Vigilance, Anti-dredator strategy, *Loxodonta Africana*, *Equus Quagga*

Introduction

Mixed-species groups are observed in various ecosystems and across a wide range of taxa (e.g. ungulates, Fitzgibbon 1990; cetaceans, Frantzis & Herzing 2002; birds, Caro 2005, primates, Cords 1990), and these associations occur between closely related species as well as between species from different orders (Au & Pitman 1986, Stensland *et al.* 2003).

Different hypotheses explaining mixed-species groups have been suggested (see the review Stensland *et al.* 2003). These associations could (i) result from the same attracting stimulus (e.g. resource) for different species moving independently (Waser 1982), (ii) be due to species that are voluntarily associating with other specific species to take advantage of their biological abilities for foraging (Minta *et al.* 1992; Pays *et al.* 2014), or (iii) be due to species that are voluntarily associating with other specific species for anti-predator advantages (Heymann & Buchanan-Smith 2000, Schmitt *et al.* 2016; Pays *et al.* 2014). In the case of anti-predator advantages, multi-species groups are assumed to allow the species within the group to take more advantages than in monospecific group by (i) the detection ability of the other species (Bshary & Noë 1997, Heyman & Buchana-Smith 2000, Lea *et al.* 2008 Schmitt *et al.* 2016), (ii) the “dilution” effect without an increase of the competition for resources if species have different food niches (Stensland *et al.* 2003) by decreasing the risk of being predated with the presence of a more preferred preyed (Schmitt *et al.* 2014), and (iii) the strong ability of the other species for predator deterrence (i.e. the “confusion effect” Krause & Ruxton 2002, Landeau & Terborgh 1986, or mobbing behaviour Curio 1978; Struhsaker 1981, Gautier-Hion 1988). As assumed at the intraspecific level with larger group size (Pulliam 1973, Bednekoff and Lima 1998), multi-species association is expected to allow individuals to decrease the time allocated to anti-predator behaviours such as vigilance (Schmitt *et al.* 2016).

In arid and semi-arid African savanna ecosystems, surface water is a resource that becomes scarcer and limiting as the dry season progresses, leading to the aggregation of a wide range of large mammal species around these few remaining water sources (Redfern *et al.* 2003, Valeix 2011). Because large herbivores are predictably aggregated around these water sources, they represent prey hotspots in the landscape that attract large carnivores, such as the African lion *Panthera leo*, which select the habitats around waterholes (Valeix *et al.* 2010, Davidson *et al.* 2012) and make most of their kills there (Valeix *et al.* 2009a, Davidson *et al.* 2012). Waterholes are therefore places where herbivores have to deal with both water

requirements and heavy predation pressure, which are increasing over the dry season (Valeix *et al.* 2009b). It was suggested that even if mixed-species groups are formed just by chance, it does not mean that species within these groups could not get the advantages discussed above (Stensland *et al.* 2003). To our knowledge, only one study focused on mixed-species groups and the associated effects on vigilance behaviour in this context (Périquet *et al.* 2010). Ferry *et al.* (2016) revealed an increasing aggregation pattern of zebras and African elephants *Loxodonta africana* at waterholes as the dry season progressed and suggested that a possible underlying mechanism could be a protective effect of elephants, called here the “bodyguard hypothesis”. Indeed, African elephants are megaherbivores (>1000kg, sensu Owen-Smith 1988) and whereas calves are susceptible to be predated (Loveridge *et al.* 2007a) adults are able to deter predators such as lions *Panthera leo* by mobbing behaviour (McComb *et al.* 2011; pers. obs.). Zebras, which are preyed by lions (Davidson *et al.* 2013) could therefore take advantage of this mobbing behaviour by being close to the elephants, leading to a decreased perceived predation risk. This would result in lower period allocated to vigilance behaviour.

Here, we designed a field play-back experiment to test this “bodyguard hypothesis”. To determine how elephant presence affects perceived predation risk and antipredator response, we tested how zebras behave in response to playback of roaring of lion in presence and in absence of elephant. We predicted that, after the lion roaring, vigilance level will be lower in presence of elephants than when they are absent. In addition, we predicted that zebras will aggregate to elephants after the lion roaring. We further assess if the zebra drinking behaviour was impacted.

Materials and methods

Study site

Hwange National Park (HNP hereafter) covers ~15 000 km² of semi-arid dystrophic (low nutrient soil) savanna in northwestern Zimbabwe (19°00' S, 26°30' E). The vegetation is primarily woodland and bushland savanna. 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 HNP where lion density is estimated around 4.3 individuals/100 km² (Loveridge *et al.* 2016), elephant density is estimated above 2 individuals/km² (Chamaillé-Jammes *et al.* 2008) and zebra density is estimated at 0.6 individuals/km² (Grange *et al.* 2015).

Experimental design

Experiments were performed in 2016 (annual rainfall = 438.3 mm) at the end of the dry season (between August and November) at four artificial waterholes. Playback experiments with simulated predator presence (lion roaring) or control treatment (car engine sound) were conducted in two elephant-contrasted situations (presence/absence). We avoided any temporal effect during our experiments by randomly distributed the different playbacks across the study period. To avoid habituation, a minimum period of 2 days was left between playbacks to the same waterhole. The behavioural responses of the adult zebras to playback were recorded on video, alongside live commentary, using a camera. Observers were inside the stationary car parked at approximately 100m from the waterhole to minimize disturbance while maximizing the quality of the video recording. Data were filmed mainly by one observer (N.F.) and were supplemented by a second observer who recorded the zebra' behaviour. We started to film when a zebra group entered the "waterhole area", defined with the spatial boundary set where grasses are replaced by sand, avoiding potential foraging activity of zebra during the observation. Zebra group size, presence of elephants and wind strength were recorded. The playback was played when one of the zebras from the focal group started drinking and lasted for 1 minute. The stimulus of presence of predators consisted in lion roaring, and the control treatment was the sound of 4x4 car engine, as this sound is assumed to be neutral for herbivores in the context of a protected area with touristic activities. We matched the acoustic properties (i.e. frequency characteristics and temporal structure) of the roaring and sound of car engine playbacks by visually comparing their spectrograms. We checked that there were no differences in the overall frequency characteristics between the two playbacks (see Appendix 1). Recordings were in 16-bit WAV format and analysed with Avisoft SASLab software (Avisoft Bioacoustics, Berlin, Germany). Four shared acoustic properties were measured on each call sound track: (1) peak frequency (the frequency for which amplitude (Hz) is maximum); (2) maximum frequency (highest frequency of the call in Hz); (3) minimum frequency (lowest frequency of the call in Hz); (4) frequency bandwidth (differences in Hz between maximum frequency and minimum frequency measure on a linear amplitude spectrum (threshold -20 dB)) (Fast Fourier Transformation (FFT) length of 1024 samples). We stopped filming when all zebras had left the waterhole area. The experiments were performed in two elephant-contrasted situations: when elephants were absent and when elephants were present. Four experiment

combinations were therefore conducted: (i) zebras only with control treatment ($n=8$), (ii) zebras only with lion treatment ($n=9$), (iii) zebras and elephants with control treatment ($n=7$), and (iv) zebras and elephants with lion treatment ($n=8$). We conducted only one playback experiment per waterhole per day in order to avoid monitoring zebras that were near the waterhole during a previous experiment and would have already been affected by the stimulus. Tests involved a mean of 11.4 individuals per video experiment. The ranges of group sizes of zebra-only and zebra with elephant groups were similar (i.e. from 2 to 20 and 6 to 20 individuals, respectively).

Choice of Experimental Stimuli and Playback Materials

We broadcast sound tracks using MegaVox Pro MEGA—7500 loudspeaker (Anchor®). Concerning the signal used during playback, we used roaring and sounds of 4x4 car obtained from online sound banks. To avoid pseudoreplication (Hurlbert, 1984; Kroodsma, 1989, 1990), roaring from 3 lions and sounds from 3 car engines were used. Playback sequences were constructed using Avisoft-SASLap Pro software.

Spatial data

In the situation with elephants, the aggregation behaviour of zebras was assessed by recording, with a telemeter and a compass, the distance from the car and the angle to the north of the pair of closest zebra-elephant. Euclidean distances between individual zebras and the nearest elephant were then calculated. This distance was calculated just before the beginning of the playback and after the playback, if zebras had moved closer to elephants.

Vigilance and drinking data

From video analysis, we assessed two principal behaviors that described the responses of each individual (up to ten random individuals were monitored per group) in the focal group: the induced vigilance (sensu Blanchard & Fritz 2007) and the drinking behaviour. This analysis was performed with JWatcher software (Blumstein *et al.* 2006) by 1 identifiers (E.M.). We then obtained for each individual, the number of events for each behaviour and the duration of each event, the total duration and the proportion of time for each of the four behaviours. Because we were interested in whether there are fine-scale differences in vigilance and drinking behaviors in response to different playbacks, we analyzed each response variable separately.

Analyses

Spatial analyses - Spatial data were eventually not analysed because zebras never got closer to elephants after the playback treatment (lion or control).

Vigilance and drinking analyses – We first assessed the effect of the stimulus of the presence of lions on zebra induced vigilance behaviour by performing three mixed models on: (i) the logit-transformed proportion of time spent in induced vigilance, (ii) the number of events of induced vigilance, and (iii) the mean duration of an induced vigilance event. Explanatory variables were the zebra group size, the period (before vs. after stimulus), the treatment (control vs. lion) and the situation (zebra only vs. zebra with elephant). A two-way interaction was tested between group size and period, and a three-way interaction was tested between period, treatment and situation. We then assessed the effect of the stimulus of the presence of lions on zebra drinking behaviour by performing three mixed-models on: (i) the logit-transformed proportion of time spent drinking, (ii) the number of drinking event, and (iii) the mean duration of a drinking event. We considered the same explanatory variables as in the models for induced vigilance except the period (before vs after stimulus) which was removed as stimulus was played when zebras began to drink. The only interaction in this model was the two-way interaction between treatment and situation. In all analyses, we considered the focal group and the playback used as random effects. For all the analyzes, mixed-models were performed except for the number of events were generalized mixed-models with poisson family were done (log-normal function link). These analyses were performed with the package lme4 (Bates *et al.* 2007), and p-values were estimated using the package lmerTest (Kuznetsova *et al.* 2015) based on the Satterthwaite approximation for denominator degrees of freedom. Analyses were done on R statistical software 3.3.2 (The R Foundation for Statistical Computing, Vienna, Austria).

Results

Induced vigilance –There was no difference in the proportion of time spent in vigilance before the stimulus whatever the treatment and the situation (Tab. 1, Fig. 1). The control treatment increased the time spent in vigilance when there were zebras only (i.e. no elephant, $\beta_{\text{Period}} = 0.447$, $t = 2.35$), and this increase was higher in presence of elephants ($\beta_{\text{Period} * \text{Situation}} = 0.70$, $t = 3.15$). The lion treatment had a higher effect than the control treatment on the time spent

in vigilance ($\beta_{\text{Period} * \text{Treatment}} = 0.42$, $t = 2.01$) and this effect was independent of the presence or absence of elephants (i.e. no significant three-way interaction). The group size effect on the proportion time spent in induced vigilance was detected only after the treatment (lion or control) as only the interaction group size-period was significant ($\beta_{\text{Group size} * \text{Period}} = -0.037$, $t = -2.46$). Results on number of events of vigilance and mean duration per event are presented in Appendix 2. We observed the same pattern for the number of events of vigilance, but not for the mean duration per event.

Table 1: Results from the mixed-model with logit-proportion of time passed in vigilance. Bolded variables are those with significant p-value.

Variables	Estimate	SE	t	P-value
Period	0.45	0.19	2.35	0.02
Treatment	0.05	0.31	0.16	0.88
Situation	-0.21	0.28	-0.77	0.45
Period*Treatment	0.42	0.21	2.01	0.045
Period*Situation	0.70	0.22	3.15	0.002
Treatment*Situation	-0.53	0.38	-1.39	0.18
Period*Treatment*Situation	0.31	0.31	1	0.32
Group size	0.02	0.02	1.08	0.29
Group size*Period	-0.04	0.01	-2.46	0.014

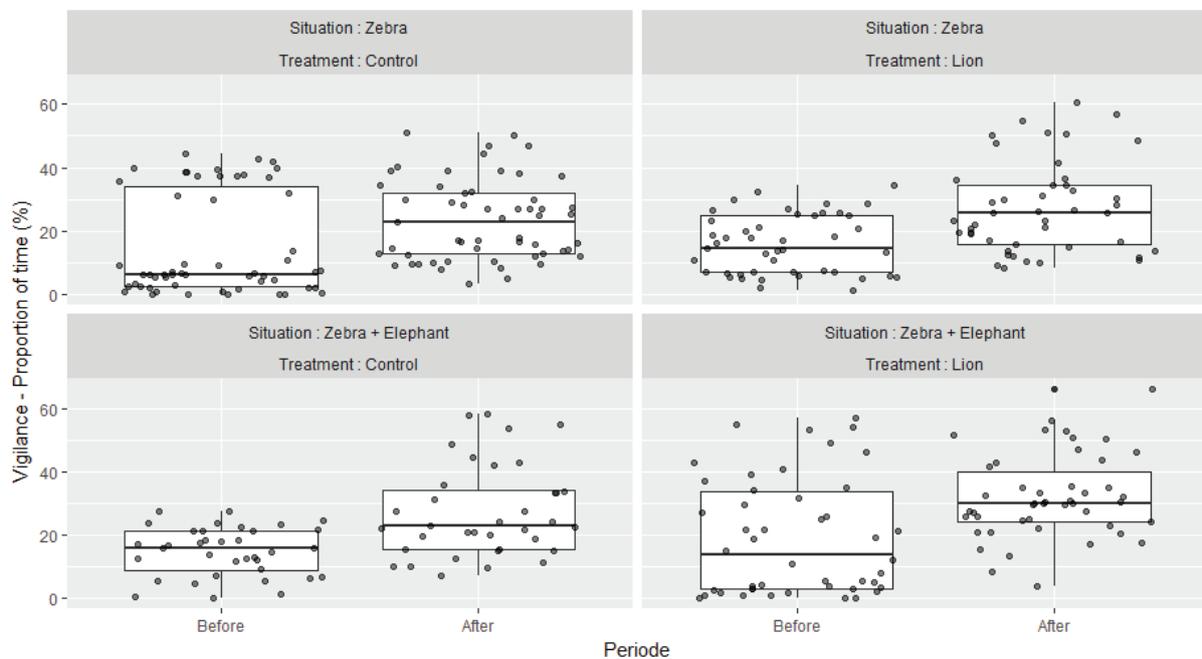


Figure 1 : Proportion of time passed in vigilance upon the treatment (control vs lion), the situation (zebra vs zebra + elephant) and the period (before vs after). The box and whisker plots display the median value and 25 and 75% quartiles; the whiskers are extended to the most extreme value inside the 1.5-fold interquartile range.

Drinking – We did not detect any significant effect of the group size, treatment (lion or control) and situation (with elephant and without elephant) and the interaction between treatment and situation neither on the logit-transformed proportion of time spent drinking, neither on the number of drinking event nor on the mean duration of the drinking event.

Discussion

In the present study, we tested the effects of elephant's presence on the vigilance and drinking behaviours of zebras. We showed experimentally that zebras vigilance increases with perceived predation risk, with the presence or the absence of elephants. We also showed that zebras responded to the presence of elephants by increasing their vigilance after the control treatment. We did not observe any change in the drinking behaviour (as observed in Périquet *et al.* 2010).

Reactive adjustments occur when prey have detected an immediate threat, i.e. encountered either the predator or cues of its presence (Creel and Winnie 2005, Wirsing & Ripple 2010). Prey species alter their behaviour in response to predation risk (Turchin and Kareiva 1989) by retreating to safe habitats (Kotler *et al.* 1991, Sih 1997), altering group size (Caro 2005, Creel and Winnie 2005), or increasing vigilance (Brown & Kotler 2004). Zebra population of Hwange National Park, seems to be under top-down control by lions and currently declining due to a high predation pressure (Grange *et al.* 2015) even if they are not the main prey of lions (Davidson *et al.* 2013). In this system, lions represent therefore one of the main threats zebras can face during they daily activity, particularly areas surrounding waterholes (Valeix *et al.* 2010). During our experiment, zebras responded to the lion roaring. This response was not represented by fleeing behaviour after the lion roaring (except during the only situation where we observed a zebra alone which directly fled away from the waterhole, pers. obs.). It seems to confirm results from Courbin *et al.* (2016), where zebras were less prone to flee away after an encounter with lion in open area such as grassland whatever the distance from waterholes. Regarding the two other anti-predator behaviours (vigilance and group size change), in our situation, grouping is considered as a proactive response to the use of dangerous habitats (Creel *et al.* 2014) letting zebras to adjust their anti-predator behaviour only with vigilance. Périquet *et al.* (2010) did not observed vigilance increase from zebras when lions were in the vicinity of waterholes (< 2km) whereas we

observed an increase of the vigilance level after the lion roaring. It is unlikely that this vigilance increase was only due to the emission of sound as we controlled it with the car engine sound. An explanation could be that zebras react negatively to the presence of lions (as see in Courbin *et al.* 2016) but either i) zebras did not detect lion's presence in Périquet *et al.* (2010), although kudus seemed to do detect it, either ii) zebras detect lions but respond negatively only to direct visual/auditory signal of the presence of lions. Interestingly, zebra's vigilance increased after the car treatment, whereas it was assumed to be neutral in term of predation (poaching being very limited inside the park for zebras). It confirms the importance to disentangle between the response to the simple emission of a signal (kind of "surprise effect" and the response to the real stimulus (here lion roaring) in such experimental field studies. It is interesting to note that the differences of time proportion passed in induced vigilance are owing to the number of event and not to the duration of the event (Appendix 1).

Contrary to expectations, after the playback of lion, the presence of elephant did not result in a decrease of the vigilance response level of zebras. In addition, zebras never aggregated to elephants after lion roaring. The "bodyguard hypothesis", under which thanks to their mobbing behaviour elephants are considered as pledge of security against predators at the waterhole, is not supported by our results which do not explain the aggregation pattern observed in Ferry *et al.* (2016). Further, it was observed (Ferry N. pers. obs) that in rare occasions, after the treatment (control or lion) elephants fled away from the waterhole when zebras stayed. These results would tend to the conclusion that zebras would not take advantage of the presence of elephants at waterholes in this context. On the contrary the presence of elephants would be a source of increased vigilance for zebras when a sound is played. Indeed, zebras were more vigilant after the control treatment when elephants were present. Interestingly, this increase was not more important when the treatment was lion roaring (contrarily of the situation without elephants were the increase of vigilance was more important with lion roaring than with control treatment). Either, elephant presence does not have the same effect for zebras upon the auditory cues, either they reached a maximum threshold of vigilance level and cannot pass beyond.

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Supporting information

Appendix 1

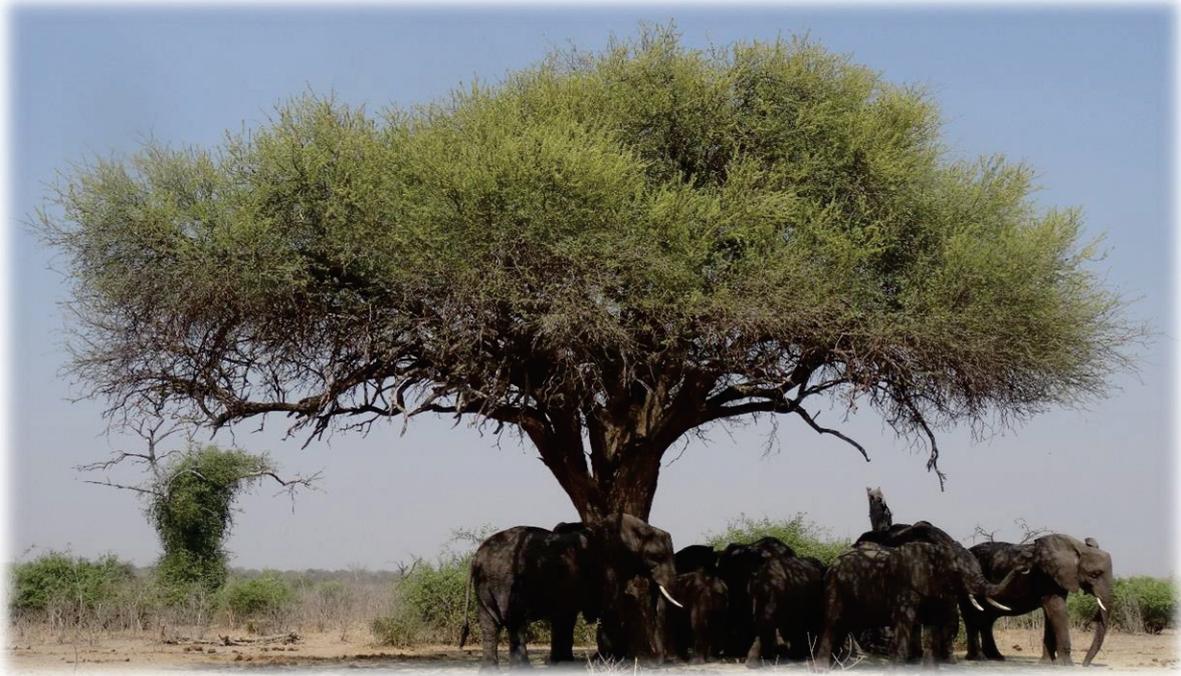
Frequency characteristics of the roaring and the sounds of car

Treatment	Frequency characteristics (Hz)			
	Peak	Minimum	Maximum	Bandwith
roaring	140	113	1190	1076
car	120	26	1040	1015

Appendix 2

a) Results from the generalized mixed-model with number of event passed in vigilance. b) Results from the mixed-model with mean duration of event passed in vigilance.

a)				
Variables	Estimate	SE	z	P-value
Period	0.61	0.09	7.1	< 0.001
Treatment	-0.01	0.19	-0.07	0.94
Situation	-0.3	0.28	-0.07	0.94
Period*Treatment	0.25	0.09	2.7	0.006
Period*Situation	0.37	0.1	3.56	< 0.001
Treatment*Situation	-0.26	0.29	-0.92	0.35
Period*Treatment*Situation	0.38	0.15	2.6	0.009
Group size	0.02	0.01	1.69	0.09
Group size*Period	-0.02	0.007	-3.5	< 0.001
b)				
Variables	Estimate	SE	t	P-value
Period	-15.96	10.7	-1.49	0.14
Treatment	-10.4	17.4	-0.6	0.57
Situation	-16.88	17.76	-0.95	0.35
Period*Treatment	11.68	11.68	1	0.32
Period*Situation	26.9	12.5	2.1	0.03
Treatment*Situation	-10.68	24.6	-0.43	0.67
Period*Treatment*Situation	-2.68	17.7	-0.15	0.88
Group size	0.26	1.17	0.22	0.83
Group size*Period	-0.51	0.84	-0.62	0.54



AXIS 2.

Indirect effect of elephants on lion's spatial distribution,
through competition/facilitation with other herbivores.



*« L'homme qui marche derrière un éléphant n'a rien à
redouter de la rosée. »*

Massa Makan Diabaté

Chapter 4: Assessment of food competition between African elephants and other large herbivore species through spatial segregation at multi-scale level.

This chapter combines results based on road censuses carried out for 10 years (from 2004 to 2014) in 3 study areas of Hwange National Park to assess the spatial distribution of African elephants *Loxodonta africana* and other large mammalian herbivores, and discuss interspecific competition mechanisms in light of the spatial niche partitioning observed. This work is a collaborative work between Elise Say-Sallaz¹ and **Nicolas Ferry¹**, under the supervision of Stéphane Dray¹, Hervé Fritz¹ and Marion Valeix¹.

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Abstract

In community ecology, interspecific spatial patterns allow exploring the existence of interspecific interactions, such as competition or facilitation. Studies of spatial patterns are very insightful especially when experiments are too difficult to carry out, which is typically the case of large mammalian communities in protected areas. Here, we tested the hypothesis that the African elephant (*Loxodonta africana*), a megaherbivore, has a competitive effect on other herbivore species in a semi-arid savanna ecosystem. As interspecific competition leads to niche partitioning, we assessed the impact of elephants on other herbivore species at three scales: (i) landscape-scale spatial segregation, (ii) habitat partitioning, and (iii) fine-scale spatial segregation. We did not find any landscape-scale spatial segregation between herbivores and elephants. We did not find neither any habitat partitioning, and unexpectedly impalas selected habitats that were intensively used by elephants. Finally, we did not demonstrate any within-habitat scale spatial segregation. At this point, no competitive effect of elephants on other herbivores has been demonstrated, but it does not mean that it does not exist at all. This effect might happen at two other dimensions of niche partitioning not investigated in this work: resource partitioning and temporal segregation.

Keywords: spatial pattern analysis, niche partitioning, interspecific competition, *Loxodonta africana*, large mammalian herbivores

Introduction

Interspecific competition is an important biotic filter leading in some circumstances to competitive exclusion (Chase *et al.* 2002), which is translated by local extinctions or a change in the resources used by the non-dominant species (Volterra 1926; Gause 1934; Hardin 1960). Nowadays, interspecific competition is recognised as a major process in the establishment and structuring of communities (Cornell & Lawton 1992; Amarasekare 2002). Two types of interspecific competition exist: exploitative competition and interference competition (Case & Gilpin 1974; Connell 1983; Schoener 1983). Exploitative competition is an indirect process where some species, by using some resources, are cutting off associated benefits to competitors (Schoener 1983). Interference competition is a direct process where individuals are preventing their competitors to have access to a resource, by the mean of their presence, physical aggression, or by releasing toxic chemicals (Schoener 1983; Gyimesi *et al.* 2010). It induces numerous costs such as injuries (Janson & Van Schaik 1988) or a decrease of the intake rate, which is difficult to measure in the field as it is due to an avoidance behaviour (Janson & Van Schaik 1998; Gyimesi *et al.* 2010).

To avoid or minimize the costs of competition and thus coexist, competing species can use the environment differently (e.g., in space or time) and specialise on different resources. This is the concept of niche partitioning (Schoener 1974; Connell 1980). Niche partitioning can be effective on different resources shared by the competitors, and can lead to (i) spatial segregation, whereby one species spatially avoids the competing species (Connell 1980; e.g. Stewart *et al.* 2002 for cattle and rocky Mountain mule deer and elk), (ii) habitat partitioning, whereby two species can be found in the same area if they do not use the same habitat (Connell 1980; e.g. depth that plant roots are occupying in the soil), (iii) resource partitioning whereby two species use the same habitat but different types of resources or different resource items (Schoener 1974; e.g. seed size for species with a granivore diet), or (iv) temporal partitioning, whereby two competing species are found in the same area, use the same habitat, and potentially the same resources, but not at the same time (e.g. Kotler *et al.* (1992) showed that two competing species of gerbils used the same resource patches but at different times of the night). Species are thus involved in complex interspecific interactions that can occur along different niche axes (Di Bitetti *et al.* 2010).

This study focuses on the role of interspecific interactions in a community of large mammalian herbivores (herbivores hereafter). Herbivory has important impacts on ecosystems (Ripple *et al.* 2015) including impacts on plant diversity, plant tolerance to herbivory, and nutrient cycle (Augustine & McNaughton 1998). Among herbivores, megaherbivores (> 1000 kg) have interesting characteristics: they are generalists and ecosystem engineer species (Owen-Smith 1992; Ripple *et al.* 2015; Coverdale *et al.* 2016). Ecosystem engineers can physically transform the abiotic or biotic material (Jones *et al.* 1994; Wright *et al.* 2002; Soulé *et al.* 2005), and other species are expected to respond to these environmental changes, which can thus affect the distribution and abundance of other species in ecosystems (i.e. niche construction Odling-Smee 2003). While threatened by poaching in several African ecosystems (Wittemeyer *et al.* 2014; Chase *et al.* 2016), some populations of African elephants (*Loxodonta africana*) remain stable or are increasing in southern and eastern Africa (Chase *et al.* 2016), due to habitat fragmentation (Archie *et al.* 2012; Ripple *et al.* 2015) and efficient conservation (creation of protected areas). In these ecosystems, elephant populations can reach high densities and concerns have arisen about their impact on the structure and functioning of communities and ecosystems because of the large amount of vegetation they process and their potential important role as ecosystem engineers (Paine 1992; Soulé *et al.* 2005). A growing number of studies have therefore focused on the role of elephants in their ecosystems. For instance, it has been suggested that elephants can have a negative effect on browsers (i.e. species feeding on ligneous vegetation) by decreasing trophic resource availability (Fritz *et al.* 2002; Valeix *et al.* 2008; de Boer *et al.* 2015). Contrarily, other studies have shown that elephants can have facilitative effects on browsers on the short term. Indeed, when elephants break trees, these broken trees tend to resprout and the number of shoots produced by the plant at a height available for browsers such as impala (*Aepyceros melampus*) increases (this is the concept of browsing lawns - Rutina *et al.* 2005; Makhabu *et al.* 2006; Fornara & du Toit, 2007). Elephants might also have a direct competitive effect on water acquisition for other herbivores when water resources are scarce during the dry season (Valeix *et al.* 2007; Ferry *et al.* 2016).

In Hwange National Park, Zimbabwe, since culling stopped in 1986, the elephant population doubled in less than ten years, and its abundance is now fluctuating around 30 000 individuals (Chamaillé-Jammes *et al.* 2008). At the same time, changes in the abundance of the populations of other herbivore species were observed. Some species abundances increased before 1986 and started decreasing after elephant culling stopped. Other species abundances decreased when the elephant population abundance increased and stabilized when the elephant population abundance stopped increasing and started to stabilize and fluctuate (Valeix *et al.* 2008). These changes in species abundances can result from the climatic conditions that occurred between 1985 and 1995 in Hwange National Park (low dry season rainfall), but a competitive effect of elephants cannot be ruled out (Valeix *et al.* 2008). In this study, we therefore tested the hypothesis that elephants have a competitive effect on other herbivore species, particularly browsers, which would result in niche partitioning between these species and elephants. We specifically investigated spatial avoidance (at different scales) and habitat segregation. Using a transect-based long-term study (10 years), we focused on habitat and spatial use by elephants and the other sympatric herbivore species. We first described spatio-temporal variation of the composition of herbivore communities at the landscape scale to assess if spatial segregation occurs between elephants and other herbivore species at a large scale. We then considered environmental data to study habitat selection and detect habitat segregation between elephants and other herbivore species. Finally, we investigated at finer spatial scales whether herbivores avoid being close to elephants when using the same area at the same time as elephants.

Material and methods

Study site

The study site was carried out in Hwange National Park in northwestern Zimbabwe (19°00'S, 26°30'E) (Fig.1). The park covers ~ 15 000 km² of dystrophic semi-arid savanna mainly composed of woodlands and bushlands (Dudley *et al.* 2001; Appendix 1A). The dominant vegetation species in the park are *Acacia* spp., *Colophospermum mopane*, *Combretum* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). There are two contrasting seasons, the dry season, from May to October, and the rainy season, from November to April. The long-term mean annual rainfall is ~ 600mm, and the long-term mean dry season rainfall is 8,7mm. There is no perennial water in the park, although a few rain-fed pans hold water for much of the year in an average rainfall year. Water is artificially supplied to some waterholes during the dry

season (Appendix 1B). Most of the artificial waterholes, and hence most animals in the dry season, are in the northern sector of the park (Appendix 1B). In this study, we focused on three areas in this northern sector: (from West to East) Sinamatella, Main Camp and Ngamo (Appendix 1). These three areas cover about 4 000km² of the park.



Figure 1: geographic position of Hwange National Park (green) in Zimbabwe (<http://www.za-hwange.cnrs.fr/>)

Data

Road censuses

Road censuses were carried out during 10 years, from 2004 to 2014, to assess the abundance and spatial distribution of herbivores in the three study areas. The censuses followed the line-transect method and most available roads of the study areas were considered as transects (Appendix 1B). All observations of herbivores (species, group size) along transects were reported with the GPS coordinates of the observers on the transect, the angle to the North of the observation, the distance to the road of the animal(s), in order to calculate the exact positions of observations. The transect number, the activity of the herbivores (e.g. foraging, resting, moving), the perpendicular distance to the road, the date, and the time of the observation were consistently recorded. Two census sessions were carried out per year: one in May/June corresponding to the beginning of the dry season and one in September/October corresponding to the end of the dry season. For each session, two repetitions by transect were done.

Environmental data

Environmental data were extracted from a map of the artificial waterholes and a raster map (raster format) of the different vegetation types (Appendix 1). The vegetation raster map was created based on satellites images (see Courbin *et al.* 2016 for details). Seven categories mainly based on openness were considered: grassland, open bushland, bushland-mopane, bushland-other, woodland-mopane, woodland-evergreen (mainly composed of *Acacias* spp.) and woodland-other. The proportion of each vegetation category for each transect in a buffer of 50m was determined with the QGIS software (QGIS 2.14.5). Similar method was performed to evaluate for each transect the proportion of four classes of distance to water (0-1km, 1-2km, 2-5km, >5km). Distance to water and proportion of grassland, which is the most open habitat in the Hwange ecosystem, were correlated with grasslands predominantly found close to waterholes (Appendix 2). Therefore, collinearity between vegetation type and distance to water were assessed in further analyses.

Analyses

All statistical analyses were performed with open source Software R 3.3.1 (R Development Core Team 2014) unless otherwise specified.

Detection probability

We first computed the detection probability function for each herbivore species using Distance Sampling software (Thomas *et al.* 2010). As most of Hwange ecosystem is characterized by rather densely wooded habitats, detection probabilities decreased rapidly with the distance to the road. Therefore, for our analyses, we selected observations that were in a buffer zone of 50m from the road in order to have a detection probability of at least 0.7 for all species (with the exception of the very small species, such as steenbok (*Raphicerus campestris*) and duiker (*Sylvicapra grimmia*) that have a detection probability of only 20% at this distance, so these species will not be used for analysis).

Landscape-scale spatial segregation

We first investigated (1) spatial segregation between elephants and other herbivore species, and (2) relationships between environmental factors (distance to waterhole, vegetation type) and species communities in the study areas. Multivariate analyses were performed (ade4 package, Dray & Dufour 2007) on the species abundance, on each transect for a given session.

We preliminarily performed a classical Principal Component Analysis (PCA) on the log-transformed species abundances. We then assessed the temporal variability of the herbivore community between year by performing a between-class PCA with “Year” as factor. Spatial variability between transect was assessed in similar way, with “Transect” as explanatory variable. Finally, a Principal Component Analysis with respect to Instrumental Variable (PCAIV) was performed on the spatial between-class PCA to quantify the proportion of the total spatial variability explained by the environment. Three zones were highlighted that correspond to the three study areas, i.e. Sinamatella, Main Camp and Ngamo. Sinamatella is very different from the two other areas in terms of both vegetation composition (Appendix 3a) and herbivore community composition (see after). Only data from the Main Camp and Ngamo areas were therefore used for subsequent analyses. In addition, analyses were performed on the five most common species: two mixed-feeders (elephant and impala), two browsers (giraffe (*Giraffa Camelopardalis* and kudu *Tragelaphus strepsiceros*), and one grazer (zebra *Equus quagga*, Appendix 3b).

Habitat selection and partitioning

Habitat selection of the five herbivore species was assessed, as well as whether the intensity of elephant utilization affects habitat selection of other herbivores in Main Camp and Ngamo areas. Only observations when herbivores foraged were used. Resource Selection Functions (RSF, Manly *et al.* 2007) were performed for each herbivore species (with presence of animal(s)= 1 and available = 0). We define (sp package, Bivand *et al.* 2013) available habitat with random locations (same number as the real observations) in the 50m buffer along transects. We used four explanatory variables: vegetation type, distance to water, sampling season (May and October), and the intensity of elephant utilisation. For this last variable, the locations and the abundance of elephant were used to build a raster layer of the intensity of utilization by elephants (ranging from 0 to 400 elephants for each pixel). This last variable was not used for the analysis of elephant habitat selection. To select the best model, we used the Bayesian Information Criterion (BIC) that selects for the most consistent and parsimonious model, whereas the Akaike Information Criterion (AIC) maximise the accuracy (Aho *et al.* 2014). Model parameters were then estimated with a model averaging (on models with $\Delta BIC < 2$, MuMIn package, Bartoń 2016, Burnham & Anderson 2004). Estimates of the model

parameters were used to calculate the selection strength (or relative probability of selection) for each variable. In order to avoid collinearity issues due to the structure of the habitat (Appendix 2), we calculated the variance inflation factor (VIF package, Lin 2012) for parameters in every model. All the VIF values were below 4, so we considered that the correlation between the proportion of grassland and the distance to the water was not a statistical issue (O'Brien 2007).

Fine-scale spatial segregation

Fine scale spatial segregation was assessed between elephants and the four other most common herbivore species (giraffe, kudu, impala, zebra) in Main Camp and Ngamo areas. Considering one focal species, for each observation of this species the distance to the closest elephant (D_{elephant}) was calculated, as well as the distance to the closest individual of each of the three other species when possible (D_{other} ; up to three measures of D_{other} can therefore be recorded). For each observation, only observations recorded on the same transect during the same day were used to calculate distances (Fig. 2). Because all herbivores tend to aggregate in the vicinity of waterholes in the dry season (Redfern *et al.* 2003; Valeix *et al.* 2009), segregation was expected at a certain distance to water and distance to elephant (D_{elephant}) was considered according to distance to water. Similar process was used for the distance to the other species (D_{other}). In order to compare the two distributions, the distance to elephant (D_{elephant}) was ranked according to all the D_{other} relevant on the same transect the same day. The probability to be equal or inferior to the D_{elephant} was then calculated. For each of the four classes of distance to water (0-1km, 1-2km, 2-5km, >5km), we combined all the probabilities by performing an unweighted Z-transform test (Stouffer *et al.* 1949). This test allows combining probabilities from k independent tests with identical null hypothesis and calculate a Z value that indicates whether the segregation between herbivores and elephants is significant.

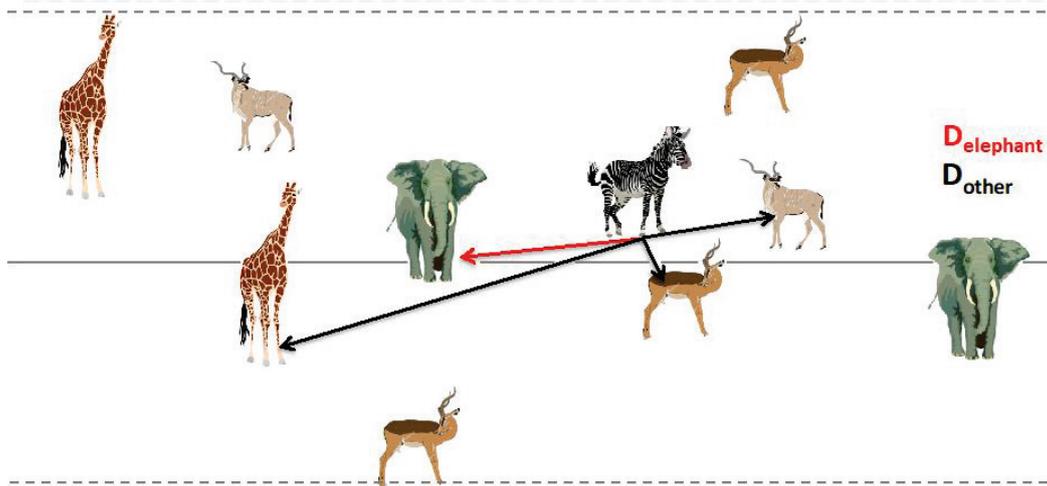


Figure 2: Example of observations of herbivores inside the buffer (dotted grey lines) of 50 m from the transect (solid grey line). In this example, the species of interest is the zebra, the red line represents the Euclidean distance to the closest elephant observation (D_{elephant}), and black lines represent the Euclidean distances to the closest observation of all other herbivore species (D_{other}). In this example, D_{elephant} would occupy the 3rd rank (after impala and kudu) regarding the distances calculated, the probability to be equal or inferior would therefore be 0.75.

Results

Landscape-scale spatial segregation

The PCA revealed a temporal stability of the herbivore community composition between seasons (Appendix 4) and between years (Appendix 4). The between-year PCA confirmed this temporal stability at the inter-annual scale, with only 3% of the total variability explained by differences between years. Regarding spatial variability, the PCA revealed a spatial structuration of the community to a certain level, corroborated by the between-transect PCA where 30.1% of the total variability is explained by differences between transects. The PCAIV highlighted that 60% of these 30.1% are due to environmental factors. Impalas are located in environments that are different from the environments of all other herbivore species (Fig. 3a). They are indeed preferentially located in areas characterized by mopane vegetation, which is typical of the West of the park in the Sinamatella area (Fig. 3c). All the other species are preferentially located in the Eastern part of the park (Main Camp and Ngamo areas, Fig. 3c), characterized by all the other vegetation types (Fig. 3b, c; see also Appendix 3). The second PCAIV's axis allowed to identify a second group of species (giraffe and kudu) preferentially located in the Main Camp area (Fig. 3d), where woodland vegetation dominates (Fig. 3b). All other species appear to co-occur in the same areas. Overall, no spatial segregation between elephants and other herbivore species appeared at the landscape scale.

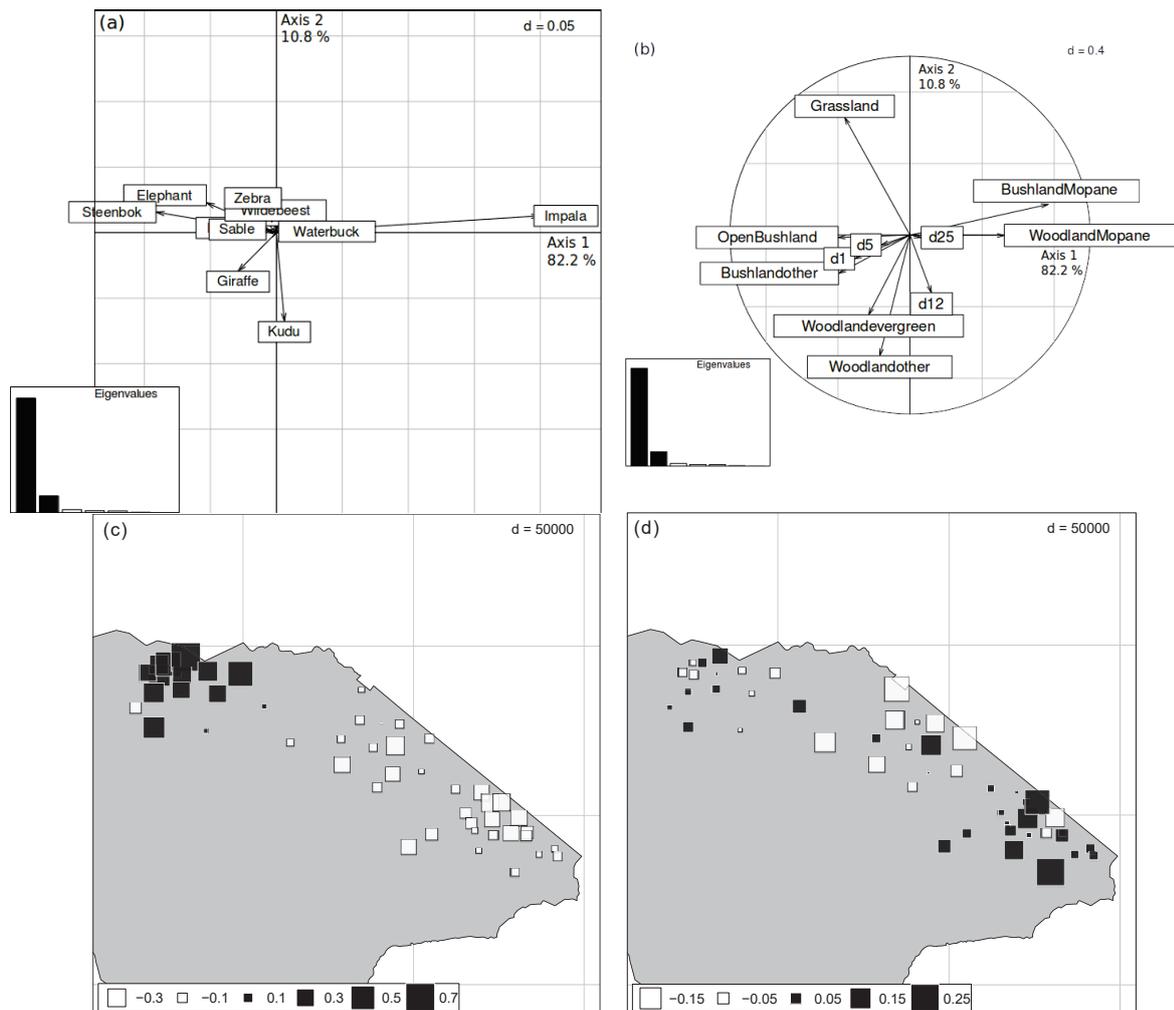


Figure 3: a) Factorial map of the PCAIV, the first axis is explaining 82.2% of the total variability and the second one is explaining 10.8% of the total variability. B) Correlation circles with environmental parameters (distance to water and vegetation classes). C) Spatial representation of PCAIV's first axis distinguishing impalas and other species. d) Spatial representation of PCAIV's second axis distinguishing kudus and giraffes.

Habitat selection and partitioning

The model selection approach indicated that elephants did not select any type of vegetation. In addition, neither the season nor the distance to water seemed to influence elephant habitat selection (the null model was the best model; Appendix 5A), which confirmed that elephants are generalists. Regarding the four other species, models including season as an explanatory variable were never selected. For giraffe, the best model to explain habitat selection was the null model (Appendix 5B). For kudu, habitat selection was best explained by the model with the variable 'distance to water' only (Appendix 5C).

For impala, two best models were selected: one including 'distance to water' and the interaction between 'vegetation type' and 'the intensity of use by elephants', and another including 'distance to water' only (Appendix 5D). Model averaging was therefore performed for impala. For zebra, the best model to explain habitat selection was the model with the additive effect of 'distance to water' and 'vegetation type' (Appendix 5E).

Distance to water influenced habitat selection for zebra (estimate \pm SE = $-3.453e-04 \pm 8.595e-05$; fig. 4a), impala (estimate \pm SE = $-3.72e-04 \pm 1.05e-04$; fig. 4b) and to a lesser extent kudu (estimate \pm SE = $-2.62e-04 \pm 8.17e-05$; fig. 4c). All species selected habitats close to water but the effect was weak for kudus.

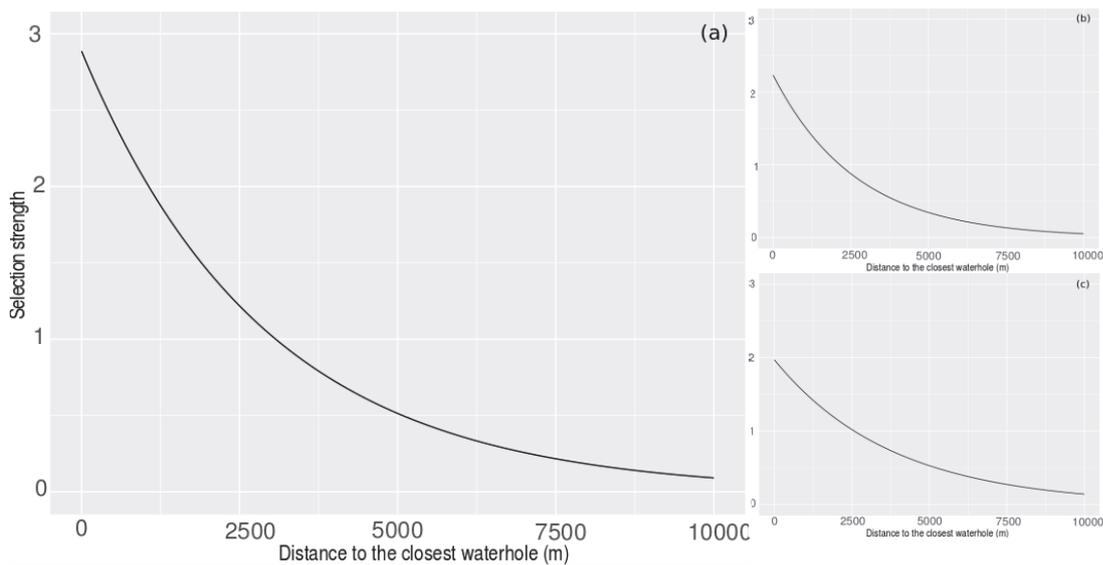


Figure 4: Selection strength according to the distance to water for a) zebra, b) impala, and c) kudu.

Vegetation type had an effect on both impala and zebra habitat selection. Both species selected grassland over other vegetation types (estimate \pm SE = 1.29 ± 0.6 and 1.51 ± 0.31 for impala and zebra respectively; fig. 5). Further, for impalas the vegetation type was in interaction with the intensity of elephant utilisation where impalas selected area with higher intensity of elephant utilisation (Fig. 5a). Finally, the other species did not avoid or select areas intensively used by elephants.

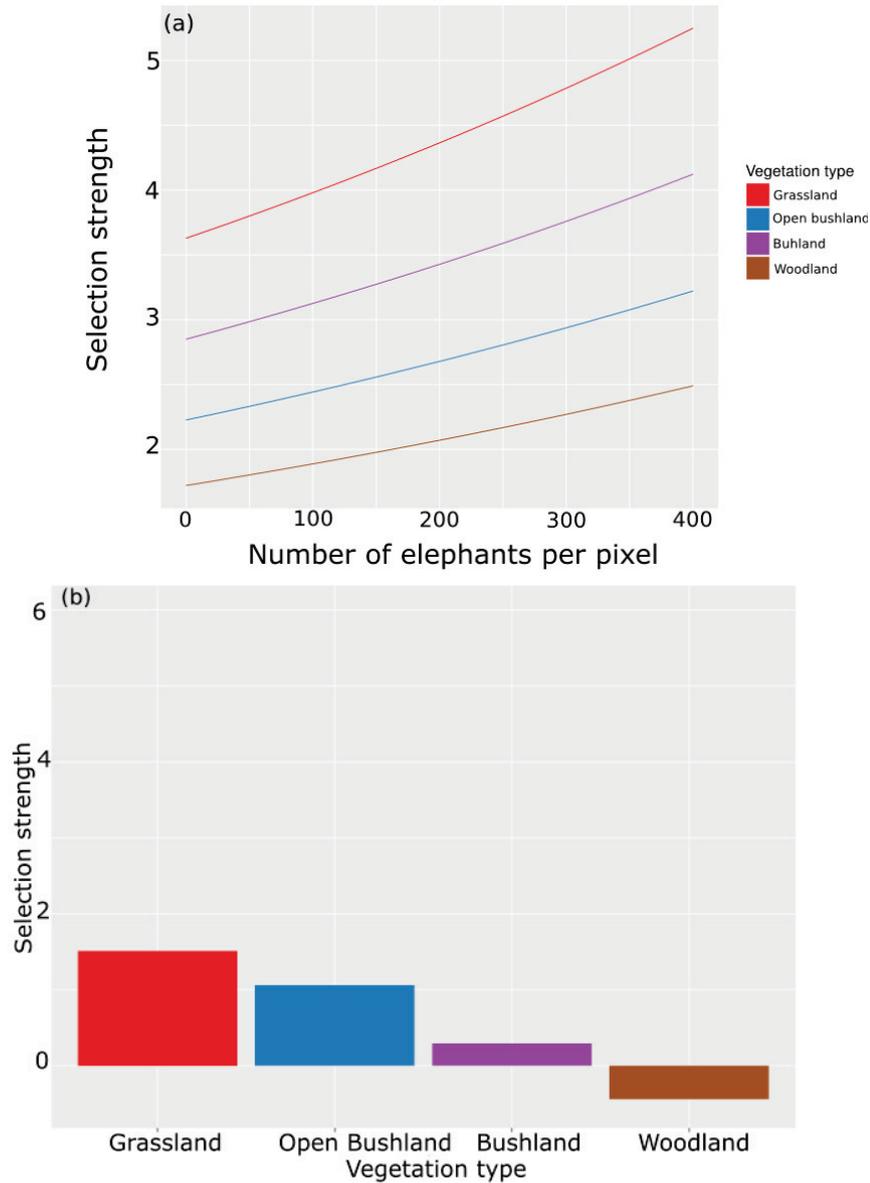


Figure 5: Selection strength of a habitat for a) impala according to the intensity of the elephant utilization and vegetation type, and b) zebra according to the type of vegetation only.

Finer-scale spatial segregation

No segregation from elephant was revealed at finer scales neither. For all the species and all the classes of distance to water, the Z-values had non-significant p values, which means that no spatial segregation could be demonstrated (fig. 6). Even though non-significant, there seems to be a trend for segregation between giraffes and elephants when close to a waterhole.

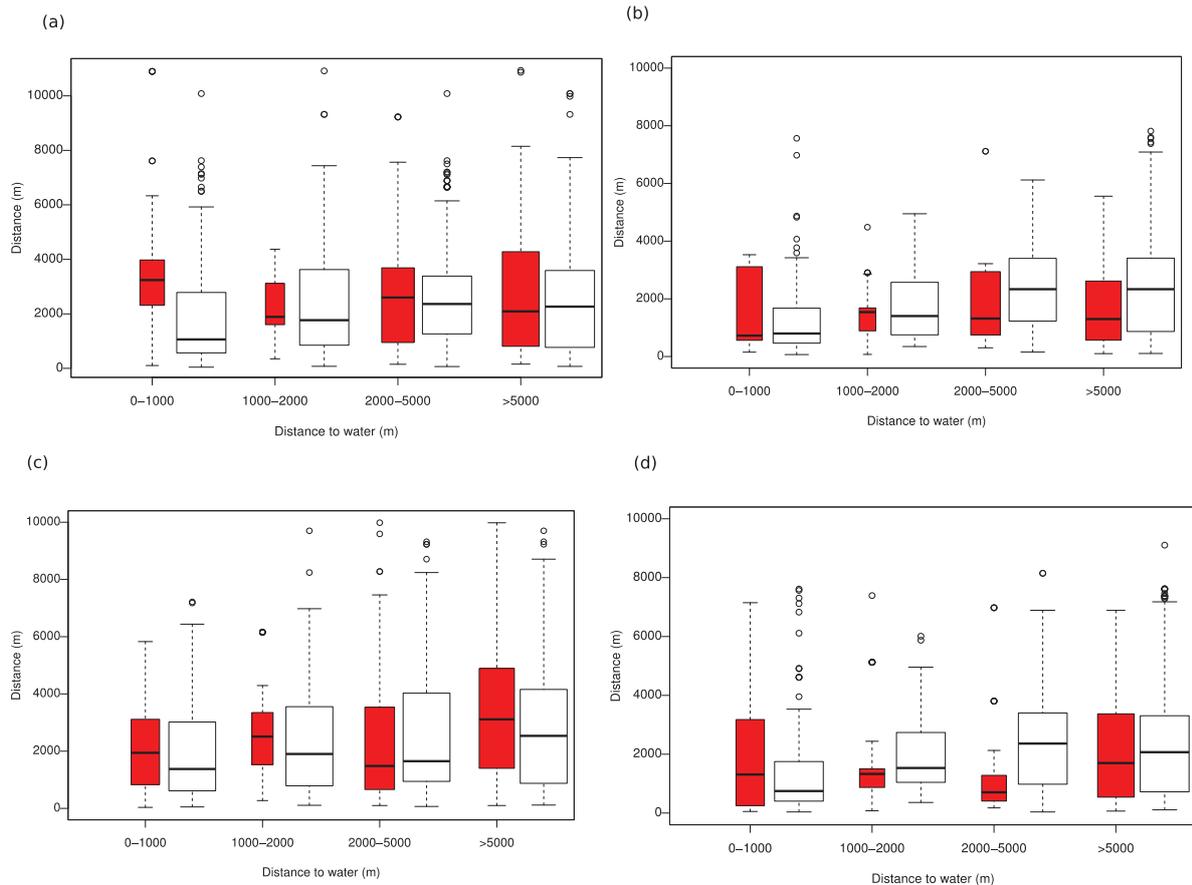


Figure 6 Distributions of the distances to the closest elephant observation (D_{elephant} - red boxplots) and of the distances to the closest other herbivore observation (D_{other} - white boxplots) for a) giraffe, b) impala, c) kudu, and d) zebra according to distance to water. Distances were calculated for real time observations, i.e. animals present the same day on the same transect.

Discussion

Landscape-scale spatial segregation

We initially made the hypothesis that elephants have a competitive effect on herbivores species that can lead to niche partitioning. At the landscape scale, we assessed whether there is spatial niche segregation between elephants and herbivores. The multivariate analyses highlighted the temporal stability of the herbivore community composition over the 10-year study period (2004-2014), which is consistent with previous work focusing on community composition at waterholes in the park (Chamaillé-Jammes *et al.* 2016). Our analyses further revealed that the herbivore community had a spatial structure. Sinamatella, the most western study area characterized by mopane vegetation on rich basaltic soil, showed a very specific species community dominated by impalas contrarily to the two other study areas (Main Camp and Ngamo), which were dominated by elephants and on Kalahari sands, which are poor quality soils. Because elephants and impalas are both mixed feeders, this result may suggest the existence of a spatial segregation between these two species at large scale. However, our results on habitat

selection showed that impalas selected sites intensively used by elephants in Main Camp and Ngamo areas, and therefore provide little support for a competitive scenario between these two species. Instead, the Jarman-Bell principle states that mammalian herbivores with a large body mass can afford to eat lower quality food (but needed in large quantities) compared to smaller herbivores that have to eat higher quality food (but can afford low quantities) (Bell 1971, Jarman 1974, Müller *et al.* 2013). Indeed, larger species can increase their intake without increasing their basal metabolism compared to smaller ones (Müller *et al.* 2013). Considering the body mass gap between impala (female body mass = 45 kg) and elephant (female body mass = 2800 kg), this could explain why impalas are preferentially found in the area with the soil of better quality and elephants in the areas with the soil of poorer quality. Impalas are preferentially found in Sinamatella area, as they seem to preferentially select plant species found in the Mopane habitat type (Kos *et al.* 2012).

Results from the multivariate analyses also showed that most of the other herbivore species were preferentially located in Main Camp and Ngamo areas, despite some of them having small body masses. A hypothesis could be that elephants, through their trophic activities, increase the quality of the trophic resources for other herbivores and allow them to thrive on poor quality soils. This would corroborate the findings on the facilitative effects of elephants for browsers through the creation of browsing lawns (Makhabu *et al.* 2006). Hence, contrary to our predictions, no spatial segregation occurred between elephants and other herbivores at the landscape scale.

Habitat selection and partitioning

The fact that the null model was selected for elephant habitat selection corroborates that the elephant is a habitat generalist (Owen-Smith 1992). Indeed, as megaherbivores, elephants have a capacity to digest a wide range of vegetal species, due to their long digestive tractus (Demment & Van Soest, 1985). However, we cannot rule out a scenario whereby elephants would normally select for a certain habitat type but given the very high abundances encountered in Hwange, it is likely that intraspecific competition is high and a portion of the elephant population is constrained to sub-optimal habitats. Overall, other species cannot segregate their habitat selection from elephant habitat selection as elephants are found in all habitats. However, the PCAIV presented in the first section of results was based on abundances and suggested that the density of elephants in the park is slightly uneven over

Main Camp and Ngamo areas. It also highlighted the fact that elephant abundance is constrained by short distances to waterholes. One explanation would be that using presence/availability data is not as effective to model habitat selection as using abundance data.

There was no effect of distance to water on giraffe habitat selection and only a weak effect for kudu. This may result from the fact that both species are browsers feeding on leaves that supply water, especially during the dry season (Owen-Smith 1979; du Toit *et al.* 1990; Omphile & Powell 2002). For zebra and impala, our results showed a selection strength that increased when the distance to water decreased. These two species are recognized as water-dependant species (Redfern *et al.* 2003).

Interestingly, whereas giraffe and kudu were preferentially found in the Main Camp area, vegetation type did not influence habitat selection for these two browser species. Giraffes mainly eat *Acacia* spp. (du Toit *et al.* 1990; Parker & Bernard 2005), which is likely to be present in different vegetation types especially in grasslands and open bushlands which are dominant in Main Camp and Ngamo areas (Rogers 1993). This might explain why we do not find any pattern of habitat selection for that species at that scale. A limit of our study is that when herbivores were foraging, we do not know on which plant species they were foraging, and the available vegetation map is mainly a vegetation structure map so information on plant species composition is lacking. For both impala and zebra, vegetation type influenced their habitat selection. Impala selected more intensively grasslands and bushlands, which makes sense because impala is a mixed feeder spending the rainy season grazing, and the dry season browsing. Zebra selected more intensively grasslands and open bushlands, the two most open habitats where it is easier to graze.

Finally, for impala, for which the elephant-related explanatory variable was in the best habitat selection model, the selection strength of a habitat type increased with the intensity of utilization by elephants, which was contrary to our expectations. This result does not support a hypothesis of a competitive effect of elephants on impalas. It does support however results from previous works in the Chobe ecosystem, Botswana, where elephant-induced

browsing lawns have been revealed suggesting a short term facilitative effect of elephants on other browsers in non-Mopane woodlands (Rutina *et al.* 2005; Makhabu *et al.* 2006). The fact that we did not show an impact of elephant on other herbivore habitat selection does not mean that elephants have no competitive effect at all as this may occur at a finer scale of the niche (trophic resources, resource items) or temporally. Some studies highlighted the fact that there is a very small resource overlap between elephants and other herbivore species for the plant that they browse on at the Chobe riverfront in Botswana (Makhabu 2005). In fact, there is a differentiation in the species eaten by herbivores along a C3/C4 gradient (Tilman & Borer 2015). If there is a resource partitioning, herbivores are not eating the same species as their competitor and that allows coexistence between them and no habitat segregation (Tilman & Borer 2015). With our data, we cannot assess if there is resource partitioning between herbivores and elephants, as we do not have the information about what trophic resource they eat.

Finer scale spatial segregation

The goal of this last section was to determine if there is spatial segregation between elephants and other herbivores at a finer scale than the habitat, which would be linked to interference competition mechanisms. In African savanna large mammalian communities, studies on interference are rare and the few existing studies were carried out at waterholes. They revealed temporal segregation between elephants and other herbivore species (Valeix *et al.* 2007), and fine-scale spatial segregation for some species only at the onset of the dry season (Ferry *et al.* 2016). Here, we expected a negative impact of elephants on other herbivores due to interference in habitats away from waterholes (as we focused on the habitats that species used to forage), which would result in a spatial avoidance of elephants by other herbivores at fine scales away from waterholes (Chesson 2000; Amarasekare 2003). We were not able to detect any segregation from elephants, and we did not highlight any spatial aggregation to elephants either.

Conclusion

In this study, we focused on herbivore spatial distribution patterns and interpreted our results in the light of possible interactions with elephants. Overall, we did not find any spatial segregation pattern between elephants and other herbivores (whether at the landscape scale, at the habitat scale or at a finer scale). Our results therefore do not support our predictions based on a competitive effect of elephants on other herbivores. This can arise from the absence of competition between elephants and other herbivores (facilitation even seems to be suggested between elephants and impalas from our results on habitat selection) or because competition occurs along niche axes that are not investigated in this work (e.g. resource items, time). This work underlines the importance of scales when studying spatial patterns and inferring what may cause them.

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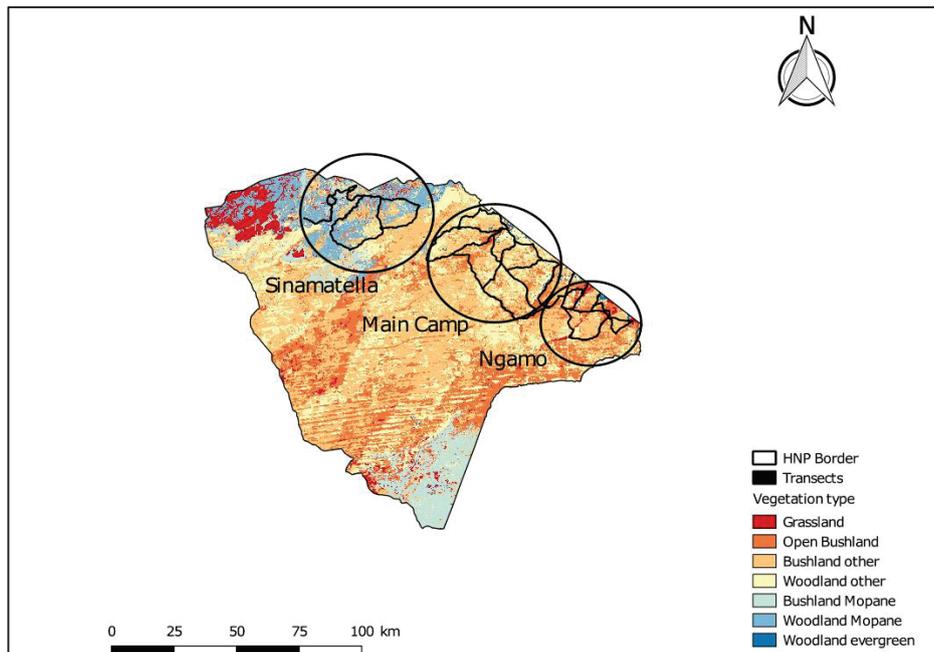
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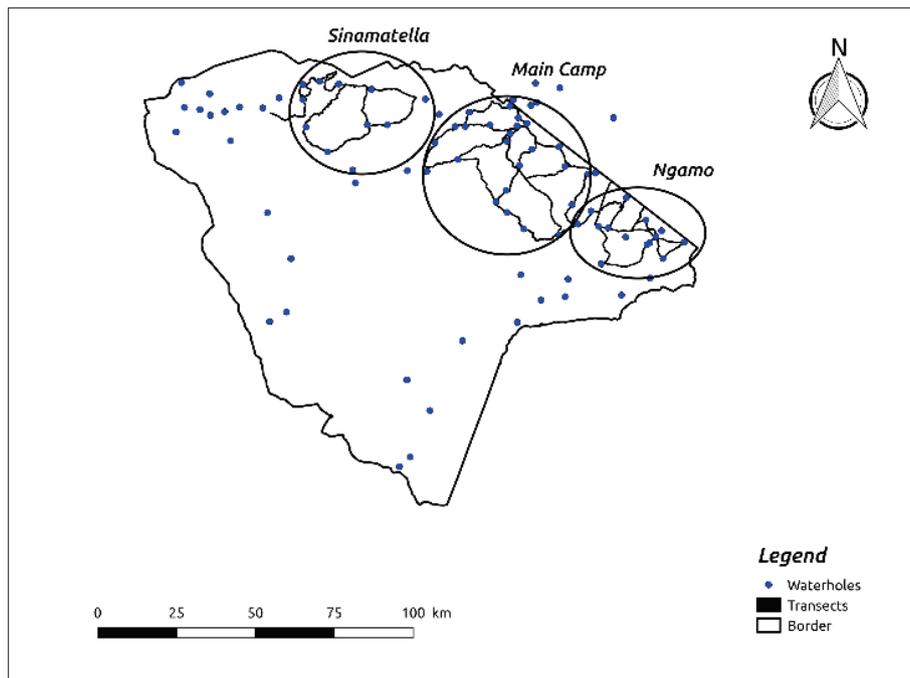
Supporting information

Appendix 1: A) Raster layer used to extract environmental data (QGIS software). It represents the seven general types of habitat (i.e. vegetation types) that can be found in the park. The border of the park and the transects of the study site are represented in black. The three areas of the study site, Sinamatella, Main Camp and Ngamo are circled. At this level the differential composition in vegetation type between Sinamatella and Main Camp and Ngamo is notable. Indeed, the Mopane habitat type (Bushland Mopane and Woodland Mopane) appears to be dominant in Sinamatella area. B) Map of Hwange National Park, Zimbabwe, with transects (black lines), the artificial waterholes (blue dots), and the three study areas (black circles). The map was created with the QGIS software.

A)

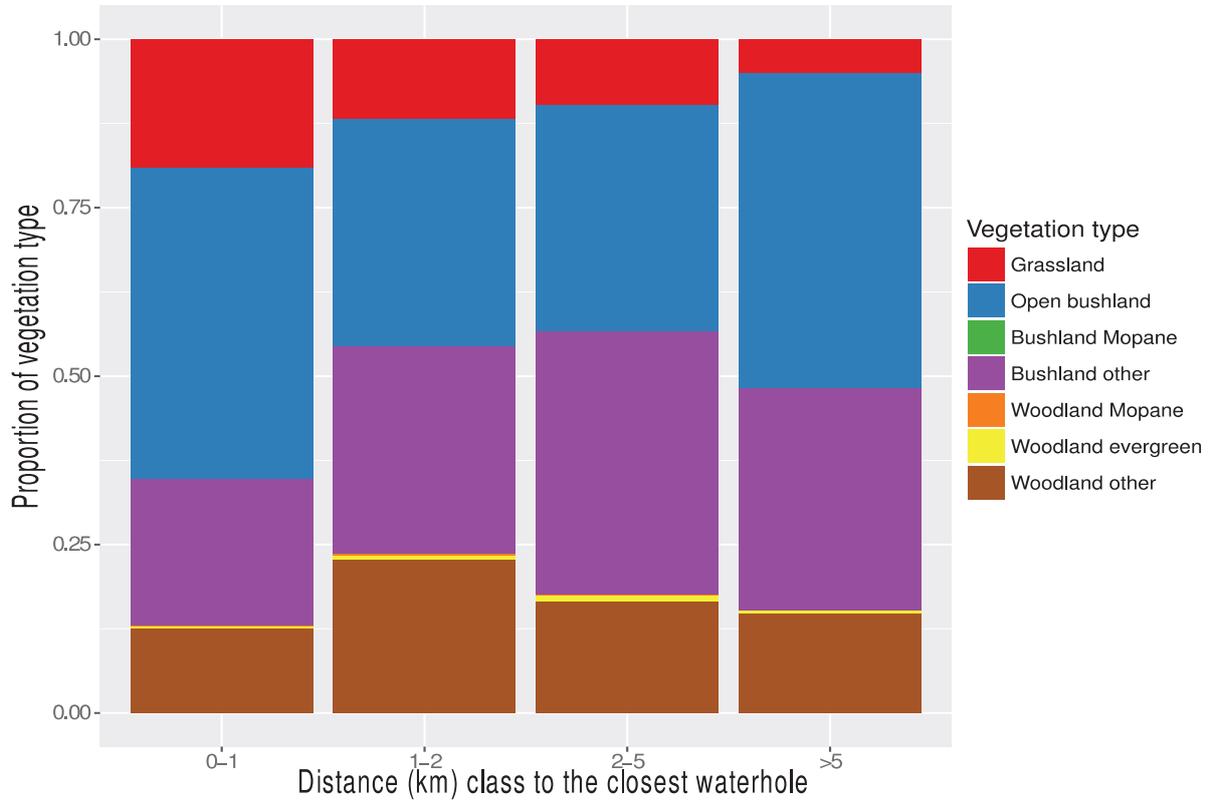


B)



Chapter 4 : Assessment of food competition between African elephants and other large herbivore species through spatial segregation at multi-scale level

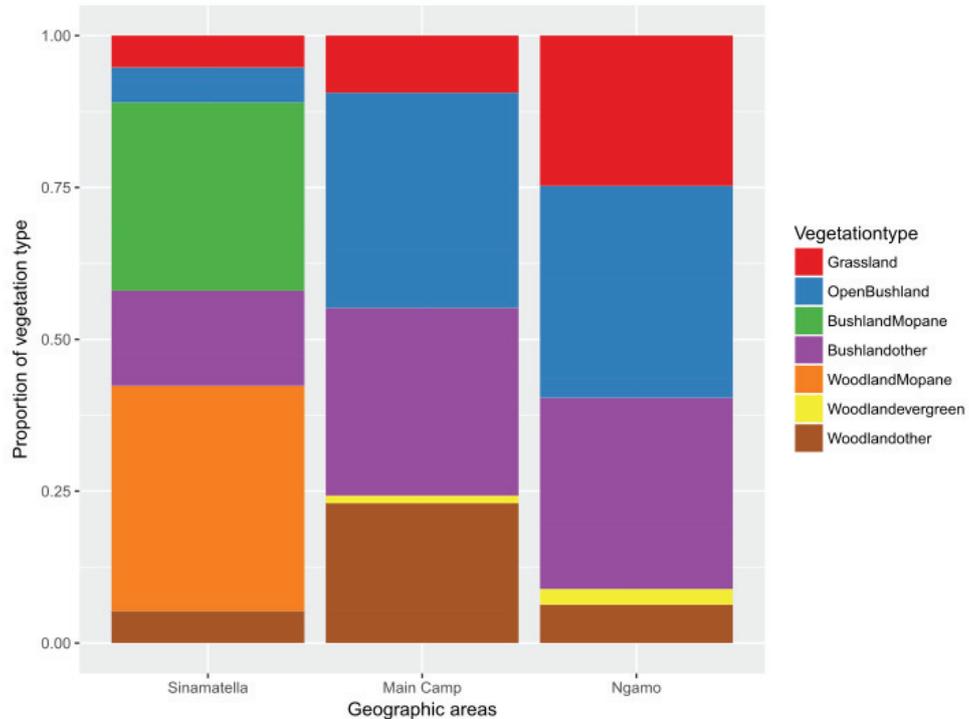
Appendix 2: barplot of the proportion of each habitat type according to distance classes to a waterhole. Vegetation types are sorted along a gradient of habitat's openness, from the more open (Grassland) to the more closed habitat (Woodland-other).



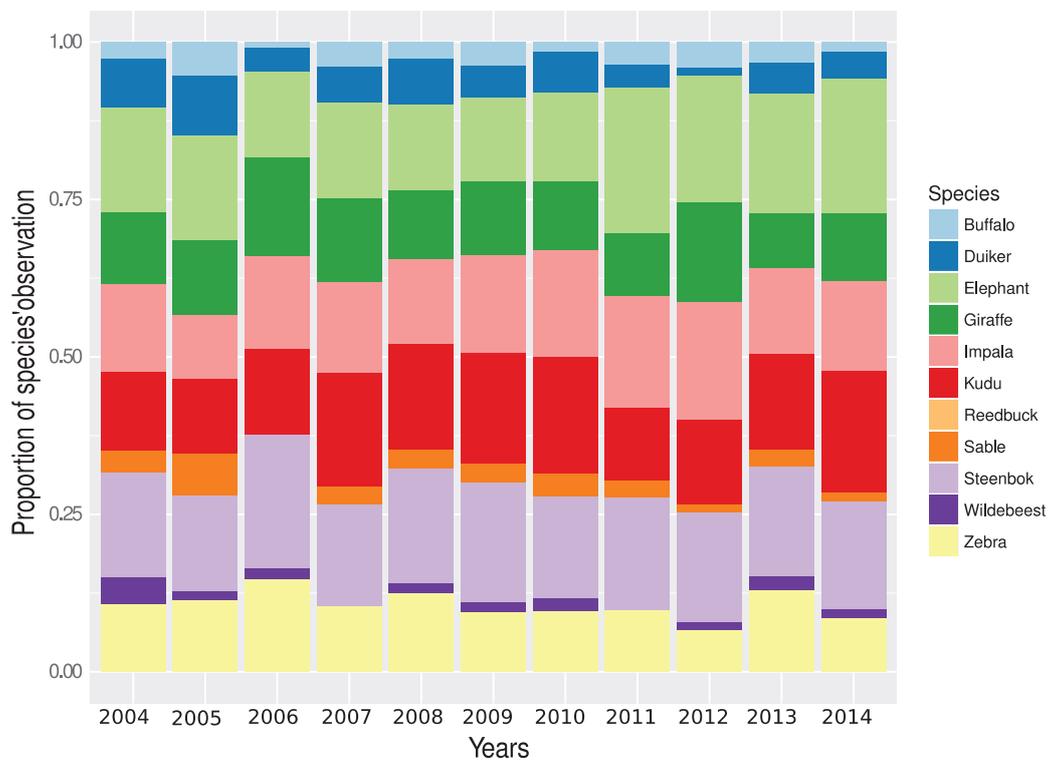
Chapter 4 : Assessment of food competition between African elephants and other large herbivore species through spatial segregation at multi-scale level

Appendix 3: A) Vegetation composition for each study area. Sinamatella area is composed of 80% of Mopane vegetation, which clearly differs from Main Camp and Ngamo areas. Although Ngamo is more open than Main Camp, the same vegetation types characterize these two areas. B) Proportion of observations for the ten most abundant herbivore species in the study site over the years of the study.

A)

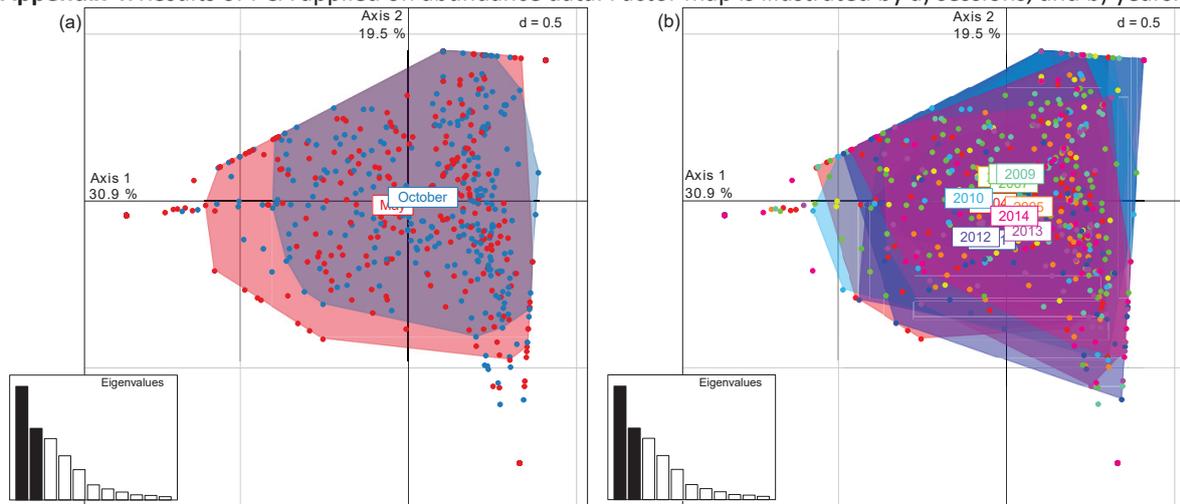


B)



Chapter 4 : Assessment of food competition between African elephants and other large herbivore species through spatial segregation at multi-scale level

Appendix 4: Results of PCA applied on abundance data. Factor map is illustrated by a) sessions, and b) years.



Chapter 4 : Assessment of food competition between African elephants and other large herbivore species through spatial segregation at multi-scale level

Appendix 5: Table of the four best habitat selection models in Main Camp and Ngamo areas for A) elephants, B) giraffes, C) kudus, D) zebras, and E) impalas. The best model is indicated in bold. Distance to water is the distance to the closest waterhole, season represents the two sampling sessions (May and October), and vegetation stands for vegetation structure types. If there are models with a delta BIC value inferior to two, a model averaging was performed to estimate average parameters.

A)	Explicative variables	BIC	Delta BIC	Weight
	null	949.2	0.00	0.880
	distance to water	954.1	4.86	0.077
	season	955.7	6.52	0.034
	vegetation	959.7	10.46	0.005

B)	Explicative variables	BIC	Delta BIC	Weight
	null	488.3	0.00	0.653
	distance to water	490.8	2.54	0.184
	elephant_use	492.5	4.20	0.080
	season	494.1	5.85	0.035

C)	Explicative variables	BIC	Delta BIC	Weight
	distance to water	488.3	0.00	0.654
	null	490.8	2.49	0.188
	distance to water + elephant_use	492.5	5,16	0.050
	distance to water + season	494.1	5.20	0.049

D)	Explicative variables	BIC	Delta BIC	Weight
	distance to water	488.3	0.00	0.654
	null	490.8	2.49	0.188
	distance to water + elephant_use	492.5	5,16	0.050
	distance to water + season	494.1	5.20	0.049

E)	Explicative variables	BIC	Delta BIC	Weight
	distance to water + elephant_use * vegetation	291.2	0.00	0.406
	distance to water	291.5	0.30	0.350
	distance to water + vegetation	295.2	3.97	0.056
	distance to water + elephant_use	295.7	4.53	0.042



AXIS 3.

Indirect effect of elephants on lion foraging behaviour through vegetation modification



« Quand l'éléphant trébuche, ce sont les fourmis qui en pâtissent. »

Proverbe africain

Chapter 5: Effects of long-term exposure to high elephant densities on semi-arid African savanna woodland structure, species composition and functional traits. Is savanna woodland attaining a new equilibrium state?

Article *in prep.* for submission in *Functional Ecology*

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Abstract

Herbivory is known to strongly shape African savanna ecosystems. Among herbivores, the effect of the African elephant *Loxodonta africana*, considered as a megaherbivore (>1000 kg) and an ecosystem engineer, on the vegetation was extensively studied. Debate are still ongoing about the negative or positive effect elephants could have on diversity and structure which seems to be context-dependent. However, very few studies assessed the long-term dynamic of the vegetation constantly exposed to high elephant densities. Elephants impacts on woody vegetation and correlated effect on structure, species and functional trait composition were monitored during a long period of high elephant density (2001, 2008 and 2015) in Hwange National Park, Zimbabwe. We showed that elephant impacts (mainly broken trunk) accumulated over the years but was not correlated to changes neither in dominant species neither in mean functional trait. However, we observed changes in composition of rare species. Finally, we did not reveal strong changes in the vegetation structure (height, crown diameter and stem girth), except in the 50-200 cm height layer where the crown diameter was highly reduced in almost all vegetation type considered. Our study suggests that under high elephant pressure, impacts on woody vegetation accumulate but do not lead to global modification of the vegetation.

Key-words: vegetation dynamics, species and functional trait composition, vegetation structure, high African elephant density, ecosystem engineer.

Introduction

Savanna ecosystems are complex and heterogeneous landscapes with a high diversity of habitats and plant species shaped by different interacting factors such as soil, rainfall, frost, fire and herbivory (Sankaran *et al.* 2005). Due to their very high plant biomass consumption (Owen-Smith 1988), African elephants *Loxodonta africana* are known to exert strong top-down control on the vegetation in savanna ecosystems (see reviews in Kerley and Landman 2006, Guldemond and van Aarde 2008). They are generalists in their diet with a wide range of food items (grass, leaves, twigs, roots, bark; Barnes 1982, O'Connor *et al.* 2007), and have the physical potential to significantly impact trees (from pollarding to breaking trunks and uprooting trees, O'Connor *et al.* 2007). For all these reasons, African elephants are considered as ecosystem engineers (*sensu* Jones *et al.* 1994) and have the ability to significantly alter their environment.

Adult African elephants are virtually immune to natural predation (Sinclair *et al.* 2003), but because of their body size and the growing demand for ivory, they are particularly vulnerable to human threats (e.g. habitat fragmentation, human-wildlife conflicts, hunting, poaching; Macdonald *et al.* 2013). African elephant populations have changed tremendously in the past century with some populations collapsing due to poaching for ivory (Chase *et al.* 2016) while others in well protected populations have increased to very high densities (Blanc *et al.* 2005). Increasing elephant populations have led to profound changes in African savanna ecosystems (Skarpe *et al.* 2004). Concerns have been raised regarding elephant-induced vegetation changes as they can influence a wide range of processes, such as grass-tree coexistence (Sankaran *et al.* 2005), fire dynamics (Langevelde *et al.* 2003), habitat selection by other species (Valeix *et al.* 2011), animal biodiversity (Pringle 2008), and predator-prey relationships (Loarie *et al.* 2013).

Several previous key studies have shown elephants to negatively (*sensu* Guldemond & van Aarde 2008) affect vegetation structure, diversity and composition (the so-called “elephant problem”; Laws 1970, Caughley 1976), however it is now recognized that elephant effects are complex and dependent on the spatio-temporal scales considered (Guldemond & van Aarde 2008, Coverdale *et al.* 2016). Many of these studies showing elephants to exert

strong negative effects on the vegetation were conducted in small and closed reserves (O'Connor & Page 2014) in contrast to open systems where elephants naturally use wide areas to roam (Loarie *et al.* 2009). These results are difficult to generalize as long-term studies in fenced areas seem to show more negative impacts from elephants than studies in non-fenced areas (Guldemon & van Aarde 2008). Furthermore, many of these previous studies were either once-off (Ben-Shahar 1993) or short-term (Ben-Shahar 1998) and failed to assess the long-term vegetation dynamics. Longer-term studies that have been conducted were often carried out during periods of changing elephant populations (Conybeare 1991, Mosugelo 2002, van de Vijver *et al.* 1999). The long-term effects of consistently high elephant densities on vegetation dynamics are still not clear. Debates are still ongoing, and given the rapid changes occurring in many elephant populations, there is an urgent need to better understand how elephants affect woody vegetation (species composition, functional traits and structure) over the long-term in large natural savanna ecosystems.

To our knowledge, few studies have assessed the long-term cumulated impacts of high elephant densities on community compositions and structure in large areas, and even fewer have focused on the functional trait compositions of the woody plant communities (Wigley *et al.* 2016). In this study, we use field data from twelve long-term (15 years) vegetation plots set up in areas of very high elephant densities in Hwange National Park, Zimbabwe, to specifically test for the long-term effect of consistently high African elephant densities on savanna woodland species and trait composition, as well as structure. With an estimated average elephant population density > 2 individuals.km⁻¹ (Chamaillé-Jammes *et al.* 2008) over the last two decades, Hwange National Park, offers an excellent opportunity to study the long-term cumulated effects of elephant on woody vegetation.

Previous studies have found that elephants feed selectively on woody plant species (Guy 1976, Viljoen 1989, O'Connor *et al.* 2007), with food selection being mainly driven by plant functional traits such as leaf chemistry (Jachman & Bell 1985, Jachman 1989, Holdo 2003). If we assume that most of elephant impacts on trees (e.g. broken trunk, uprooted tree) result from foraging processes and not from other behaviour (e.g. musth for the male, Poole 1987), we expect elephant impacts to be greater in preferred plants (hypothesis ES1 Table 1). Further, if elephants select plant species according to their functional traits, e.g. leaf nutrient

content, the intensity of impact is expected to be related to these traits (hypothesis ES2 Table 1). As consequences of this continuous selection, we expect the woodland plant community to change, especially because woody plant species are also expected to be differentially vulnerable to elephants (O'Connor *et al.* 2007). This raises concerns about plant diversity losses as well as landscape changes (Owen-Smith *et al.* 2006, Landman *et al.* 2007, O'Connor & Page 2014; Coetsee & Wigley 2016). Holdo (2007) used a simulation model to investigate the possible effects of elephants, fire and frost on vegetation composition during a 50-year period. In his model, Holdo (2007) showed a shift of the community composition towards species highly resistant to disturbances, mainly unpalatable scrub vegetation such as *Ochna pulchra* and *Erythrophleum africanum*. We expect that the continuous pressure by elephant has selected communities dominated by unpalatable species or species responding well to damages (hypothesis CS1 Table 1). If elephants select woody plant species according to their functional traits, with even potential extirpation (O'Connor *et al.* 2007), the loss of diversity in the functional trait composition of the community (hypothesis CS2 Table 1) could have important consequences for the ecosystem functioning (Augustine & McNaughton 1998, Diaz & Cabido 2001).

For structural changes, the effects of elephant can be major in these semi-arid savanna woodlands, mostly through decrease in the total basal area, crown area and tree density (e.g. Conybeare 1991, Mosugelo 2002, Holdo 2007). According to Holdo (2007), elephants were not expected to convert woodland to complete grassland as often suggested/observed in East African savannas (Beuchner & Dawkins 1961, Laws 1970), but revert and maintain the vegetation at a scrub phase. Holdo (2007) suggested an asymptotic relationship between elephant impacts on vegetation structure and elephant density, which allows to predict a structural change in favour of shrub canopy cover as well as lower total tree cover (hypotheses S1 and S2, Table 1). This change in structure could be associated with changes in the availability of resources such as refuges for some species (Pringle 2008), or food items for other browsing species (Fornara & du Toit 2007), as well as habitat features important for predator-prey relationships (e.g. visibility, Tambling *et al.* 2013). We therefore tested specifically if the most significant changes in vegetation structure occurred in the height layer functionally critical to other large mammals (i.e. the 50-200 cm height layer, hypothesis S3, Table 1).

Chapter 5: Effects of long-term exposure to high elephant densities on semi-arid African savanna woodland structure, species composition and functional traits

Table 1: Hypotheses on effect of elephant impacts on vegetation structure, species composition and functional trait composition.

	Hypothesis	References	Analysis
<u>El – Elephant Impacts</u>			
<i>El – Elephant impacts</i>	Elephants' impacts increased over the study period		Mixed logistic model
<u>ES – Elephant Selection</u>			
<i>ES1 - Species</i>	Elephants select woody plant species.	Guy (1976), Vlijoen (1989)	Jacob's index
<i>ES2 - Functional trait</i>	Plant selection by elephants is linked to plant functional traits	Jachman & Bell (1985), Holdo (2003), Olivier (1978)	Mixed logistic model
<u>CS – Community Shift</u>			
<i>CS1 – Species composition</i>	Elephant impacts lead to a shift in woody plant species composition	Holdo (2007), O'Connor <i>et al.</i> 2007	Co-inertia analysis
<i>CS2 – Functional trait composition</i>	The species composition shift, related to elephants' impacts, is associated to a shift of the functional trait composition	Augustine & McNaughton (1998)	RLQ
<u>S - Structure</u>			
<i>S1 – Tree abundance</i>	Tree abundance is decreasing over the study period	Conybeare (1991)	Paired Wilcoxon's test
<i>S2 – Height, Stem diameter, Crown Surface (Trees > 200 cm)</i>	Elephants open woody habitats by decreasing the height, stem diameter and the crown diameter of trees	Holdo (2007)	Unilateral Jonckheere's test
<i>S3 - Crown Surface (Trees < [50, 200] cm)</i>	Elephants alter vegetation structure in the layer important for predator-prey relationships (50-200 cm height)		Bilateral Jonckheere's test

Material and methods:

Study site

Hwange National Park (HNP hereafter) covers an area of 14 600km², extending from 18°30' to 19°50'N and from 25°45' to 27°30'E. The study took place in the Main Camp area, in the North-eastern part of HNP in 2001, 2008 and 2015. Rainfall is markedly seasonal, from November to March, with an annual mean of \approx 600 mm and a range of 324 to 1160 mm (Appendix 1). The mean annual temperature is 20.3°C. October is the hottest month with a mean daily maximum of 33.2°C, and July is the coldest with a mean daily minimum of 4.1°C. In the Main Camp area, the four dominant vegetation types monitored are *Baikiaea plurijuga* woodland, *Combretum* bushed-woodland, *Colophospermum mopane* bushland and *Acacia / Terminalia* bushed-woodland (Rogers 1993). Elephant population in Main Camp area were estimated at more than 2 individual / km² and stayed around this level until 2015 (Chamaille-Jammes *et al.* 2008, Fritz 2015).

Data

In each of the four vegetation types, three plots of 25x 50 m were monitored between May and August in 2001 and 2015. In 2008, only plots in the *Baikiaea plurijuga* woodland and *Combretum* bushed-woodland were monitored. Each plot was delimited and marked by two concrete blocks: one block was placed in the middle of the plot (GPS coordinates are provided in Appendix 2), the other block marked the north-western corner. Each plot was defined in area assumed to be intensively used by elephants in late dry season (close to permanent waterholes, mean distance to water = 1271 m, Table S1).

Vegetation structure, composition and elephant impacts

To determine the vegetation species composition and structure an exhaustive inventory of woody plants was conducted in each plot. For each woody plant, we recorded the species, height, two perpendicular measures of the crown diameter to calculate an average crown diameter and stem diameter measured at breast height (DBH hereafter) and recorded for woody plants with a stem girth > 6 cm. For individuals with a height <1.5m, heavily damaged and/or with several stems, diameter was measured on the largest stem, at the height of the first twig. In addition, for each plant the degree of utilization by elephants was recorded through several binary variables: trunk broken, twigs browsed, uprooted, root

used, bark removed (between 1.5m and 5m in height, according to the height potentially reachable by elephant, Höft and Höft, 1995) and dead tree. If twigs were browsed or bark removed on the plant, a quantitative assessment of the impact was recorded (percentage of twigs browsed/ bark removed). A last variable was “Used” if at least one elephant impact was present on the plant. The different impacts were qualified as old or young (less than one-year-old, see Coetzee *et al.* 1979 and Ben-Shahar 1998 for the age classification method).

Functional traits

Six functional traits were measured: three physiological traits; percentage of leaf nitrogen (N), carbon (C) and phosphorous (P) and three anatomical traits; the leaf dry matter content (LDMC), the stem density (SD) and the type of spinescence (no spines, spine or thorn). Functional traits data were gathered from a combination of sources which included the TRY database, the Global ¹⁵N Database (Craine *et al.* 2009), the Seed Information Database, TROBIT West Africa (Domingues *et al.* 2010), The Americans N&P Database (Kerkhoff *et al.* 2006), Global Wood Density Database (Zanne *et al.* 2009), William Bond’s database. Species for which data were missing were filled by a fieldwork session in May, 2016, according to the methods outlined in Wigley 2013. Functional trait data were gathered for a total of 26 species which accounted for 90% of the standing abundance in the plots (Appendix 3).

Analyses

All analyses were performed using R Software (R Development Core Team, 2004).

Dynamics of elephant impacts

To evaluate whether elephant impacts on the woody vegetation increased over the study period (hypothesis EI, Table 1), we performed a mixed logistic model (using the “lme4” package, Bates *et al.* 2015), with the binary variable “Used” as the response variable (1= “Yes”, 0= “No”), the variable “Plot” as a random effect and the variable “Year” as a fixed effect.

Species and functional trait preference

Species preference - For each species, a Jacobs’ index (Jacobs 1974) was calculated (Eq. 1) for each plot and for each year, based on the variable “Used”, to get a descriptive overview of the differential utilization of the vegetation species by elephants (hypothesis ES1, Table 1).

$$D_{ij} = \frac{r_{ij}-p_{ij}}{r_{ij}+p_{ij}-2r_{ij}p_{ij}} \quad (\text{Eq. 1})$$

Where r_{ij} is the proportion of the total number of plants used by elephant for the species i in the combination plot-year j and p_{ij} is the proportional availability of the species i in the combination plot-year plot j . Jacobs index ranges between -1 (highly avoided), 0 (used in proportion to availability) and 1 (highly selected). A weighted mean of this Jacob's index was calculated for each species (Eq. 2).

$$W_i = \frac{1}{N_i} \sum_1^j D_{ij} n_{ij} \quad (\text{Eq. 2})$$

Where N_i is the total abundance of the species i , D_{ij} is the Jacobs index and n_{ij} the abundance of the species i in the combination plot-year. Only species with at least 30 individuals were kept to calculate the index representing 34 species in total for this analysis. Further, we assessed if the weighted Jacob's index was correlated to the difference of abundance between 2001 and 2015.

Functional trait preference - To evaluate whether elephants select for functional traits (hypothesis ES2, Table 1), we performed a linear model with the weighted Jacob's index as the response variable and the six functional traits as fixed effects.

Species and functional trait composition dynamics

Species composition dynamics - We performed a co-inertia analysis (Dolédec & Chessel, 1994) to evaluate the link between the two tables describing species composition and elephant impacts (per plot per year, hypothesis CS1, Table 1). Species abundances were log-transformed and within-class analyses were applied prior to co-inertia analysis to remove the effect of 'plot' on the variations in species compositions or elephant impacts. Analysis were performed with the *ade4* package for R (Dray and Dufour 2007).

Functional trait composition dynamic - We applied a partial-RLQ analysis (Wesuls *et al.* 2012), using the "ade4" package (Dray & Dufoure 2007) to determine how functional trait composition varied with elephant impact (Hypothesis CS2, Table 1) after controlling for plot differences. This allowed us to identify if and which types of elephant impacts mainly drive differences in functional traits among communities. Rao's quadratic entropy index (RQE) was also calculated for each combination plot-year to evaluate the functional trait composition diversity dynamics, as follows:

$$RQE_i = \sum_{j=1}^s \sum_{k=1}^s d_{jk} p_j p_k$$

Where i is the i -th combination plot-year, s is the number of species in the plot-year; p_j and p_k are the proportion of respectively j -th and k -th species in the plot-year, d_{jk} is the dissimilarity of species j and k ($d_{jj} = 0$, i.e. dissimilarity of each species to itself is zero).

Effect of elephant impacts on vegetation abundance and structure

Vegetation abundance - A paired Wilcoxon test was performed comparing species abundances between 2001 and 2015 in all plots, with the simple alternative hypothesis of a difference between the two years (Hypothesis S1, Table 1).

Vegetation structure - For these analyses, all trees below 50cm height were removed as we assumed that they did not substantially affect the structure of the habitat and would therefore not influence predator-prey relationships. Furthermore, these small plants can bias analyses on height, stem diameter and crown surface. We distinguished the stratum above 200 cm height and the one between 50 and 200 cm height for the crown surface as this variable could have a particular effect on visibility for herbivores and predators. In each plot, for the height, the stem diameter at breast height and the crown surface (> 200 cm height), a non-parametrical Jonckheere test of global trend was performed (Jonckheere 1954) with a decrease over time as the alternative hypothesis (hypothesis S2, Table 1). For the variable "Crown Surface – 50-200cm height" the alternative hypothesis was a simple difference (hypothesis S3, Table 1).

Results

Dynamics of elephants impacts

The proportion of plants used by elephants increased over the study period (Fig. 1) in 2008 and in 2015 ($\beta_{2001-2008} = 0.53$, $z_{2001-2008} = 9.2$, $\beta_{2001-2015} = 0.82$, $z_{2001-2015} = 21.3$), with an overall increase in the proportion of broken plants. Over the year, the main impact by elephants was trunks broken with 87% of the "Used" trees in 2001, 85% in 2008 and 88% in 2015. The other impacts were browsed twigs with 21 % of the used plant being browsed in 2001 (37% in 2008 and 58% in 2015), and bark utilization with only 1% of the used plant having bark partially removed in 2001 (2.7% in 2008 and 2.6% in 2015). Uprooted trees and root utilisation were almost never recorded. Indeed, only 12 individual plants uprooted were

observed in 2001, 2 in 2008 and 5 in 2015 and only 1 plant in 2001 and 1 plant in 2015 were observed with root utilised.

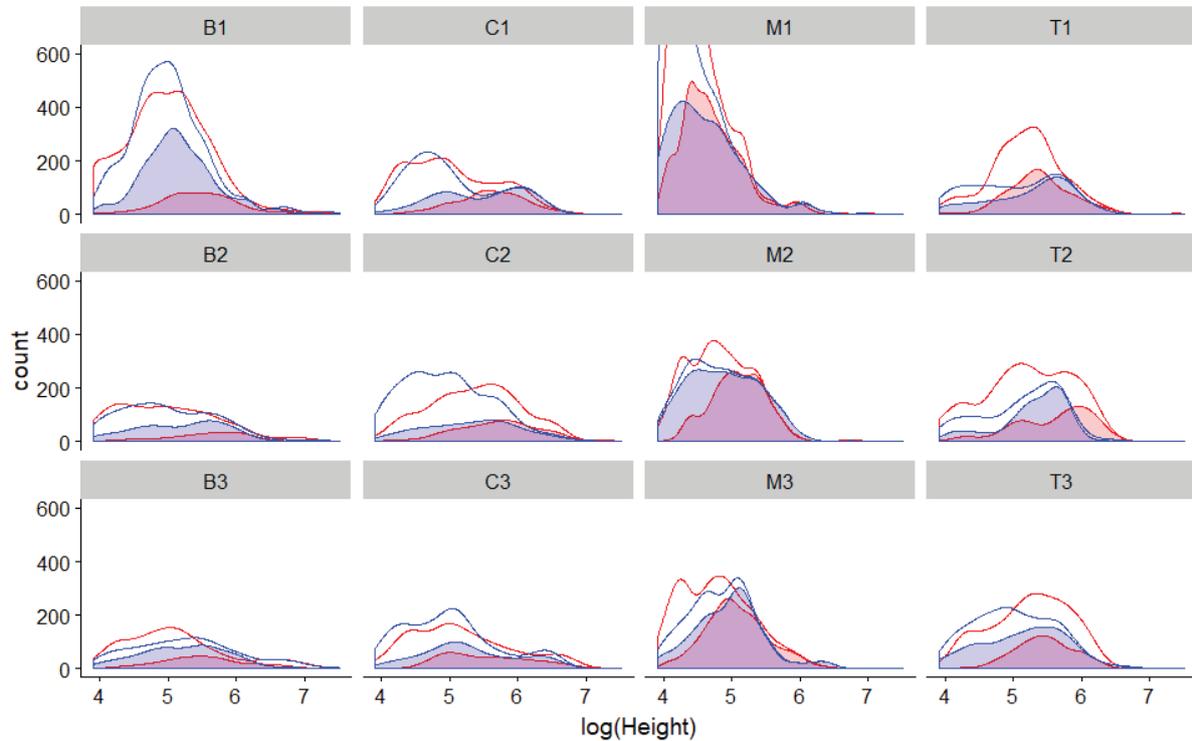


Figure 1: Height density distribution for the three plots monitored (1, 2 and 3) for each of the four vegetation types (B = *Baikiaea plurijuga* woodland, C = *Combretum* bushed-woodland, M = *Colophospermum mopane* bushland and T = *Acacia/Terminalia* bushed-woodland). Red density distributions represent 2001 and blue density distributions represent 2015, for visual convenience 2008 was not represented here. Simple lines represent density distributions for all plants whereas full-coloured density distribution represents plants used by elephants.

Species and functional trait preference

Species preference

Of the 34 plant species considered, *Colophospermum mopane* was the only species to be highly selected for by elephants (Jacob's index >0.5 , Fig. 2.a), while 11 other species were slightly selected for (Jacob's index >0 but <0.5). Nine species were highly avoided (Jacob's index <-0.5) and 12 were slightly avoided (Jacob's index <-0.5 but <0). There was no significant relationship between the change in abundance between 2001 and 2015 of each species and the Jacob's index of each species ($t=1,7$, $df = 32$, $cor = 0.29$, Fig. 2b).

Functional trait preference

Elephants avoided species with higher leaf N concentrations ($\beta = -0.26$, $z = -2.65$, $p = 0.01$). They did not select for nor avoid any of the other considered traits.

Chapter 5: Effects of long-term exposure to high elephant densities on semi-arid African savanna woodland structure, species composition and functional traits

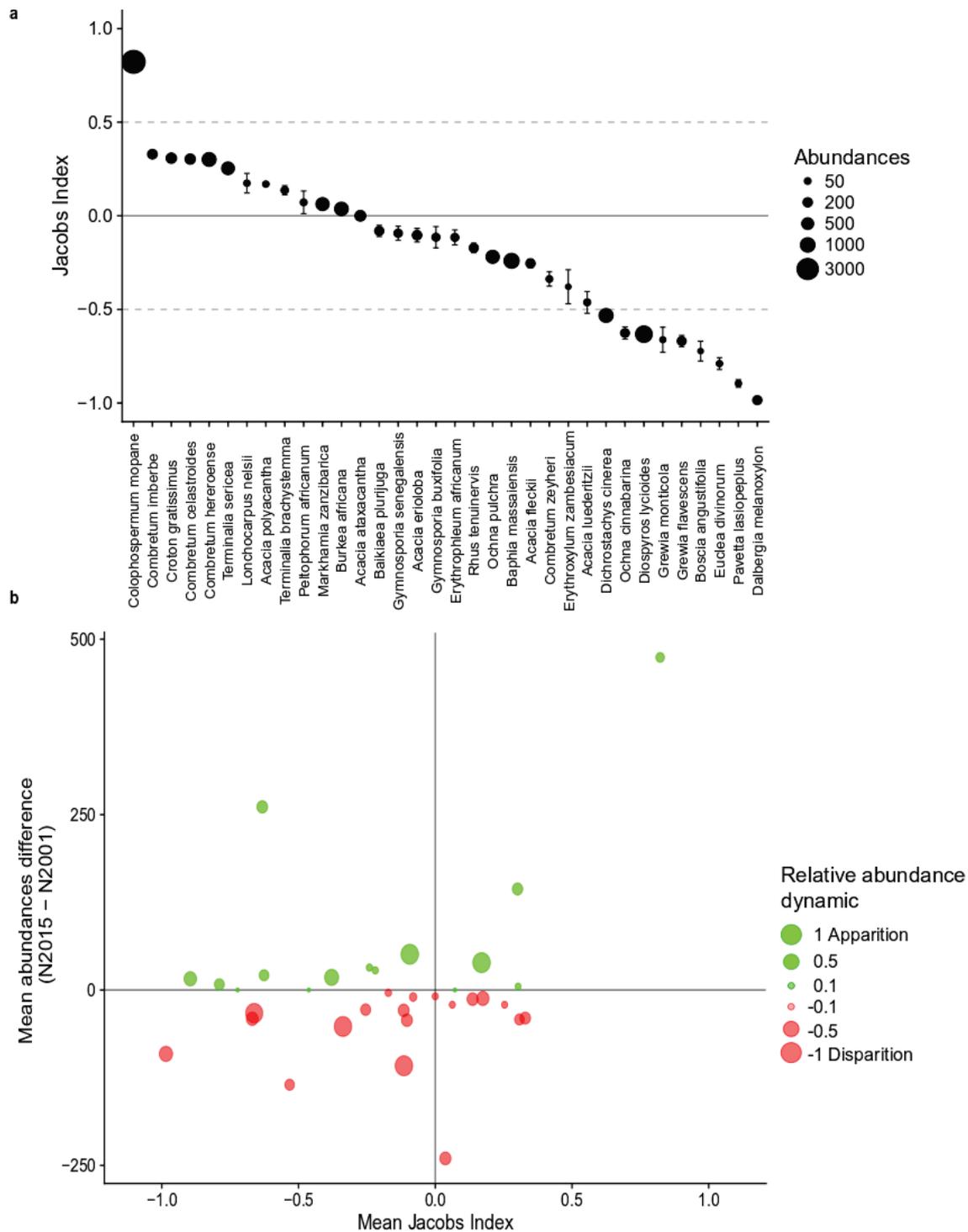


Figure 2: a) Weighted mean Jacob's selection index per species, with error bar corresponding to standard error. Jacob's index ranged from -1 to 1, representing respectively a negative and a positive selection for the species. b) Relationships between the weighted mean Jacobs index and temporal dynamics of each species (absolute difference between 2015 and 2001 on y-axis and relative difference index with the size and color of points).

Functional trait composition dynamics

When looking at the functional trait composition, no temporal change was detected (permutation test 1 $p > 0.05$, permutation test 2 $p = 0.78$). After variations among plots had been removed, there was no temporal shift in the functional trait composition of the vegetation resulting from an increase in elephant impacts. In addition, when looking at the Rao's quadratic entropy index, no change in the functional trait diversity was observed over the years.

Effect of elephant impacts on vegetation abundance and structure

Vegetation abundance

No significant difference of plant abundance was observed between 2001 and 2015 for all species combined ($W = 38$, $p = 0.97$, see Appendix 4 for detailed abundances).

Vegetation structure

There was a slight alteration of the vegetation structure when considering the height (in 4 plots the height decreased, see Table 2 for the height median in 2001 and 2015 for these plots, Fig. 1), but almost no change was observed when looking at the DBH (Table 2, Table S4) and the crown surface for >200cm height trees (Table 2, Fig. 4). However, a strong decrease of the crown surface for trees between 50-200 cm height was observed in almost all plots, except in Mopane plots where an increase was observed (Table 2, Fig. 4).

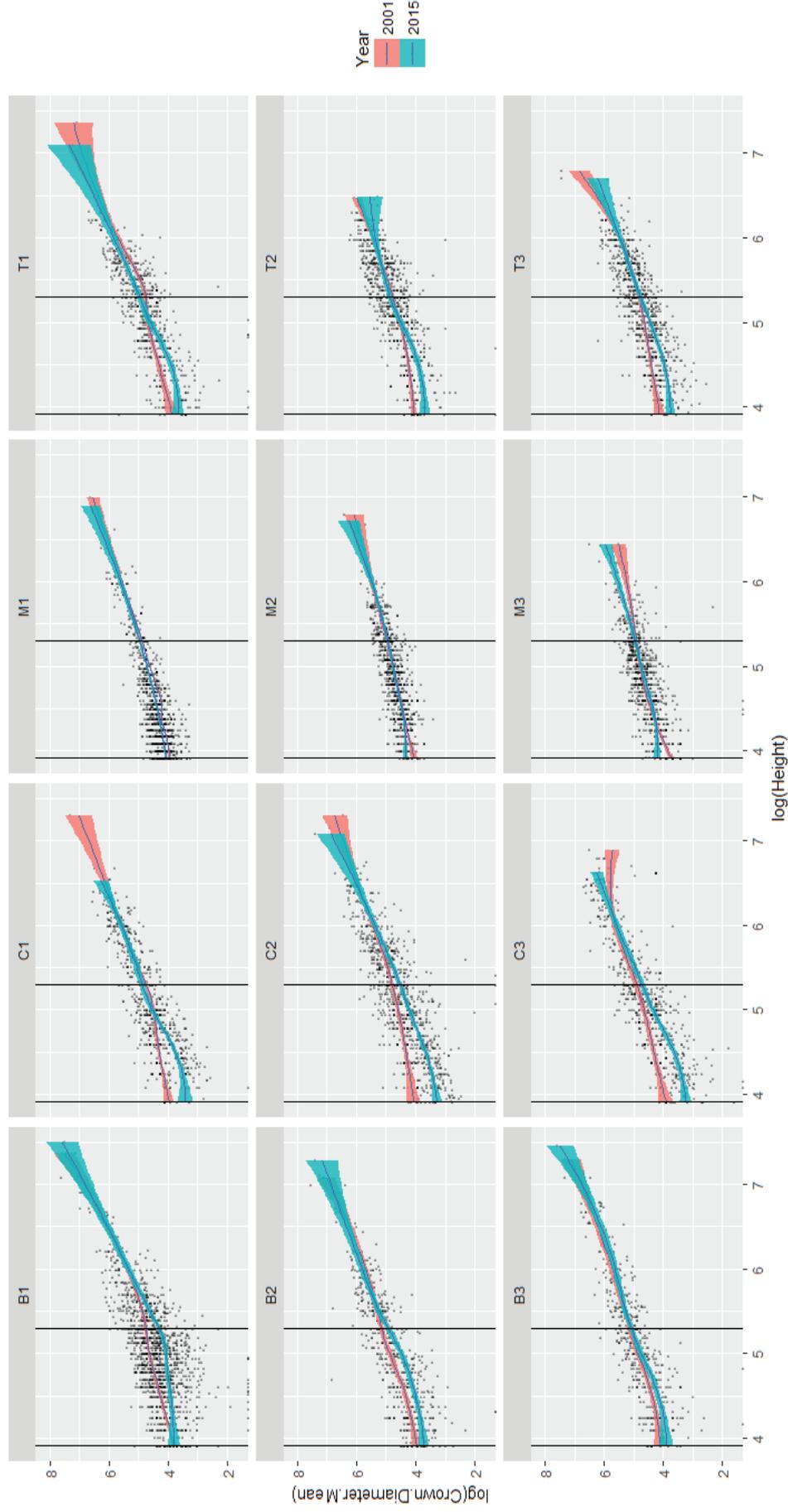


Figure 4: Representation of the log-transformed mean crown diameter function of log-transformed height of all plants for the three plots monitored (1, 2 and 3) for each of the four vegetation types (B = *Baikia plurijuga* woodland, C = *Combretum* bushed-woodland, M = *Colophospermum mopane* bushland and T = *Acacia/Terminalia* bushed-woodland). Are represented predicted values with confidence interval (using local polynomial regression fitting “loess” smoothing method) in red for 2001 and in blue for 2015. Vertical lines represent the log-transformed 50 cm and 200 cm thresholds.

Table 2: Results from analyses on vegetation structure. For each vegetation type and each plot, the dynamic of each structural variable was assessed with a Jonckheere's test, with the alternative hypothesis as a decrease of the structural characteristics over the study period except for the variable "Crown Surface (m²) 50-200 cm height", where the alternative hypothesis was a simple difference. Only significant results are represented ($\alpha = 0.05$) with the median value of the structural characteristics in 2001 and in 2015. * represents the particular case of the *Mopane* plots where an increase of the "Crown Surface (m²) 50-200 cm height" was observed.

	#	Baikiaea	Combretum	Mopane	Terminalia
Height (cm)	1		H ₂₀₀₁ =220, H ₂₀₁₅ =135	H ₂₀₀₁ =80, H ₂₀₁₅ =80	H ₂₀₀₁ =200, H ₂₀₁₅ =145
	2		H ₂₀₀₁ =150, H ₂₀₁₅ =145		
	3				
Stem Diameter (cm)	1		D ₂₀₀₁ =2.86, D ₂₀₁₅ =1.67		
	2				
	3				
Crown Surface (m ²) > 200cm height	1		C ₂₀₀₁ =3 .14, C ₂₀₁₅ =2.17		
	2				
	3				
Crown Surface (m ²) 50-200 cm height	1	C ₂₀₀₁ =0.5, C ₂₀₁₅ =0.24	C ₂₀₀₁ =0.38, C ₂₀₁₅ =0.22	*C ₂₀₀₁ =0.38, C ₂₀₁₅ =0.44	C ₂₀₀₁ = 0.75, C ₂₀₁₅ = 0.29
	2	C ₂₀₀₁ =0.5, C ₂₀₁₅ =0.27	C ₂₀₀₁ =0.5, C ₂₀₁₅ =0.16	*C ₂₀₀₁ =0.5, C ₂₀₁₅ =0.72	C ₂₀₀₁ = 0.5, C ₂₀₁₅ = 0.3
	3	C ₂₀₀₁ =0.79, C ₂₀₁₅ =0.6	C ₂₀₀₁ =0.38, C ₂₀₁₅ =0.22		C ₂₀₀₁ = 0.5, C ₂₀₁₅ = 0.32

Discussion

Elephant impact dynamics

The elephant population was already high in 2001 (Chammaillé-Jammes 2008) and so were elephants impacts, showing a strong cumulated effect of elephants on all vegetation types considered, mostly through broken tree trunks. Most of the observed impacts were qualified as old whereas few were characterized as fresh, as these impacts can be observed for a long time after they appeared (e.g. broken trunk). This supports our hypothesis that the observed increase in elephant impacts is an accumulation of these over the years rather than an increase in the elephant impacts rate during the study period.

Species and functional trait preference

Among the main species present in the study plots, only *Colophospermum mopane* was highly selected for. Mopane is a species which is known to be subject to high rates of elephant utilization (Ben-Shahar 1998) and is almost exclusive in the Mopane plots (>90% of relative abundance). It is interesting to note that *Colophospermum mopane* which was the most utilized species was also the species for which we observed the strongest abundance increase. However, as *Colophospermum mopane* is known as a wind dispersed species and not as an animal dispersed species the role of elephant in this increase in abundance remains unclear, although elephants are known to be crucial in the fruit dispersion of some woody species (Campos-Arceiz & Blake 2011). Other species were clearly avoided (such as *Dalbergia melanoxylon* contrarily to what was observed in van de Vijver *et al.* 1999, Wigley *et al.* 2014). However, 70% of the 34 considered species were neither selected for, nor avoided (Jacob's index between -0.5 and 0.5) suggesting opportunistic foraging behaviour by elephants (not supporting ES1). This tendency of a generalist feeding behaviour is also observed when focusing on the selection for functional traits: contrary to other studies on elephant preferences (Jachman & Bell 1985, Jachman 1989, Holdo 2003), we did not detect associations between elephant selection and the functional plant traits measured in this study (*not supporting ES2*). However, our results corroborate previous studies at the population level of *Colophospermum mopane*. (Anderson & Walker 1974, Thomson 1975; see also Ben-Shahar & Macdonald 2002). An avoidance of species with high N leaf content was nevertheless observed in complete opposition to expected herbivore preferences (Crawley 1983, Herms & Mattson 1992, Pérez-Harguindeguy *et al.* 2003). An explanation of this surprising result could be that the

composition of N in the leaf could be associated with other functional traits (e.g. secondary metabolite compounds, Herms & Mattson 1992) which would lower the palatability of the species with high leaf N leaf content. However, we did not have the data to assess this hypothesis.

Species and functional trait composition dynamics

We revealed a slight shift in the plant community composition over the fifteen-year period which was highly correlated with increased elephant impacts. At the species level, plant species selected for or avoided by elephants are not those characterized by the most important absolute or relative abundance change between 2001 and 2015 (Fig. 2b). Elephant impacts appear to have led to shifts in community compositions, not for the common species such as *Colophospermum mopane* (despite this species being highly selected), *Baphia massaiensis* and *Diospyros lycioides* (highly avoided), but for the rare species (e.g. *Mundulea sericea*, *Trycalia alleni*, partially confirming hypothesis CS1, Fig. 3). One explanation about the absence of modification of common species could be that habitat vegetation would have already been modified before 2001 when elephant density was already high and would have attained an equilibrium state with the current elephant pressure. However, these results suggest that work on vegetation community response to elephant impacts should be particularly careful about rare species (Lombard *et al.* 2001), which seem to be more sensitive to long periods of relatively heavy elephant utilization. The overall functional trait composition did not experience a significant shift correlated to elephant impact increase (not supporting hypothesis CS2), certainly because the dominant species remained mostly the same during the study period. Furthermore, the rare species which did show changes in their relative abundance, were not present in the functional trait analyses or had lower weightings in the mean functional trait composition and in the quadratic entropy index of Rao than common species such as *Colophospermum mopane* and *Diospyros lycioides*. This study was limited in the number and diversity of functional traits analysed, as we were limited to functional traits that were previously available. The addition of missing important functional traits would most likely improve our understanding of elephant impacts on species and functional trait composition at the study sites. In addition, in further studies it would be needed to get functional trait measurements on monitored plants and not from databases as these functional traits are known to be plastic and change according to their environments and disturbance (Albert *et al.* 2011).

Vegetation structure dynamic

Our results revealed that, during the study period, elephants did not strongly alter the plant abundance and the height, the crown surface for plants above two meters and the stem diameter distribution (hypotheses S1 and S2) contrarily to what was expected from Holdo's model (2007). As for results on species composition and functional trait composition, we could not conclude if these results are due either to relatively weak effect on vegetation structure from elephants, even at very high density, either due to the fact the vegetation may have already been altered prior to 2001 as elephant densities were already high. However, our study conducted during fifteen years of high elephant density did not reveal the opening pattern of the vegetation structure as already observed in the literature (Laws 1970, Caughley 1976). We assumed that these studies were conducted in East Africa where woody savannas are dominated by *Acacia* species and were not supported in studies done in the Chobe National Park, in the Kruger National Park and the Hwange National Park, in Southern Africa, where woody savannas are more diversified (Childes & Walker 1987, Ben-Shahar 1998).

Finally, the crown surface distribution in the 50-200 cm layer changed strongly in all plots (confirming hypothesis S3). Except in *Colophospermum mopane* bushland where it increased, the crown surface decreased in all the plots of *Baikiaea plurijuga* woodland, *Combretum* bushed-woodland and *Acacia/Terminalia* bushed-woodland. The crown surface, with the height, is highly related to above-ground tree volume and biomass (Popescu *et al.* 2003). This observed decrease of the crown surface would therefore be linked to a diminution of the spatial volume occupied by trees in the 50-200 cm layer and could lead higher visibility in this height layer in these habitats. As the visibility influence the anti-predator behaviour of prey species (Fitzgibbon 1994, Gorini *et al.* 2012, Panzacchi *et al.* 2010) and the hunting behaviour of predator species (Husseman *et al.* 2003, Mills *et al.* 2004), these changes in crown surface could have consequences on predator-prey relationships, and ultimately on ecosystem functioning.

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*Chapter 5: Effects of long-term exposure to high elephant densities
on semi-arid African savanna woodland structure, species composition and functional traits*

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Chapter 6: Environment-mediated trophic interaction modification in large mammal communities: can African elephants affect where African lions kill their prey through modification of vegetation structure?

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Abstract

Ecosystem engineers can affect interspecific interactions by modifying habitats structure. Here, we assessed whether African elephants (*Loxodonta africana*), by affecting vegetation, can influence kill site selection by African lions (*Panthera leo*), a stalk-and-ambush predator. During two years, we monitored kill sites of GPS-collared lions in Hwange National Park, Zimbabwe, and characterized the visibility, the distance to a potential ambush site and the presence of elephant impacts at these sites (n=209). We first showed that elephant-impacted sites had slightly higher visibility and longer distance to a potential ambush site than non-impacted sites. We then assessed lion kill site selection (1) at a large scale, by comparing lion kill sites to random sites distributed in habitats intensively used by lions, and (2) at a fine scale, by comparing each lion kill site to a paired random site in the nearby habitat (within a 150m radius). At the large scale, lions killed more in elephant-impacted habitats when compared to other intensively used habitats. However, at the fine scale, lion kills were located in sites with lower distance to a potential ambush site than the available nearby habitat. Our study suggested that ecosystem engineers can indirectly mediate trophic interactions, but that mechanisms are scale-dependent.

Keywords: ecosystem engineer, ecosystem functioning, habitat structure, large carnivores, megaherbivores, predator-prey relationships.

Introduction

Species cohabiting in 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 both 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 predator effects mediating interspecific prey competition - Preisser & Bolnick, 2008). In these cases, the interaction between two species can be modified by a third species (hereafter “interaction modification”, Wootton 1993). Further, this process can appear through 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 within which the interaction takes place (i.e. environment-mediated interaction modification, Wootton 1993, 2002, Dambacher & Ramos-Jiliberto 2007).

Questions have arisen about how habitat changes (diversity and/or physical structure) may affect interspecific interactions (Petren & 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 deeply affect habitats (Crooks, 2002), and ultimately interspecific interactions (Marquis & Lill, 2007). Arditi et al. (2005) even designated ecosystem engineer species as “interaction modifiers” thanks to their capacity to modulate their environment. Interaction modifications were shown to drive population and community’s dynamics in system with few species (Werner & 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 & Werner 2001, Okuyama & Bolker 2007). A greater understanding of how they influence population dynamics will be a key part of improving 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 considered a keystone (sensu Bond, 1994) and ecosystem engineer species. While the effects of elephants on vegetation structure through their foraging activity and movements start to be well understood (Guldemon & van Aarde, 2008), the consequences of elephant-induced vegetation changes on the whole ecosystem remain obscure as a diversity of indirect effects is documented (Pringle, 2008; Valeix et al., 2011; Coverdale et al. 2016). In particular, almost nothing is known about the environment-mediated trophic interaction modification by elephants (but see Tambling et al., 2013), in spite of the importance of predation as an ecosystem process with cascading effects down the food chain (Estes et al. 2011), and in spite of the fact that predation is well-known to be strongly mediated by physical features of habitats (Bell, 1991; Kauffman et al., 2007).

Here, we investigated whether elephants, through their impacts on vegetation structure, can influence predator-prey interactions between African lions (*Panthera leo*) and their prey in savanna ecosystems. Lions are stalk-and-ambush predators that rely on features of the microhabitat (typically dense vegetation) providing concealment to approach and attack their prey (Hopcraft et al., 2005; Loarie et al., 2013; Davies et al., 2016). Therefore, microhabitat characteristics are expected to play an important role in kill site selection by lions (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 meters of a potential ambush site (Loarie et al., 2013). Elephants were observed to decrease crown diameter of trees and shrubs between 50 cm and 200 cm over a 15-year period of monitoring in Hwange National Park, Zimbabwe (Ferry et al. unpublished data). The crown surface, with the height, is highly related to above-ground tree volume and biomass (Popescu et al. 2003). By modifying vegetation structure, elephants are therefore expected to affect the visibility and the distance to a potential ambush site (DPAS hereafter), and are thus likely to affect where lions hunt and/or successfully hunt (i.e. kill) their prey. The aim of this study is two-fold: (1) to confirm that elephant impacts on the vegetation are associated with an increased visibility and an increased distance to potential ambush sites as often assumed in the existing literature, and (2) to test the hypothesis that lions kill less in areas impacted by elephants (as we expect them to kill more in areas with denser vegetation and associated lower visibility, and more potential ambush sites, and thus greater opportunities for concealment). This second part was investigated at two different scales: (i) at a large scale, we assessed if among all habitats used

by lions (represented by random sites within areas where lions killed and rested), kill sites, were characterized by denser vegetation and no elephant impact, and (ii) at a fine scale, we assessed if lions killed more in closed habitats that were not impacted by elephants compared to the surrounding habitat directly available (< 150 m). Together, the results will allow assessing to which extent elephants can induce environment-mediated trophic interaction modification.

Material and methods

Study site - Study site - Hwange National Park covers ~15 000 km² 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 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 (~7 000km²) where lion density is estimated around 4.3 individuals/100 km² (Loveridge et al., 2016), and elephant density is estimated above 2 individuals/km² (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 GPS radio-collars. The lions' locations were available hourly and for some lions every two hours, day and night. Potential lion kill sites were attained by identifying clusters of coordinates that had more than 4 hours of sequential locations within a defined proximity (150 m, see also Tambling et al., 2010). These clusters were searched for carcasses in a 50m radius around the GPS point identified as the start of the cluster. Clusters were classified as kill sites based on the forensic evidence of a kill. We confirmed 209 lion kills using several supporting indicators including: lion tracks, hair and scats, indications of a struggle visible in broken and trampled vegetation, the positioning of the carcass remains and the condition of any remaining hide bearing claw and bite marks typical of lion predation. Carcasses found at clusters were classified to species based on the presence of identifiable material, such as horns, jaws, bones and hair and teeth wear. We recorded for each cluster (confirmed or not as a kill site) a paired random site (with a random direction and random distance between 50 and 150m from the GPS point identified as the start of the cluster). For each kill site and random site, the DPAS (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 x 50 cm white boards. The two boards were set so that one board was at 10–60 cm (representative of the height of a sitting lion) and the other was at 100–150cm (representative of a standing lion). One person stood at the location of the carcass for a kill site 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). Elephant impacts were assessed within 25m radius of the site (Appendix 1). 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): 0 - no impact, 1 -]0;25], 2 -]25;50], 3 -]50;75] and 4 -]75;100]. For each of these classes, the number of study sites (kill sites and random sites) was respectively: 197, 97, 76, 34, and 12.

Analyses – Kill sites from grassland habitat were removed from the analyses as there is very little woody vegetation, and we were interested in the elephant impacts on the woody vegetation, which are the ones modifying the structure of habitats. Hence, 168 kill sites were used in the analyses (Appendix 2). 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, Fritz & Madzikanda 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 habitat structure - Visibility at 100-150cm was highly correlated to visibility at 10-60cm ($r = 0.96$, $t = 139.65$, $df = 1587$), so only results on the visibility at 10-60cm (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 data and on (2) the DPAS with a truncated linear regression as data distribution was left truncated at 0 m (‘truncreg’ package from open source Software R 3.3.1 R. Development Core Team, 2014).

Kill site selection of lions - For the analyses on kill site selection by lions, two scales were considered. First, we focused on a large scale by comparing characteristics of the habitats of

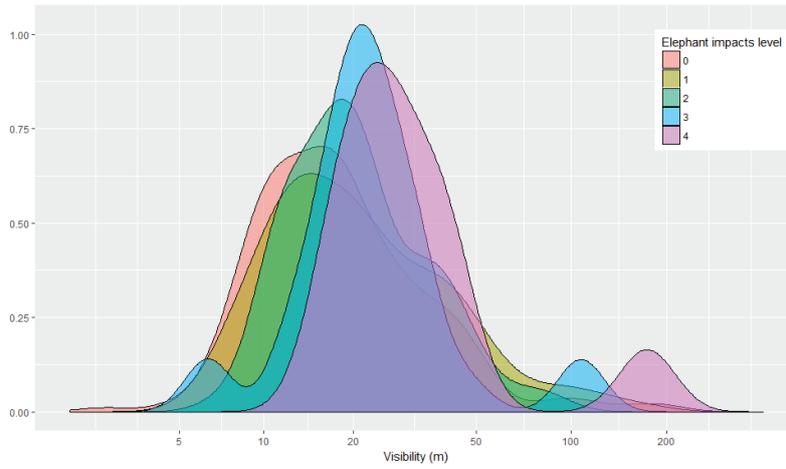
lion kill sites with characteristics of the habitats across a range of sites intensively used by lions (represented by all random sites). We used logistic regressions to develop resource selection functions (RSF), with the dependent variable being 1 for kill sites and 0 for random sites. Explanatory variables were the level of elephant impacts, the visibility and the DPAS, without interaction between them. No strong correlation was observed between these three variables which were therefore kept for the analyses. (Pearson's correlation coefficient: Impacts-Visibility = 0.15, Impacts-DPAS = 0.18, Visibility-DPAS = 0.38). A model selection was performed using the function "dredge" ('MuMin' package) using the Bayesian Information Criterion (BIC) for a compromise between the explanation power and the parsimony of the models and model averaging was performed on the 95% confidence set (Burnham & Anderson, 2004). Second, we focused on kill site selection by lions at a fine scale, by comparing the characteristics of habitats of lion kill sites with the characteristics of the direct surrounding habitat available (represented by the random site associated to each kill site). A paired Generalized Estimating Equations (GEE) model was performed using the package "gee" to remove all the variability between the pairs (kill versus paired random) and focus only of the variability within each pair (Liang & Zeger, 1986). For this analysis, the quasi-likelihood criterion (QIC) was used (Liang & Zeger, 1986) and a model averaging was performed on the 95% confidence set.

Results

Kills were not evenly distributed upon the habitat openness (Appendix 2). 27% of the prey killed by lions were greater kudu *Tragelaphus strepsiceros*, 20% African buffalo *Syncerus caffer* and 12% plains zebra *Equus quagga* (Appendix 2). DPAS and visibility for each species killed are presented in Appendix 3.

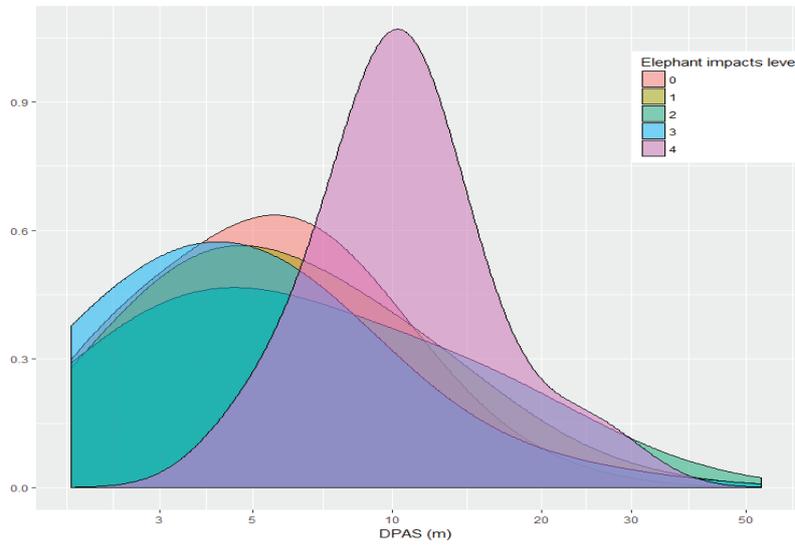
Effect of elephant on habitat structure - The effect of the level of elephant impacts was assessed on each habitat variable. Log-visibility was higher when the level of elephant impacts increased (estimate \pm SE = 0.09 ± 0.026 , $t = 3.322$, $p < 0.001$, Table 1a, Fig. 1a). Log-transformed DPAS was higher when the level of elephant impacts increased (estimate \pm SE = 0.12 ± 0.03 , $t = 3.78$, $p = 0.001$, Table 1b, Fig. 1b). In this last case, we observed a particular increase of the log-DPAS with the higher level of elephant impact.

a)



	2.5 %	Mean	97.5 %
a			
0 – None	16.5	18.1	19.7
1 -]0,25]	16.5	20.9	26.5
2 -]25,50]	16.1	20.7	26.5
3 -]50,75]	16.6	22.7	30.9
4 -]75,100]	19.8	30.9	47.9

b)



	2.5 %	Mean	97.5 %
b			
0 – None	3.3	3.7	4.3
1 -]0,25]	3.2	4.6	6.5
2 -]25,50]	3.5	5.1	7.3
3 -]50,75]	2.6	4.5	7
4 -]75,100]	5.8	10.5	18.5

Figure 1: Distribution of a) the visibility and b) the distance to a potential ambush site (DPAS) according to the level of elephant impacts.

Table 1: Estimated mean and confidence interval at 95% for each level of elephant impacts of (a) the visibility (m) and (b) the DPAS (m).

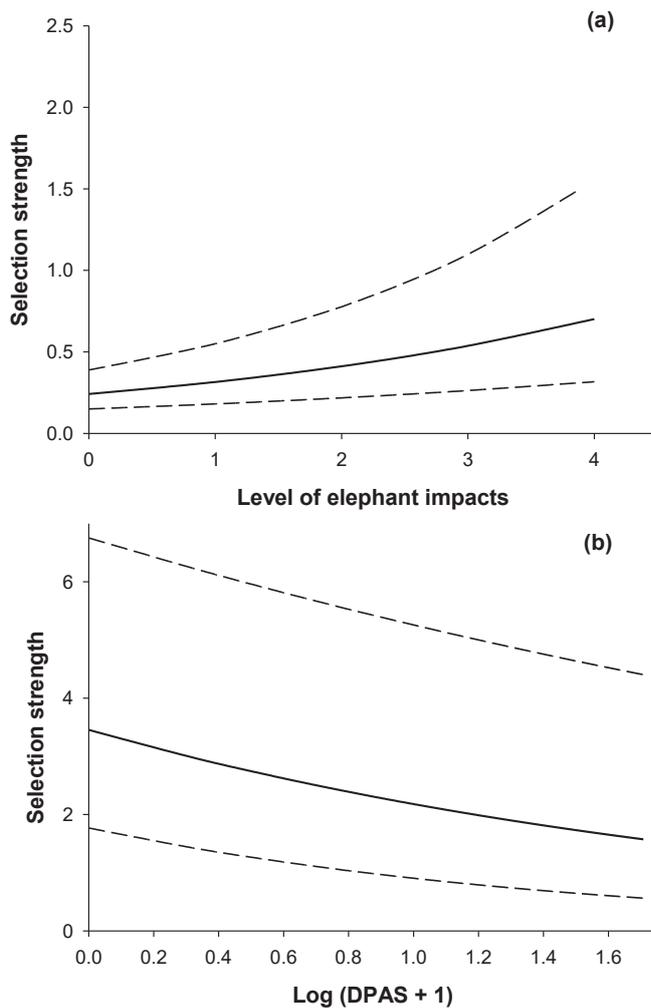


Figure 2: (a) Relationship between the level of elephant impacts and the strength of kill site selection for lions at the large scale. (b) Relationship between the log-transformed DPAS (for DPAS ranging from 0 to 50m) and the strength of kill site selection for lions at the fine scale. The selection strength is $\exp(\beta_0 + \beta_1 \cdot \text{level of elephant impacts})$ at the large scale and $\exp(\beta_0 + \beta_1 \cdot \log(\text{DPAS} + 1))$ at the fine scale, where β_0 is the intercept estimate and β_1 is the estimated coefficient for the level of elephant impacts at the large scale and for $\log(\text{DPAS} + 1)$ at the fine scale.

Kill site selection by lions - For these analyses, the sites in *Colophospermum mopane* were removed as they did not show any response to elephant impacts. At the large scale, model averaging over the 95% confidence set of best-ranked logistic models revealed that the presence of elephant impacts was the only variable to clearly explain lion kill site selection (Table 1a). Lion kills were preferentially located in habitats impacted by elephants (estimate \pm SE = 0.69 ± 0.21 , Fig. 2a). At the fine scale, model averaging over the 95% confidence set of best-ranked logistic models revealed that the DPAS was the only variable to clearly explain lion kill site selection (Table 1b). Lion kill sites were preferentially located in habitat characterized by a reduced DPAS (mean_{Kill} = 5.8 m) compared to the direct nearby habitat available (mean_{Random} = 7.6m, estimate \pm SE = -0.42 ± 0.24 , Fig. 2b).

Table 1: 95% confidence set of best-ranked logistic models (models whose cumulative BIC weight, $\text{bcc } w_i, \leq 0.95$ (a) and models whose cumulative QIC weight, $\text{qcc } w_i, \leq 0.95$ (b) examining the effect of the presence of elephant impacts (Ele), visibility (Vis) and distance to a potential ambush site (DPAS) on lion kill site selection a) at the habitat scale and b) at the microhabitat scale. Model-averaged estimates for the three habitat variables parameters \pm standard error.

a	Candidate models	df	BIC	Δi	w_i	$\text{bcc } w_i$
1	Ele	2	696.6	0.00	0.618	0.618
2	Ele + Vis	3	699.9	3.30	0.119	0.737
3	Ele + Vis + DPAS	4	700	3.40	0.113	0.85
4	Ele + DPAS	3	701	4.42	0.068	0.918

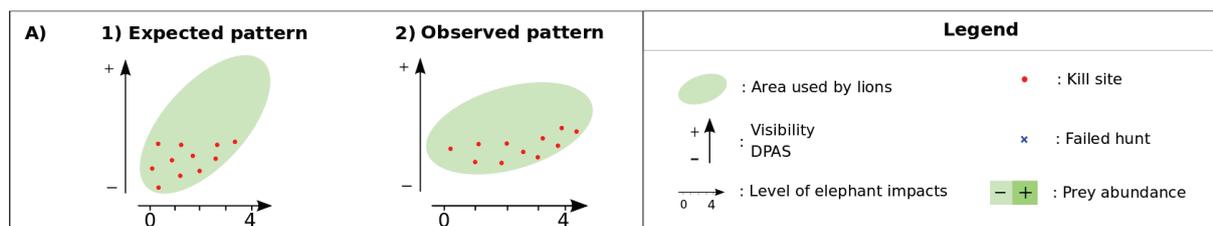
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	Ele	Vis	DPAS		
β (\pm SE)	0.27 (\pm 0.08)	0.0.9 (\pm 0.19)	-0.06 (\pm 0.14)		
b	Candidate models	QIC	Δi	w_i	qcc w_i
1	DPAS + Ele + Vis	310.4	0.00	0.233	0.233
2	DPAS + Vis	310.5	0.07	0.225	0.458
3	DPAS	310.6	0.21	0.210	0.668
4	DPAS + Ele	310.9	0.49	0.184	0.852
5	Vis	312.7	2.29	0.074	0.926
	Ele	Vis	DPAS		
β (\pm SE)	0.10 (\pm 0.12)	-0.32 (\pm 0.27)	-0.46 (\pm 0.21)		

Discussion

We assessed the effects of elephants on features of habitat structure that can be key for the ecology of predator-prey interactions. Elephant-induced vegetation changes tend to be associated with an increase in visibility (see also Valeix et al., 2011) and in DPAS. On average, there was a difference of 12.8m for the visibility (mean Level 0 = 18.1m, mean Level 4 = 30.9m) and 6.8m for the DPAS (mean Level 0 = 3.7, mean Level 4 = 10.5m) between habitats not impacted by elephants and those with the highest level of elephant impacts. However, habitats with the highest level of elephant impacts represented few sites in this study (n = 12) compared to other habitats. Even though these average differences were not very large, they can make a difference in dense habitats considering the visibility scale for lions when killing their prey (e.g. within 9 meters of a potential ambush site - Loarie et al., 2013). Further, elephants, by altering visibility and DPAS, are likely to affect where lions choose to hunt and/or where they happen to hunt successfully. Following the ambush-habitat hypothesis (Hopcraft et al., 2005), lions should kill more in habitats with lower level of elephant impacts and characterized by lower visibility and a shorter DPAS, thus more favourable to lion hunting success (Fig. 3a).

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 of kill site selection observed based on four different parameters: probability of prey presence, probability to hunt depending on prey presence and/or habitat openness, and probability to hunt successfully and kill a prey in the different habitats (Fig. 3b). Following the ambush-habitat hypothesis, our initial hypothesis assumed an equal probability of presence of prey in all habitats and a probability to hunt not linked to the probability of prey presence. However, it stated that lions would have either a higher probability to hunt in closed habitats (Fig. 3b – Patterns 9), either a higher probability to kill in closed habitats (Pattern 3), either both (Pattern 11), observing therefore more kills in less elephant-impacted habitats (Fig. 3a – 1).



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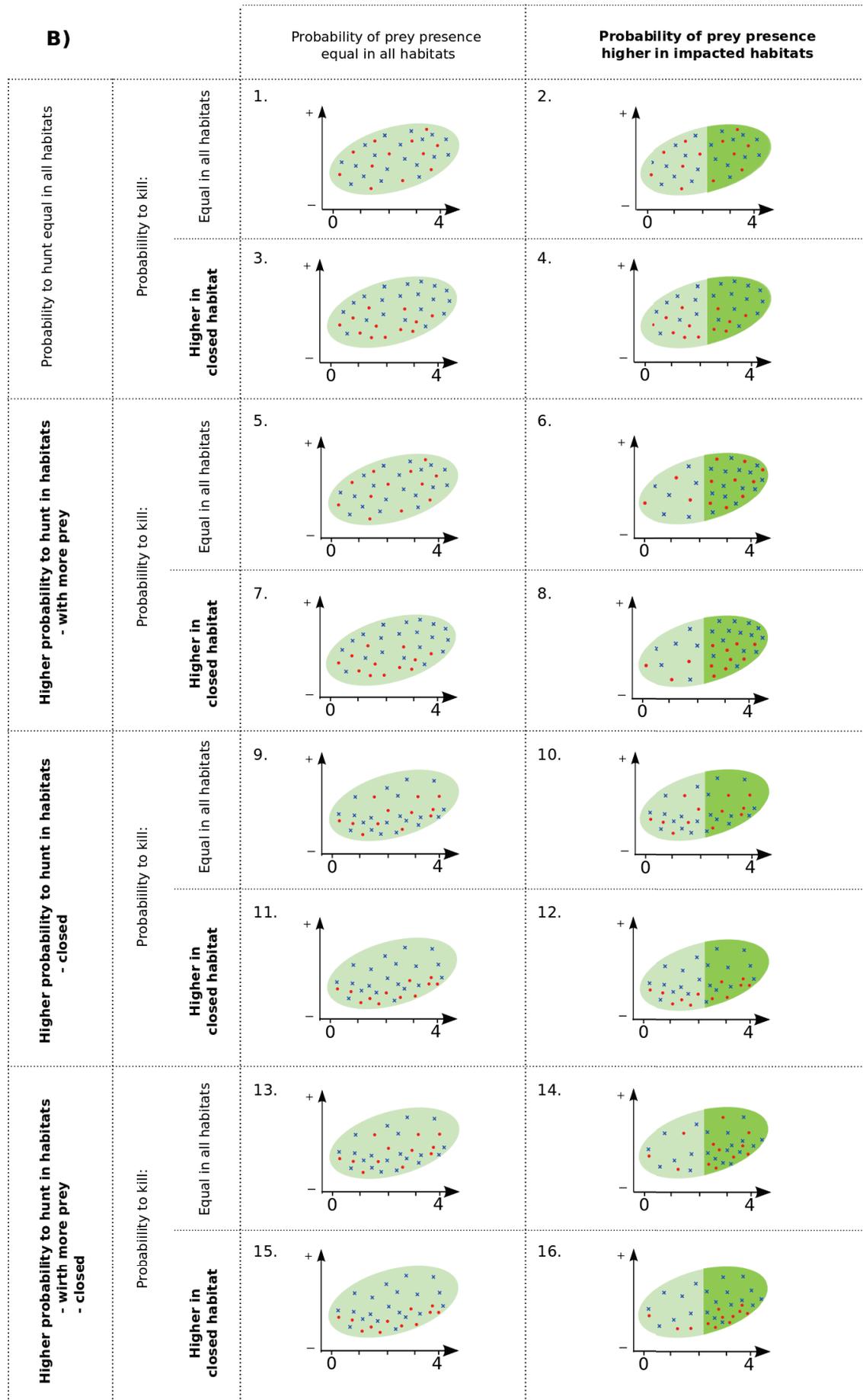


Figure 3: A) Representation of the expected pattern under our initial hypotheses and the observed pattern. 1) Under our initial hypotheses, we expected higher visibilities and DPAS in habitats with higher levels of elephant impacts, as well as more lion kill sites in habitats characterized by a lower visibility and a shorter DPAS, and thus more kills in non-impacted habitats. 2) 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 fine scale, lion kill sites were more in habitat characterized by a lower DPAS. B) Representation of the different scenarios envisaged to explain the observed pattern. We played on the combination of four variables : 1) the probability of prey presence, depending on if herbivores select for elephant-impacted habitat (Patterns 1, 3, 5, 7, 9, 11, 13, 15) either via vegetation engineering by elephants (following findings from Valeix et al. 2011), either by coincidence or not (Patterns 2, 4, 6, 8, 10, 12, 14, 16), 2) the probability that a hunt will occur, with lions hunting more in high prey abundance habitat (following the prey-abundance hypothesis, Patterns 5-8, 13-16) or not (Patterns 1-4, 9-12), 2) the probability that a hunt will occur, with lions hunting more in closed habitats (following the ambush-habitat hypothesis, Patterns 9-16) or not (Patterns 1-8) and 3) the probability of a successful hunt, i.e. of a kill, with lions having a higher success rate in closed habitat (following the ambush-habitat hypothesis; Patterns 3, 4, 7, 8, 11, 12, 15, 16) or not (Patterns 1, 2, 5, 6, 9, 10, 13, 14). Patterns 8, 14 and 16 appear to be the most likely to explain the observed pattern.

At the large-scale, contrary to our expectations, lion kills were more located in habitats characterized by higher levels of elephant impacts, associated with a higher visibility and a higher DPAS. Because lions are more efficient hunters in closed environments (van Orsdol, 1984), this result suggests that other factors than habitat structural features drive lion hunting behaviour at this scale. Patterns 6, 8, 14 and 16 are the only ones to show this pattern, with more kills in habitats highly impacted by elephant. In these scenarios, we expect a higher probability to hunt in habitats where there are more prey, following therefore the prey-abundance hypothesis, but we also expect prey to be more present in habitat impacted by elephants. Browsers (e.g. kudu - one of the favorite prey species of lions in Hwange (Davidson et al., 2013) -, giraffe, and steenbok) and mixed-feeders (impala) have been indeed shown to select for elephant-impacted habitats in the study ecosystem (Valeix et al., 2011). The underlying mechanism is still unclear and this selection pattern may arise either from a coincidence with elephants and other herbivores using the same habitats, or from a facilitative effect of elephants through the creation of browsing lawns (Fornara & du Toit, 2007) or from a reduced perceived risk of predation in elephant-impacted habitats due to the higher visibility in these habitats (Underwood, 1982, Valeix et al., 2011). Hence, the fact that lion kills were preferentially found in elephant-impacted habitats could be explained by a selection for areas

where prey are abundant. Elephants could be considered as interaction modifiers if they influence prey habitat selection, which would be the case in they create browsing-lawns (as suggested by Rutina, Moe & Swenson 2005) or if they reduce the perceived predation risk in areas where they break trees (as suggested by Valeix et al., 2011). Evidences about the role of elephants in other herbivore habitat selection at this scale still need to accumulate.

At the fine scale, lion kills were not preferentially located in habitats highly impacted by elephants anymore. At this finer scale, lion kill sites were preferentially located in habitats characterized by a shorter DPAS. Interestingly, the visibility did not seem to be a factor as important as the DPAS. An explanation could be that, whatever the visibility, the presence of few bushes / broken trees as potential ambush sites is sufficient to lead to a higher probability of kill even in habitats with a high visibility. At this scale, Patterns 3, 4, 7-16 would be the more likely to explain the observed pattern with more kills in habitat with lower visibility and/or DPAS. All of these scenarios are conditioned by a same process: a higher probability to hunt and/or to successfully hunt (i.e. kill) in closed habitat supporting here our second hypothesis on the role of prey catchability (ambush-habitat hypothesis). Finally, when combining the two different scales, the only Patterns to explain the observed pattern with both more kills in impacted habitat at large scale and more kills in closed habitat at fine scale are Patterns 8, 14 and 16. These lasts share the same processes: more prey in elephant-impacted habitats and a higher probability to hunt in habitat with more prey (prey-abundance hypothesis). However, they differ in term of probability to hunt or to kill in closed habitat. Pattern 8 needs a higher probability to kill in closed habitat, Pattern 14 needs a higher probability to hunt in closed habitat and Pattern 16 needs both of them, suggesting therefore that lions are influenced by habitat structure during the hunting process (ambush-habitat hypothesis).

Therefore, our results together with our theoretical framework suggest that the main driver of kill site selection for lions is likely to be prey abundance at a large scale of selection, and prey catchability at the fine scale of the direct nearby habitat available (<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 behavior (Davidson et al., 2012). Therefore, by affecting the vegetation structure, elephants could play an important role in the predator-prey relationships although in complex ways, as they could act on both predators and prey's behaviour and apparently depending on the scale considered. We encourage future research to confirm that herbivores select habitats impacted by elephants because of the elephant's engineering process and not because of simple coincidence or shared. Further, a focus on identifying unsuccessful hunts will be needed. As for example here, identifying which Pattern between 8, 14 and 16 is the most likely would help to disentangle between the probability to hunt and the probability to kill in closed habitats, and therefore would help to know which process is influenced by the vegetation structure during the lion hunt. 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).

Despite remaining questions regarding the underlying mechanisms, our study revealed that (1) at the scale of the sites intensively used by lions, kill sites are preferentially found in habitats characterized by high elephant impacts, (2) visibility and DPAS increase as the level of elephant impact increases, and (3) DPAS is an important driver in lion kill site selection at a fine-scale. Hence, 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 their role of ecosystem engineer, could act on a multitude of broad-scale ecological processes in wooded savannas (Kerley & Landman, 2006). Finally, whereas previous studies of ecosystem engineers have highlighted their effects on other species abundance and richness (Jones et al., 1997), our findings suggest the importance of their indirect effect on interspecific interactions (see also Arditi et al., 2005; Marquis & Lill, 2007 and references therein). To our knowledge, our study is one of the first to assess the environment-mediated trophic interaction modification in a natural large mammal community. By showing the complexity in this process, our study clearly shows that more efforts are needed in natural ecosystems for a better understanding of ecosystem functioning.

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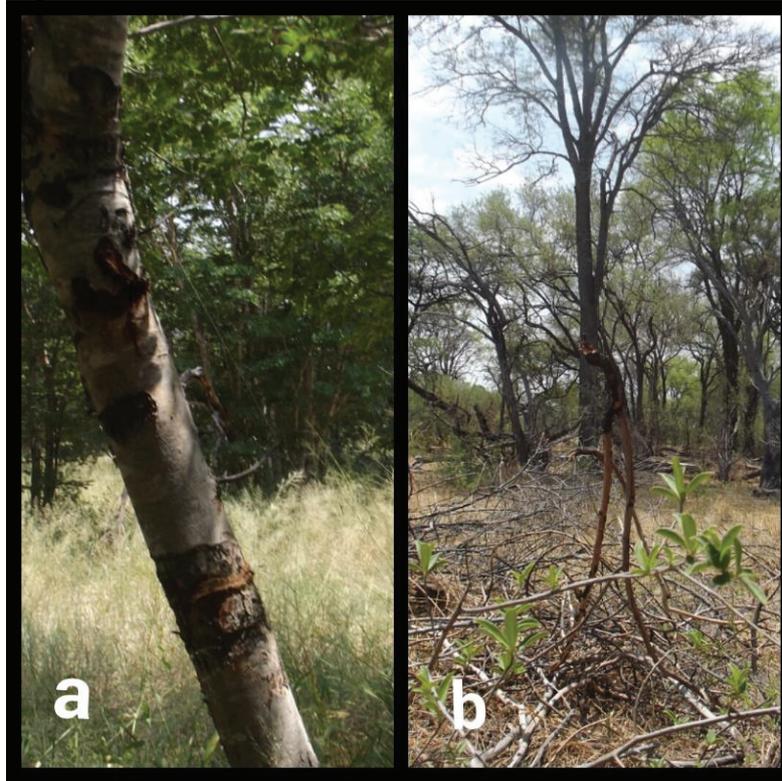
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Supporting information

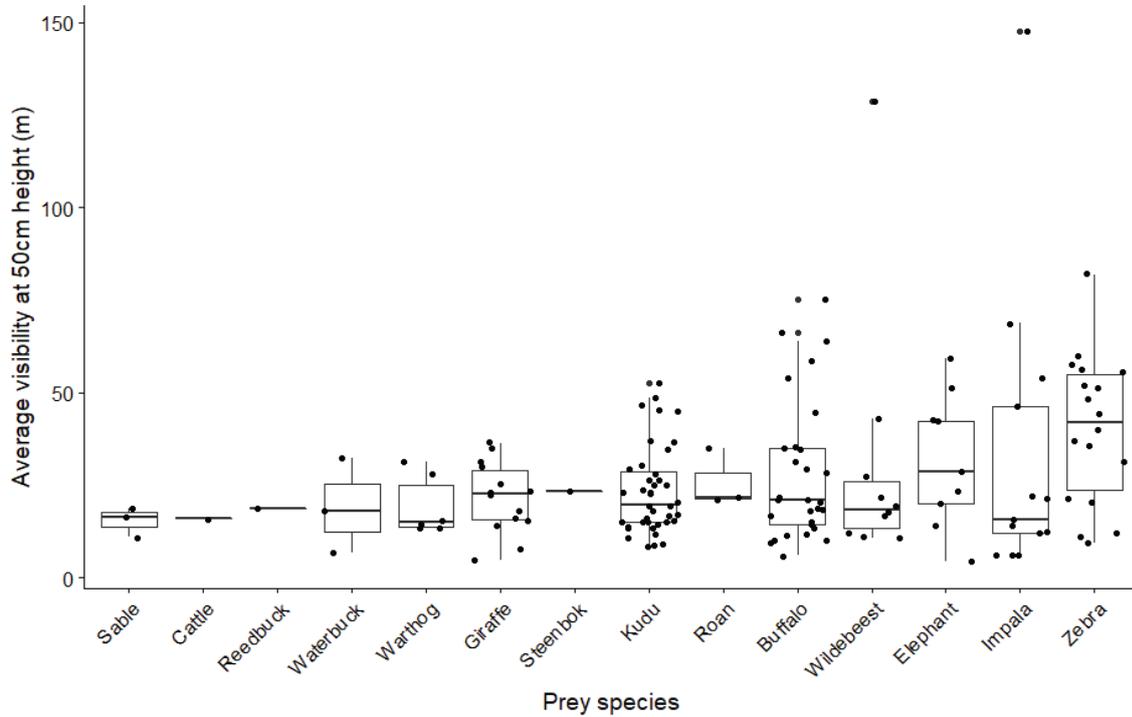
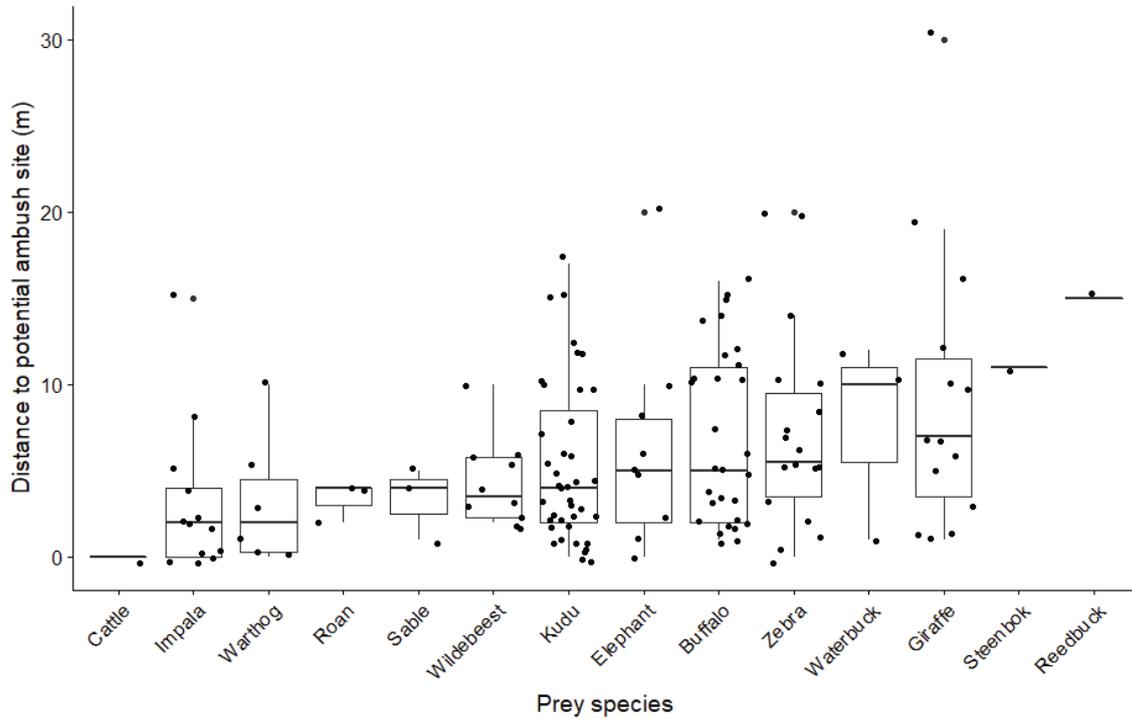
Appendix 1: Illustration of two sites with contrasted elephant impact: a) non-impacted habitat and b) elephant-impacted habitat.



Appendix 2: Distribution of the lion kills per prey species and habitat type (BW: Baikiaea woodland, ABW: Acacia/Baikiaea woodland, BEW: Burkea/Erythrophleum woodland, CBG: Combretum bushed grassland, MBG: Mopane bushed grassland, MW: Mopane woodland, OG/FPR: Open Grassland / Flood plain riverine). Data of lion kills in Open grassland / Flood plain riverine are presented here but were not used in analyses.

	BW	ABW	BEW	CBG	MBG	MW	OG/FPR	Total
Buffalo	5	3	9	13	0	5	15	50
Cattle	0	0	0	1	0	0	0	1
Eland	0	1	0	0	0	0	1	2
Elephant	4	1	3	1	0	0	3	12
Giraffe	7	3	0	4	1	0	0	15
Impala	0	1	1	11	0	0	0	13
Greater kudu	20	4	5	11	1	4	5	50
Reedbuck	0	0	0	1	0	0	0	1
Roan	1	0	2	0	1	0	0	4
Sable	0	0	1	2	0	0	0	3
Steenbok	1	0	0	0	0	0	0	1
Warthog	1	0	1	4	0	0	0	6
Waterbuck	1	0	1	1	0	1	2	7
Wildebeest	2	6	0	2	0	0	8	18
Zebra	4	1	6	7	2	0	8	28
Total	46	20	29	57	5	11	41	209

Appendix 3: Distance to potential ambush site (m) and visibility (m) for each species killed by lions.





Discussion



« Un éléphant, c'est très encombrant. Chez moi, c'est tout petit. »

Le Petit Prince (1943), Antoine de Saint-Exupéry

In this thesis, I assessed the role of the African elephant as a modifier of predator-prey relationships. I focused on three possible ways.

The first research axis evaluates the effects of elephants on other herbivore species, i.e. prey for lions, at the scale of the waterhole, and ultimately investigates the implications for lion trophic interactions at waterholes. This first research axis assesses a prey trait-mediated trophic interaction modification (General introduction - Figure 3.1).

The second research axis, constituted by Chapter 4, considers elephants either as exploitative competitors for food resources (i.e. interaction chain, General introduction - Figure 3.2A) or as an engineer species facilitating availability of resources of higher quality (i.e. trait-mediated trophic interaction modification, General introduction - Figure 3.2B), at the scale of the landscape and of the habitat.

In the third research axis, I studied the effects of elephants on lion foraging behaviour through changes in the vegetation structure (environment-mediated trophic interaction modification, General introduction - Figure 3.3).

1 – The African elephant, a modifier of predator-prey relationships?

1.1- On prey behaviour at waterholes

1.1.1- The African elephant, unfair competitor or involuntary bodyguard?

We begin to reach a better understanding of interspecific interactions between herbivores and elephants at waterholes, as well as how water availability shapes these interactions. First, there is an obvious contrast between dry years and wet years, with more elephants, coming sooner and staying longer at waterholes during dry years (Valeix *et al.* 2007b). Hence, during dry years, the probability to co-occur with elephants at waterholes is five to twenty times higher and there are five times more interactions with elephants (Valeix *et al.* 2007b, Table 1). These interactions are relatively often costly during dry years (*sensu* Valeix *et al.* 2007b, Table 1). In addition, at the intra-annual scale, the number of aggressive interactions increases as the dry season progresses (Ferry *et al.* 2016). Co-occurrence with elephants could therefore be costly for other herbivores in terms of time budget, stress response, etc. All the species facing this “elephant reality” should therefore tend to avoid temporally or spatially elephants at waterholes.

Here, I synthesize the findings from the existing studies on waterhole use by elephants and other herbivore species, together with the findings from the first research axis of my thesis. Overall, different patterns of waterhole utilisation have been revealed and three groups of herbivore species can be distinguished. For convenience, results presented below refer to Table 1 within which associated Chapters or studies are referenced. Results for which I explicitly cite the associated Chapter or study are not presented in Table 1.

The first group of herbivore species that emerges comprises impalas, warthogs, roans and sables. They are the only species for which the probability to have an interaction (or a costly interaction) increases with the number of elephants. No information about their spatial behaviour in the presence of elephants is available as they shift their circadian activity at waterholes during dry years and probably do so at the intra-annual level too (during the dry year in 2003, they experienced less co-occurrence with elephants as the dry season progressed). Additionally, in my 2016 observations, almost no simultaneous observation of these species with elephant at waterholes was recorded (*Chapter 2*). For these species, results support the hypothesis of competition for access to water with elephants, as these species appear to avoid temporally elephants to decrease the risk of interference competition with them. This group can further be separated into two sub-groups. The first sub-group comprising impalas and warthogs, which would compete with elephant for access to water in general. The second sub-group comprising roans and sables, which would compete with elephant for access to the water of good quality. Indeed, sables and roans drank close to water-troughs, almost like elephants, whereas impalas and warthogs drank further from the water-trough, almost at the maximum distance allowed by the waterhole configuration (*Chapter 2*).

The second group of herbivore species that emerges comprises kudus and zebras which had the same overall responses facing elephants. At the beginning of the dry season, both species spatially segregate from elephants, suggesting the existence of a competition with elephant for the two species. Results which seem to confirm for kudu as they shift their circadian activity during dry years, but not for zebras. However, as the dry season progresses, co-occurrence with elephants increases and the two species are closer to them than expected if distributed randomly in the waterhole area. This suggests the existence of benefits associated to be close to elephants that are higher than the possible costs associated

to the increasing aggressive interaction frequency. Neither kudus, nor zebras drink close to the water-trough, even when elephants are absent from the waterhole, which does not support the “water quality hypothesis”. A “bodyguard hypothesis” was also explored, whereby even though elephants can be aggressive towards other herbivores, they may also represent safety from predators as they are very big and able of mobbing behaviour against lions. However, the playback experiment performed in this thesis did not confirm this hypothesis for zebras. After a stimulus of lion presence, zebras did not come close to elephants. They were more vigilant indicating they responded as expected to an increase of the perceived predation risk. However, the presence of elephants did not allow decreasing the time allocated to vigilance, suggesting that the perceived predation risk did not decrease with the presence of elephants.

Finally, the last group includes giraffe only. The presence of elephants does not appear beneficial to giraffes as they have a lower drinking probability when the elephant number increases, and they spend more time to access water when elephants are present. However, they did not shift their circadian activity during dry years and they experienced more co-occurrence at the end of the dry season in 2003, with more aggressive interactions. This absence of temporal avoidance at the intra-annual scale was not compensated for by a spatial avoidance. Altogether, these results suggest that giraffe have some costs associated to with the presence of elephants (e.g. time budget), but either they are not high enough to lead to niche shift (temporal or spatial), or another constraint forces them to be at waterholes when elephants are present. Overall, giraffes tend to drink far from elephants and are particularly vulnerable when drinking.

We do not have enough information to conclude for the remaining herbivore species (buffalo, wildebeest and waterbuck). The absence of temporal avoidance, of interactions (and costly interactions) with elephants, and the apparent indifference toward elephant presence when drinking (drinking probability, time spent accessing water) would nevertheless suggest no cost associated to be with elephants for wildebeest and waterbuck. More information is needed concerning these species’ spatial and drinking behaviour.

Table 1: Results gathered from different studies on competition between elephants and other herbivores at waterholes. a indicates results from Valeix *et al.* (2007b), b from Valeix *et al.* (2007c), c from Valeix *et al.* (2009), d from Ferry *et al.* (2016), e from chapter 4 and f from chapter 5. For variables for which all species respond, only those with * were statistically significant. ** represent variable for which the study focused on a few species only. Responses of species without ** were calculated for the purpose of this discussion. *** represent variable for which the study analysed the response on all studied species confound. For this variable, responses of each species were separated calculated for the purpose of this discussion. Grey cells represent missing results (e.g. species not studied, or not enough data available).

Species	Impala	Kudu	Roan	Sable	Warthog	Zebra	Wildebeest	Waterbuck	Giraffe	Buffalo
Body mass (♀/σ kg, Owen-Smith 1988)	45/65	170/250	260/280	220/235	60/80	265/285	190/230	180/240	825/1000	520/650
Diet	Mixed	Browser	Woodland grazer	Woodland grazer	Grazer	Grassland grazer	Grassland grazer	Grassland grazer	Browser	Grazer
Inter-annual scale: Comparison between wet year and dry year										
Co-occurrence with elephant probability (Wet year - 2004) ^a	0.02	0.04	0	0.01	0.02	0.04	0.04	0.08	0.07	0.08
Co-occurrence with elephant probability (Dry year - 2003) ^a	0.41	0.43	0.59	0.43	0.51	0.45	0.3	0.49	0.54	0.62
Temporal - Niche shift (40 years database) ^a	Yes	Yes	Yes	Yes	Yes	Yes				Yes
Dry year (2003)										
Interaction probability... ^a	0.17	0.19	0.19	0.19	0.15	0.2	0.08	0	0.13	0.15
... when elephant number increase ^a	+	+		+	+					
Costly interaction probability... ^a	0.08	0.11	0.08	0.09	0.03	0.08	0	0	0.07	0.05
... when elephant number increase ^a	+		+							
Drinking probability when elephants number increases ^b			-						-	
Time spent accessing water ^b					+	+			+	
Potential drinking time when elephants ^{c*}	+	+	+	+	+	+	+		+	+
Within a dry year: behavioural dynamics over the dry season										
Temporal - Occurrence with elephant ^{d**}	-	+	-	-	-	+	=	=	+	+
Aggressive interaction dynamics ^{d***}	+	+	+	+	+	+	-	0	+	+
Spatial - Aggregation to elephants ^d		(+)				+			=	
Effect of water quality – End of dry season (2016)										
Drinking distance to water-trough (m) ^e	53.3	49.4	29.2	32.6	58.6	49.4			56.3	
Effect of elephant presence ^e	No	No			No	No				
Effect of increase perceived predation risk – End of dry season (2016)										
Aggregation to elephant ^f						No				
Effect of elephant on vigilance ^f						No				

1.1.2- Limits and perspective

We begin to have a deeper understanding of the interactions between elephants and other herbivores at waterholes. First, it seems that during wet years (e.g. 2004, 785 mm rainfall), these interactions are very rare as herbivores are not using waterholes intensively. Almost all interactions take place during dry years and particularly at the end of the dry season (between August and October), when surface water becomes very limiting in the landscape. The results from 2003 could be considered as exceptional. Indeed, 2003 was characterized by a very low annual rainfall (376 mm) and succeeded to 2002, which was also a dry year (397 mm rainfall). However, as dry years are expected to be drier in the future (Chamaillé-Jammes *et al.* 2007), two consecutive dry years or even one extreme dry year are expected to become frequent and the interspecific interactions between elephants and other herbivore species will thus occur more often.

Regarding the effects of elephant on predator-prey relationships at waterholes, the test of the “bodyguard hypothesis” carried out in this thesis did not suggest any evidence of such indirect effects. Indeed, we did not observe any effect of elephant presence on zebra’s behavioural traits (i.e. vigilance, mixed-species grouping behaviour). Does it mean that the “bodyguard hypothesis” should be definitively rejected?

First, only one prey species, zebras, was studied here (chapter 3). Kudus showed the same aggregation pattern with elephants at waterholes at the end of the dry season as zebras (chapter 1). They were not selected as a focal species for our playback experiment because the number of kudu observations was lower than for zebras in 2003. We therefore preferred to monitor zebras to guarantee enough statistical power for our experimental design. However, kudus are under heavier predation pressure from lions than zebras in Hwange National Park (Davidson *et al.* 2013) and were shown to have a vigilance behaviour particularly susceptible to an increased perceived predation risk and the presence of other herbivores at waterholes (Périquet *et al.* 2010). It would be interesting to test the “body-guard hypothesis” for this species in the future and see if the presence of elephants decreases the level of vigilance more than the presence of other herbivores in a context of high perceived predation risk.

Second, we focused on prey's trait related to anti-predation behaviour. By definition, the trophic interaction modification could also occur by a modification of a predator's trait. For instance, does the presence of numerous elephants at a waterhole leads lions to neglect at least temporarily, or even avoid, the waterhole? Fine temporal scale analysis of movements of GPS radio-collared lions (e.g. distance covered, path tortuosity, Valeix *et al.* 2010) near waterholes, contrasting waterholes where elephants are present with waterholes with no elephant, could answer this question.

Third, as herbivores are mainly preyed within 2 km from waterholes (Valeix *et al.* 2009), does the presence of elephants modify the predation pressure on other herbivores, particularly when elephants are numerous? All the propositions above could help us assess this "bodyguard hypothesis", but only partially. In Chapter 3, we focused only on prey's trait related to anti-predator behaviour, and the propositions above are made out of the same wood: either monitoring a prey's trait again, or a predator's trait. One gap will still need to be filled: the effect on the predator-prey interactions *per se*. Future research will therefore need to address the link between elephant presence/abundance and the real risk of predation for other herbivores to fully test the "body-guard hypothesis". This link is not an easy one to tackle but one possible way forward would be to combine (i) analysis of lion hunting behaviour (number of hunts, probability of a successful hunt, number of kills) thanks to accelerometer data (as discussed in Chapter 5), and (ii) contextual data of the lion hunts particularly regarding elephant presence from camera traps placed around waterholes.

Finally, it is possible that the temporal niche shift of waterhole use by herbivores between wet and dry years, due to competition with elephants, may lead prey species to travel in the "risky area" (2 km around waterholes – see Valeix *et al.* 2009) at different times of the day that may influence their availability for lions as lions are nocturnal hunters that start to hunt late afternoon and may hunt until early morning hours (Schaller 2009). Does this prey's trait modification leads lions to shift their foraging activities or their diet? Comparison of kill site repartition through the day and night hours between wet years and dry years could be a first step to investigate this point.

1.2- On prey and predator distribution in the landscape

1.2.1- The African elephant, voracious neighbour (competition) or innkeeper (facilitation)?

In chapter 4, no spatial segregation pattern between elephants and other herbivores was detected neither at the landscape scale, nor at the habitat scale. As discussed in this chapter, these results suggest that either no competition for resources occurs between elephants and other herbivores, or competition occurs along niche axes that were not investigated in this work (e.g. food Tilman and Borer 2015, time Schoener 1974). It has been hypothesized that facilitation happening during the growing season (i.e. wet season) in savanna ecosystems between grazing herbivores can compensate for the effects of exploitative competition during the dry season (Arsenault & Owen-Smith 2002). Assuming this hypothesis is true for browsing herbivores, we should expect aggregation patterns at the beginning of the dry season, and segregation or random patterns at the end of the dry season. However, no seasonal effect was detected. In addition, it is interesting to notice that neither elephants, nor impalas, which are mixed-feeders (Cerling et al. 2004 and Sonheimer et al. 2003 respectively) eating preferentially grasses at the beginning of the dry season and reporting on woody plants at the end of the dry season, showed different habitat selections when foraging according to season. Responses to elephant presence and local abundance could be species-dependent, and could differ according to diet and body mass (Fritz et al. 2002), nevertheless, according to these results, we cannot conclude that elephants are key competitors for food for any of the species studied. Further, regarding impalas, the results suggested a facilitation effect by elephants as impalas selected habitats intensively used by elephants (as reported by Rutina et al. 2005). Eventually, as we showed no general spatial pattern regarding the effect of elephants on other herbivore species spatial distribution at both the landscape and the habitat scales, we did not expect the spatial distribution of predators to be influenced by elephants and we did not investigate further the indirect effects of elephants on predator distribution.

1.2.2- Limits and perspectives

The road census data available for this study limited the investigation of niche partitioning along the resource and time axes, where competition could occur. Indeed, information about the resource consumed by herbivores during foraging activities was not collected. Better understanding trophic resource overlaps between herbivores and elephants could help assessing resource partitioning. This can be done through DNA barcoding in faecal samples (Kartzinel *et al.* 2015). However, if browser herbivores feed on different plant species than elephants, this is not represented here by a spatial segregation, meaning that the different species used by herbivores are in the same habitats. We therefore should not expect an indirect effect of elephants on predator distribution.

If competition occurs along the time axis, with temporal partitioning, it would be observed at the circadian scale as community spatial structure and herbivore habitat selection were shown to be stable over year and season. If this is the case, this would suggest the existence of interference competition rather than exploitative competition. Indeed, herbivores used the same habitats as elephants, whatever the season of the year considered. If elephants would deplete food resources (leaves, twigs, grasses) to the extent of impacting other species ecological niche, we should not observe a fine-scale temporal partitioning as food resources would not have time to regenerate at the scale of the day. We should observe either a habitat partitioning or a temporal partitioning at larger-scale than the day (i.e. month, season or year), which were not observed. If temporal competition for food resources occurs, it would therefore lead to circadian partitioning of the foraging activity of herbivores, as observed for waterhole utilisation (Valeix *et al.* 2007). This temporal partitioning could be observed either through observational studies or by elaborating a network of camera traps at resource patches to evaluate when different species use the same resources. Finally, if competition occurs due to elephant at the daytime scale, questions could arise about the effects of elephant-induced temporal partitioning of other herbivores' foraging activities on predator circadian activities.

1.3- On elephant-induced vegetation changes and predator kill site selection

1.3.3- The African elephant, engineer of the landscape of fear?

In Chapter 4, we did not observe any profound change associated to elephant impacts of the woody plant diversity and of the functional trait composition of the plant community. In addition, even with the increase of the observable damages over the years (accumulation and/or increase damage rate) mainly represented by the main stem broken by elephants, the overall structure (tree abundance, height, stem diameter, crown diameter) remained almost the same across the whole study period (2001-2015). Elephants did not “open the landscape” in this woodland savanna ecosystem (Laws 1970a), in spite of the very high elephant population density. Valeix *et al.* (2007a) compared vegetation structure at the landscape scale when elephant density was low and when it experienced a 16-fold increase, and they observed the same result. Neither when elephant populations are exploding, nor when they are stabilizing at high density the “extern morphology” of the woodland changes (Fig. 1 A-B).

However, we observed a strong decrease of the crown diameter for the 50-200 cm height layer. As the crown diameter is a good proxy of the volume occupied by the trees, it is expected to be directly linked to the visibility. In our system, and on the temporal scale considered, the elephants, by breaking trees and twigs, open the vegetation at the height of the main African herbivores, from the steenbok *Raphicerus campestris* (50 cm at shoulder height) to the greater kudu (160 cm at shoulder height). Our results therefore strongly suggest that the main impacts of elephants on woodland savanna are about the “intern morphology” of the woodland (Fig. 1 C-D). This is confirmed when looking at the visibility and distance to a potential ambush site in the vegetation impacted by elephants. Even if the size effect does not seem strong (+ 2 m for distance to potential ambush site, Chapter 6), it could represent a huge change in the perception of herbivores and predators (e.g. for the distance to potential ambush site; Fig. 2).

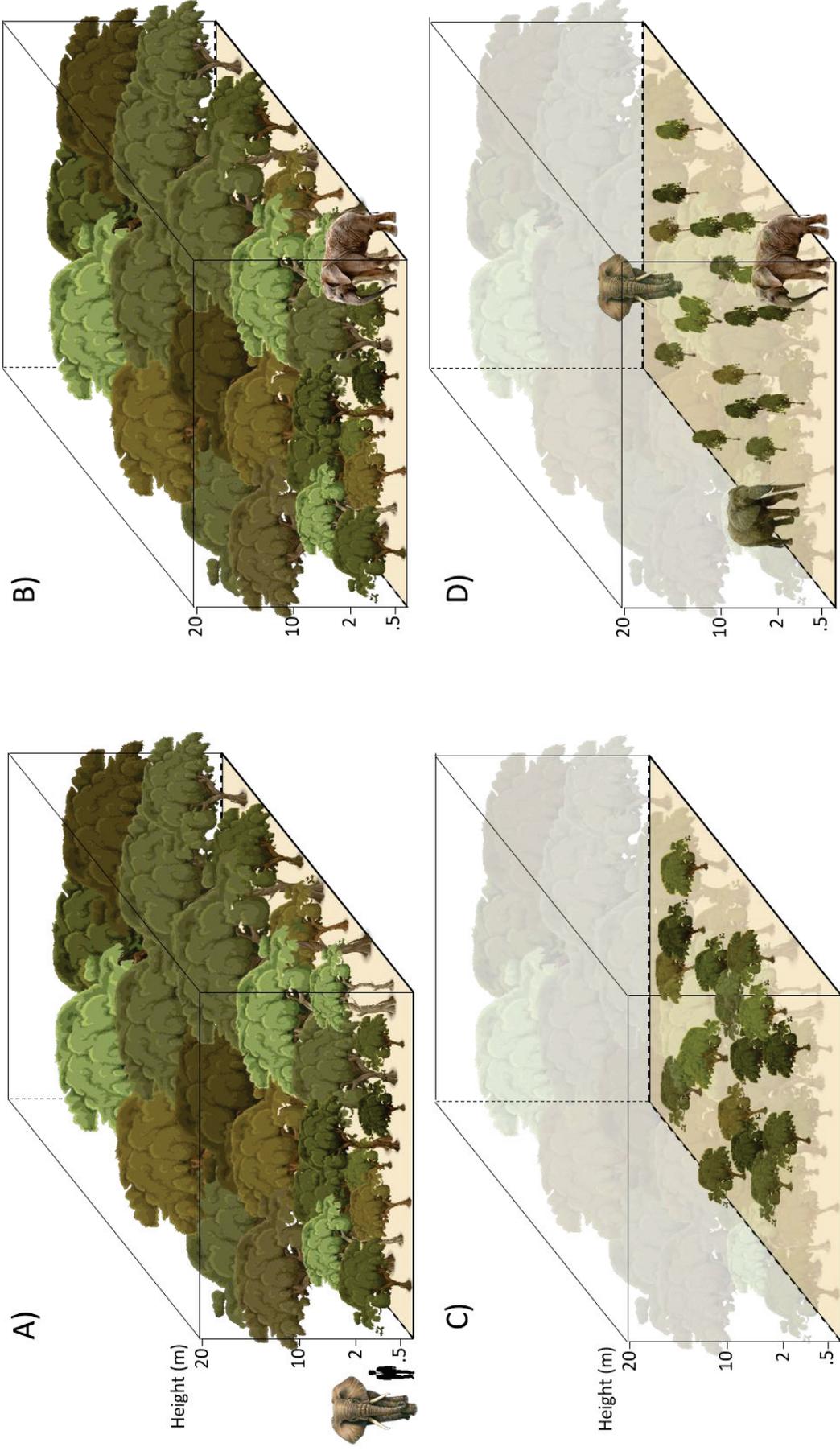


Figure 1: Schematic representation of the elephant's impact on vegetation structure, in Hwange National Park. A) and B) depict the "external morphology" of the woodland, and C) and D) the "internal morphology" of the woodland. A) and C) are habitat without elephant whereas B) and D) are habitats with high elephant density and where is observed a decrease of trees crown diameters in the 50-200 cm height layer.

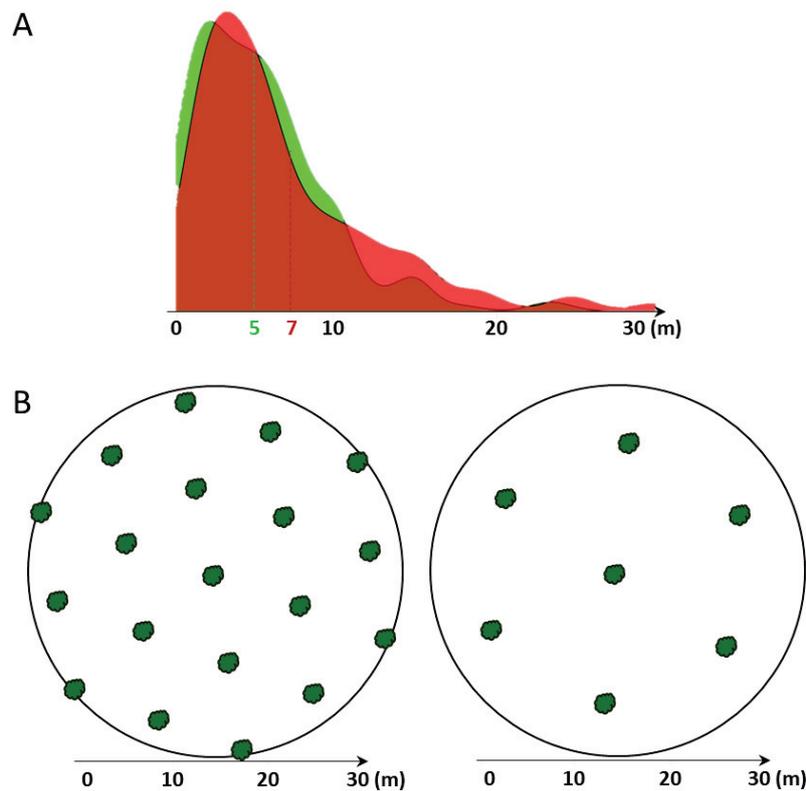


Figure 2: A) Distribution of the distance to a potential ambush site (m) for the habitats impacted by elephant (in red) and the habitats not impacted by elephants (in green). B) Representation of the difference of the distance to a potential ambush site between impacted habitat (7m, on the right) and non-impacted habitat (5m, on the left), assuming that the plants are homogeneously distributed. Green shape represents the potential ambush sites (e.g. shrubs).

When we compared the habitats where lions killed (kill sites) against the whole habitat they used and where they could have killed (used random), we observed that lions killed more in the vegetation impacted by elephants (Fig. 3 A). However, when comparing the kill sites against the directly surrounding vegetation (paired random), we observed that lions killed more in habitats with a lower distance to potential ambush sites (Fig. 3 B). While the second result could be explained by the *ambush-habitat* hypothesis, the first could not. It would be more likely that the lion kill site pattern is driven by the habitat selection of its prey. Under this scenario, lions would be disadvantaged by the elephant activity. Lions would be forced to hunt where their prey are, in the impacted habitat, but would have to deal with less ambush site and higher visibility to catch their prey. Thus, by altering the structure of the vegetation in the 50-200 cm height layer, elephants have the potential to diminish the strength of predator-prey relationships in woodland savanna habitats.

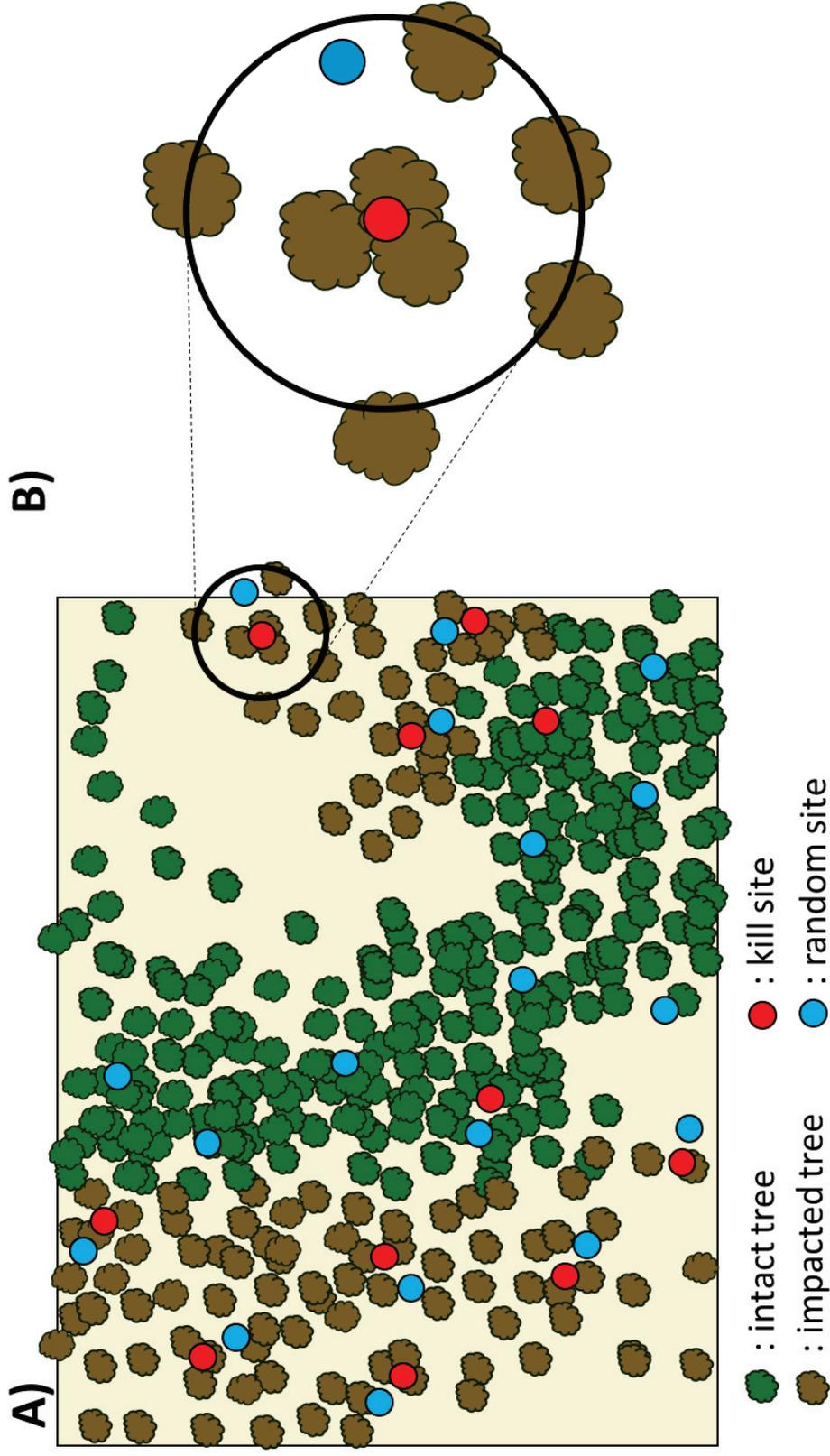


Figure 3: Lion kill site selection. Habitats not impacted are represented with intact trees (green), whereas elephant-impacted habitats are represented with impacted trees (brown). A) Comparisons between kill-sites and random sites at the scale of the areas intensively used by lions (resting, kill etc.). Lions kill sites (red circles) are located in more impacted habitats than random sites (blue circles). B) Comparison of each kill-site – random site pair (fine-scale). Lion kills are located in sites with lower distance to potential ambush sites compared to the surrounding available vegetation represented by associated random sites.

1.3.4- Limits and perspectives

As discussed in Chapter 5, we do not know what the respective roles of herbivores and predators are in the observed lion kill site patterns. Do elephant-induced vegetation changes affect predator-prey relationships by affecting prey or predators, or both? A possible way to disentangle this would be to identify the unsuccessful lion hunts. Being therefore able to identify all hunts and calculate predator hunting success would allow us to disentangle whether it is the hunting probability that is higher in elephant-impacted habitats, or the hunting success associated to these habitats, or both. A step further would then be to quantify the contextual density of herbivores when the hunt occurred. Indeed, when there are more hunts in a specific habitat, we do not know if it is a pattern driven by herbivore habitat selection or predator hunting ground selection. An alternative method to disentangle the roles of herbivores and predators would be to quantitatively model the different scenarios (and not qualitatively as in Chapter 5) taking into account the probability of prey presence, the hunting probability and the hunting success probability. If modelled patterns are well contrasted, we could identify the best model matching the observed patterns.

So far, we cannot rule out a scenario whereby there would be no causal link between elephant-induced vegetation changes and other herbivore habitat selection, and whereby herbivores would select elephant-impacted habitats only because these herbivores and elephants select the same foraging habitats. Unfortunately, we do not have experimental blocks as in Tambling *et al.* (2013) where we could assess if the resources used by herbivores and elephants are present both in the elephant-impacted and elephant-free blocks. However, Valeix *et al.* (2011) showed that elephant-impacted habitats with many broken plants present less leaves of lower quality and higher visibility. In addition, whereas the food indices did not influence habitat selection by the herbivores, the visibility indices did. These results therefore tend to support a hypothesis of herbivore habitat selection towards elephant-impacted habitats, specifically for their structure features, and do not support a hypothesis of co-occurrence of elephants and other herbivores in the same habitats because of independent selection of the same resources.

Elephants therefore have the potential to modify the landscape of fear for prey (and inversely the “landscape of hunger” for predators). By altering the structure of the vegetation in the 50-200 cm height layer, mainly by reducing the crown diameter, elephants can alter visibility and distance to ambush sites, and hence can modify, and in our study system decrease, the strength of the predator-prey relationships in woodland savanna habitats. However, this conclusion does not concord with findings from Tambling *et al.* (2013). Even if the patterns revealed between the two studies are similar (i.e. lions select woody habitats that are impacted by elephants), in their study, elephants would influence predator-prey relationships by facilitating lion’s access to dense and thorny vegetation where smaller prey

species hide. How elephants, through their impacts on vegetation, can shape predator-prey relationships is therefore not straightforward and might be context dependent. Indeed, the environment where predators and their prey live and interact can influence the response of predator-prey relationships in face of elephant activity. Starting from a very dense habitat, elephants by opening it could favour predators by increasing the accessibility to hunt small species, whereas starting from a less dense habitat, elephants by opening it could favour larger prey by increasing the visibility. However, it is difficult to compare the elephant-impacted habitats and the “intact” habitats between studies, as proxies of vegetation structure are various (e.g. visibility, tree abundances, canopy cover, etc.). Standardized protocols could help overcome this obstacle such as airborne Light Detection and Ranging (LiDAR) methods (e.g. reviewed in Bergen *et al.* 2009).

1.4- What have we learnt so far? General perspectives

The first part of this section synthesizes briefly the progresses regarding the objectives described in the general introduction and the missing steps to accomplish them. The second part presents general perspectives about indirect effects of elephants on predator-prey relationships.

In research axis 1, I studied the effect of elephants on some prey's trait at waterholes which could modify the strength of predator-prey interactions. I did not reveal changes in the anti-predator behaviour of the main study prey species (zebra). Knowledge about possible trait-mediated trophic interaction modifications by elephants at waterholes is therefore still missing, and the first step of trait modification is lacking (Fig. 4-1 – Dotted red circle) before assessing the change on trophic interactions (Fig. 4-1 – Grey dotted link). In research axis 2, I studied the competitive / facilitative effect of elephants on herbivore spatial distribution and habitat selection to ultimately assess the indirect effects of elephants on predator spatial distribution. I did not detect any spatial and habitat segregation between elephants and other herbivores (except for impala, Fig. 4-2 B), which suggests that it is unlikely that elephants indirectly affect the spatial distribution of predators through these processes (Fig. 4-2 A and B – Grey dotted arrow and gray circle). Finally, in research axis 3, I investigated the environment-mediated trophic interaction modification by elephants. I showed that elephants modify the structure of the vegetation in the 50-200 cm layer, increasing slightly the visibility and the distance to potential ambush sites (Fig. 4-3 Green shape), and could have potential effects on predator hunting behaviour (here kill site selection). However, more information is needed to know whether the trophic interaction modification is driven by the response of predators to elephant-induced vegetation changes, or if prey are the main driver (Fig. 4-3 – Grey arrow).

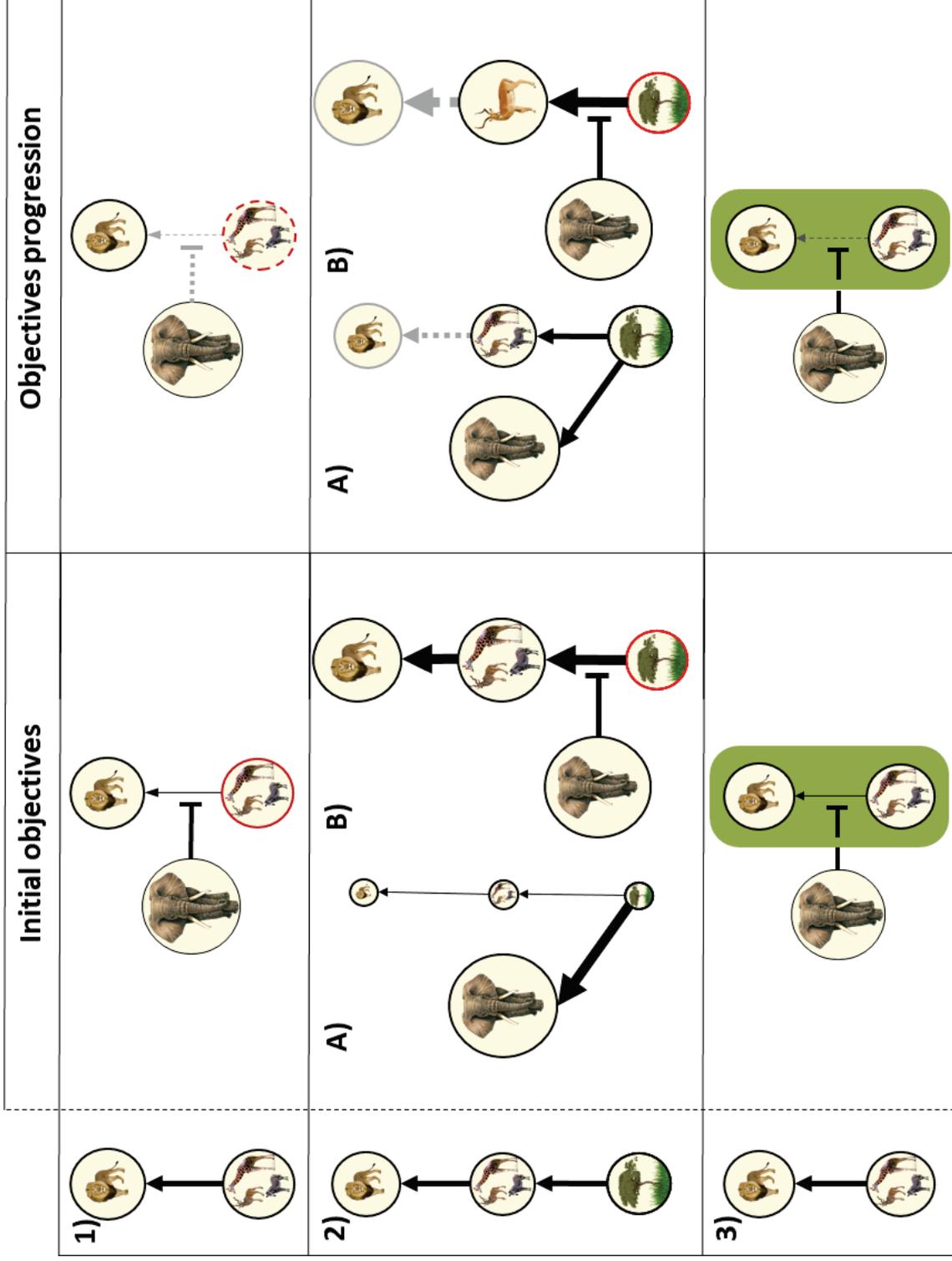


Figure 4: Synthesis of the thesis objectives and their respective progresses. Grey dotted link and red dotted circle indicate processes that are still unknown and missing steps.

Future research on the effects of elephants on trophic interactions could and should be carried on other predators than lions, particularly regarding the modification of the vegetation. Prey availability and hunting success are results of the continuous arms race in predator-prey systems resulting in a variety of predator and anti-predator adaptations (Matter and Mannan 2005). Habitat heterogeneity, by modifying prey availability along the predation process (search, encounter, kill, consumption), affects this arms race (Endler 1986). Predators select habitats that will maximize their hunting success (Hopcraft *et al.* 2005). For a stalk-and-ambush predator, the cover between itself and the prey is important (Gorini *et al.* 2012). In this thesis, I therefore assumed lions should select closed habitats, less open than those impacted by elephants. However, for pursuit, cursorial predators, the terrain through which they chase their prey is more important for hunting success than vegetation cover (Husseman *et al.* 2003, Gorini *et al.* 2012). For these predators, such as the spotted hyaena *Crocuta crocuta*, which makes up more of the predator biomass than lions in Hwange National Park (Fritz *et al.* 2011), we could expect that if elephants affect their trophic interactions through their modification of the vegetation structure, it would be the opposite way than for lions. Further, as hyaenas and lions have a high prey overlap (Hayward 2006), consequences of trophic interaction modifications by elephants on the shared prey could be confused, as these two predators would respond differently.

Finally, African elephants could influence predator-prey relationships (of lions and hyaenas) through trophic interaction chains, if they are considered as food resource in the food web. This scenario was never investigated as adult elephants are considered invulnerable to predation (Sinclair *et al.* 2003) and in most ecosystems elephants do not appear to be predated by large carnivores (e.g. Kruger, Ngorongoro and Serengeti National Parks, Fritz *et al.* 2011). However, in Hwange National Park, elephants, which represents more than 80% of the herbivore biomass, belong actively to the food web (Fritz *et al.* 2011). First, elephant carcasses due to natural mortality represent a large amount of food resource for lions and hyaenas, which are both opportunist scavengers. In addition, predation on elephants was shown to be dynamics, with elephant calves and sub-adults being more predated (active hunt or scavenging) by lions and spotted hyaenas during dry years (Loveridge *et al.* 2006 and Salnicki *et al.* 2001 respectively). Are trophic links on other herbivores also dynamics and are they synchronized to the changes in predation strength on elephants? Do predators shift their diet according to the availability of elephants as prey and do this leads predation strength on the remaining large herbivore community to be enhanced during wet years when elephants are less available for predators (Fig. 5)?

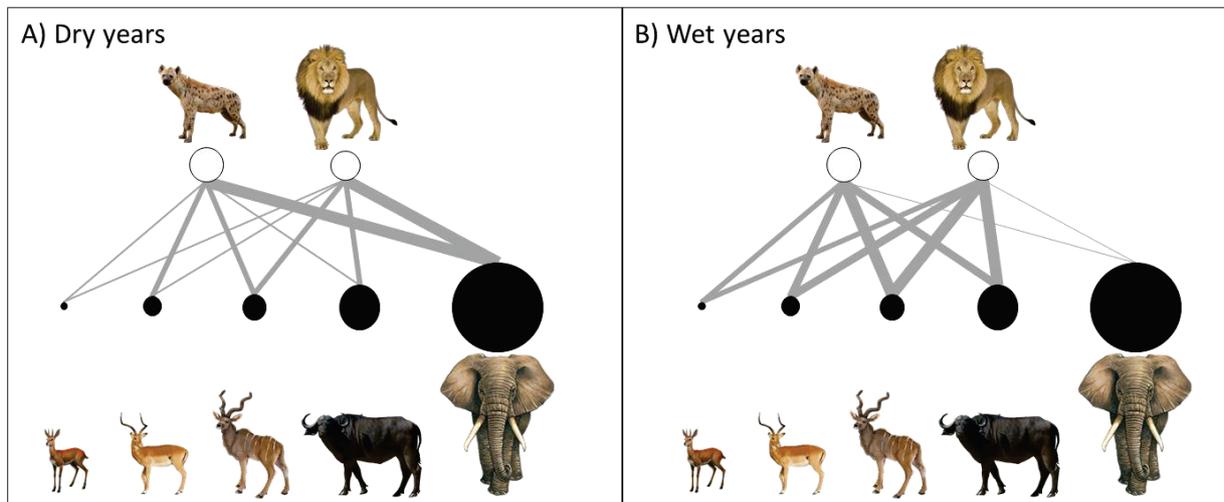


Figure 5: Expected shift of strength of the predator-prey relationships between lions and hyaenas and their prey. During dry years, sub-adult and calves' elephants are expected to represent the main food resource for these large carnivores through hunting or scavenging. During wet years, lions and hyaenas are waited to shift their diet toward smaller species (e.g. buffalo, kudu, impala, zebra) as elephants would be less available, due to higher conditions.

2 – One species to rule them all

This section of the discussion will, without surprise, focus on the role of African elephants, and its provocative title does not have the aim to minimize the effects of abiotic factors (such as fire, frost, rainfall and soil, Sankaran *et al.* 2005) and other species (e.g. impala Moe *et al.* 2014) on the structure and functioning of African savanna communities and ecosystems.

The African elephant is an iconic and charismatic species and the subject of a very profuse literature. A large part of this literature obviously concentrates on elephant itself (its physiology, behaviour, demography). More integrated views of the elephant as a component of its ecosystem have also been developed, where elephants are considered as responders to ecological changes (e.g. habitat loss Lee and Graham 2006, temporal variation of forage quality Wooley *et al.* 2009) or as agents of change in the ecosystem (e.g. on broad ecological processes, Boshoff *et al.* 2001). When looking at this last category of studies, a striking observation is the impressive attention paid to the impact of elephants on vegetation (but see Chapter 5).

In comparison, very little is known on the effects of elephants on other animal species, and the few existing studies were conducted through the role of elephant-induced vegetation changes. Laws (1970b) was the first who suggested that elephants could affect the animal community which they belong to. He raised concerns about the depletion of other wildlife in Tsavo National Park, Kenya, through elephant impacts. Barnes (1983) stated that major changes in woody vegetation density will have important implications for birds, and Hall-Martin (1990) claimed drastic reductions in bird diversities due to elephant activities in Tsavo, but as noticed by Herremans (1995) no evidence supported it. Nothing was known about elephant impact on animal communities that elephants were already labelled as agents of diversity loss... Is it the case? Debates are still ongoing (Owen-Smith *et al.* 2006) but a recent counter-view emerged as with the hypothesis of increasing species diversity and abundance thanks to ecosystem engineering by elephants.

2.1- Indirect effects of elephants on species diversity and abundance

2.1.1 On various taxa

Herremans (1995) observed a change in the bird community composition correlated to elephant impacts on vegetation in Chobe National Park, Botswana, but did not reveal a drastic loss in bird species diversity. Further, Stokke *et al.* (2014), showed in the same park a positive correlation between gallinaceous bird diversity and long-term elephant impact. Similar patterns were reported in the Addo Elephant National Park, South Africa (Chabie 1999). On the contrary, a loss of species richness for birds and ants (but not of bats) in elephant-impacted woodland was observed in the Zambesi Valley, Zimbabwe (Cumming *et al.* 1997). Pringle (2008) showed experimentally that the local density of the arboreal gecko (*Lygodactylus keniensis*) increased with the abundance of elephant-impacted trees. Further, he demonstrated that the creation of refuges attracts geckos on the impacted trees (and not increase of food resource, or just coincidence). Investigating the mechanisms underlying the patterns observed is a much-needed approach which is often lacking in such studies that mainly lead to assumptions.

2.1.2 On large mammal communities

Regarding large mammal communities, some studies highlighted correlations between elephant population changes or impacts on vegetation and changes in the population abundance of other herbivore species. In the Addo Elephant National Park, in elephant enclosure, the numbers of Cape grysboks (*Raphicerus melanotis*), bushbucks and bushpigs (*Potamochoerus porcus*) declined (Novellie *et al.* 1996). In Lake Manyara National Park, Tanzania, buffalo population growth rate increased after the removal of African elephants (through poaching), and a strong effect of resource competition on the fitness of buffalo was suggested (Prins 1996). In Amboseli basin, Kenya, an increase in the grazer biomass (zebra, wildebeest, Thomson's gazelle *Eudorcas thomsonii* and buffalo) and a decrease in the browser and mixed-feeder biomass (giraffe, impala, Grant's gazelle *Nanger granti*) were shown when elephants reduced woodlands and expanded grasslands (Western 1989). Hwange National Park and Chobe National Park have both experienced a rise of the elephant population, making them as an ideal "experiment" for studying the impact of changes in elephant abundance on ungulate communities. Historical data on herbivore population size are nevertheless often scarce and the population estimate can be far from accurate (Skarpe *et al.* 2014). Additionally, elephant abundance is not the only factor influencing other herbivore populations (e.g. dry season rainfall, Valeix *et al.* 2008). Yet, changes in the abundance of herbivore populations have been reported and occurred concurrently with the increase in the elephant population. In Chobe National Park, the abundance of buffalo and impala populations increased, and of bushbuck *Tragelaphus scriptus* population decreased in parallel to the increase of the elephant population abundance (Taolo 2003, Rutina *et al.* 2005, Dipotso 2007). In Hwange National Park, a striking synchrony between the strong increase of the elephant population abundance and the decline of other large herbivores species populations was observed after the stop of elephant culling in 1986. Indeed, mixed-feeder (impala), browser (kudu, steenbok) and grazer species (buffalo, warthog, roan, reedbuck *Redunca arundinum*, waterbuck) declined during this period (Valeix *et al.* 2008). Further, by comparing 31 natural ecosystems from East and Southern Africa, Fritz *et al.* (2002) observed negative relationships between the abundance of elephants and the abundance of mixed-feeders and browsers and suggested a strong competitive effect of elephants on mesoherbivores in savanna ecosystems with poor nutrient status.

The studies presented above mainly highlighted indirect effects of elephants on species diversity or species abundance. Hence, these studies focused on variations of the nodes (species abundance) only, and the links between the nodes (interactions) are often missing or unclear. Recent studies have been conducted to understand the role of the elephants in the observed patterns, and the processes through which elephants can affect the abundance of other species. Some hypotheses about these processes, such as competition for water (Valeix *et al.* 2007) or facilitation (Rutina *et al.* 2005, Makhabu *et al.* 2006, Valeix *et al.* 2011), were suggested and investigated.

2.2- Indirect effects of elephants on interspecific interactions

In Laikipia district, Kenya, elephants appear to reduce the competition effect of cattle on zebras. In the presence of cattle, elephants seem to facilitate the abundance of zebras by suppressing bite rates by cattle (trophic interaction inhibition), which leave the areas occupied by elephants (Young *et al.* 2005). The Addo Elephant National Park was the place of several studies focused on this issue (Kerley and Landman 2006) and are presented hereafter. Musgrave and Compton (1997) observed an increase of the phytophagous insect damages on woody plant exposed to elephant browsing, compared to woody plant in exclosures. However, we do not know if this increase is due to higher insect abundance or higher preference for impacted trees. The authors suggested an increase of the quality of browsed plants through a decline in secondary chemical compounds (e.g. tannins) but did not tested it. As Mason (1999) demonstrated that leopard and angulate tortoises preferred open habitats and avoided dense thicket, Kerley *et al.* (1999) hypothesized that elephants may increase habitat availability for tortoises, through their path and the creation of more open habitats. Kerley and Landman (2006) highlighted that the reduction of vegetation cover and density by elephants resulted in a change of the potential browse availability for black rhinoceros *Diceros bicornis*. The increase in elephant paths associated with expanded elephant densities, initially facilitates access to browse by black rhinoceros, but the subsequent dominance of the landscape by these paths results in a loss of foraging opportunities. Does this environment-mediated modification of the trophic interaction (here between rhinoceros and plants) could lead to population change in rhinoceros? In Chobe National Park, Makhabu *et al.* (2006) observed that elephants increased the number of shoots at low height levels (20-260 cm) by affecting trees. Kudus (browsers) and impalas (mixed-feeders) were observed to feed selectively on impacted trees

and at the height level with many shoots, suggesting a facilitative effect from elephants (also reported by Rutina *et al.* 2005 for impala). This food facilitation hypothesis was supported by Valeix *et al.* (2011) study but only for steenbok which used preferentially vegetation site modified by elephant characterized by higher leaf abundance. Kudus, giraffes, impalas and zebras all selected habitat modified by elephant but characterized by a higher visibility and not a higher leaf abundance. Finally, as already seen in Chapter 5, elephants could increase (Tambling *et al.* 2013) or inhibit (Chapter 5) predation strength on other herbivores by opening the vegetation.

2.3- Indirect effects of elephants on large mammals can lead to cascading effects

“Surprisingly, in the light of the history of concerns about elephant impacts in the Addo Elephant National Park, little attention has been paid to the phenomenon of ecological cascades.” Kerley and Landman (2006).

As mentioned by these authors, cascading effects of elephant indirect effects on communities were rarely investigated. For instance, if elephant activity leads to an improved access to thicket vegetation by tortoises (as hypothesised above), this could in turn increase the browsing pressure by tortoises on the low-growing succulent and geophyte flora (Mason 1999). Moe *et al.* (2014) also suggested such cascading effects in Chobe National Park, where elephants have facilitated the impala population whose density increased. This led to repercussions on the whole ecosystems (some were observed others were supposed). These cascading effects include (i) interaction chains, with facilitation and exploitative competition with other herbivore species (e.g. competition with Chobe bushbuck *Tragelaphus scriptus ornatus*, Dipotso *et al.* 2007), or maintain of rare predators feeding mainly on impala (leopard *Panthera pardus* and wild dog *Lycaon pictus*), and (ii) interaction modification, with reduction of grass cover (impala being grazers most of the year), and associated decreased in the abundance of small mammals (Saetnan and Skarpe 2006), with repercussions on the abundance of raptors and small mammalian predators (Moe *et al.* 2014).

In this second part of the discussion, I investigated indirect effect of elephants on other animals, mainly through vegetation alteration. For consistency with the topic of the thesis and because there are already lot of things to say, I considered here only interactions between organisms, and not biotic-abiotic interactions. I did not therefore encompass the effect of elephants on ecosystem processes (e.g. nutrient cycle du Toit *et al.* 2014) which could also alter communities structure and functioning. However, we can already note that much works remains to understand how elephants, beyond modifying the plant community, can indirectly affect the whole animal communities.

3 – The importance of indirect effects in communities

3.1- From food-webs to interaction-webs.

The idea that ecological communities can be viewed as linear chains of interacting carnivores, herbivores and plants (i.e. the Hairston-Smith-Slobodkin hypothesis, Hairston *et al.* 1960, or Green World Hypothesis, Pimm 1991) is considered as one of the most powerful conceptualizations of modern community ecology (Fretwell 1987, Schmitz *et al.* 2004). However, food webs exclude the many non-trophic interactions known to profoundly affect community structure and functioning (Pearson 2010). Community interaction webs were developed to incorporate non-trophic interactions into community-assembly theory (Paine 1980), but they remain underutilized (Ohgushi 2008). Food-web complexity has been addressed by partitioning webs into sub-compartments or motifs to examine the influence of different motifs on community outcomes (Rip *et al.* 2010). Conceptually, food webs could be expanded into interaction webs by incorporating hybrid motifs that include non-trophic interactions (Pearson 2010). Evidences on the importance of non-lethal, trait-mediated predator effects in trophic interactions (Peacor and Werner 2001) and trophic cascades (Schmitz *et al.* 2004, Ripple *et al.* 2016) reinforced this view. A broader integration will be achieved once it is recognized that food webs are merely a class of motifs that provide the scaffolding for more complex interaction webs (Pearson 2010, e.g. multiple plant-insect interactions on the willow *Salix miyabeana*, Ohgushi 2005, Fig. 5).

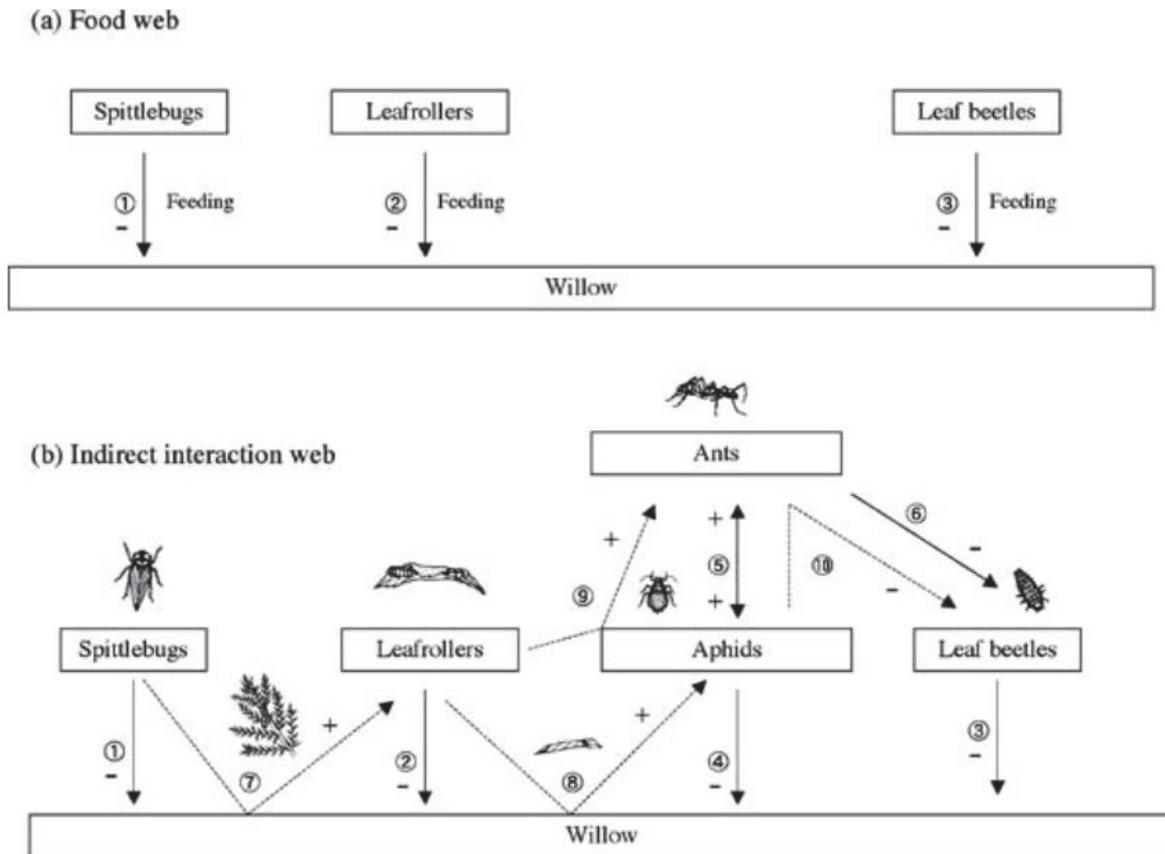


Figure 5: Comparison between a food web (*top*) and its associated indirect interaction web (*bottom*) of herbivorous insects on the willow *Salix miyabeana*. *Solid and broken lines* show direct and indirect effects, respectively. *+ and - signs* indicate positive and negative effects from an initiator to a receiver species, respectively. The spittlebug *Aphrophora pectoralis* is a specialist insect herbivore on the willow. In autumn, females lay eggs in the distal part of current shoots, which die within one week because of mechanical damage. This damage induces a compensatory shoot growth in the next year, producing longer shoots with a greater number of leaves. This enhanced shoot growth resulted in the increased density of 23 species of leafrolling caterpillars in early spring. After leafrolling caterpillars hatched and left their leaf shelters, most leaf shelters were colonized by other insects, in particular, the aphid *Chaitophorus saliniger*, which is highly specialized for utilizing leafrolls. These aphids were subjected by three species of ant that harvested aphid honeydew. The increased number of ants, in turn, reduced the larval survival of the leaf beetle *Plagioder versicolora*. From Ohgushi and references therein (2005).

3.2- From predator emphasis to herbivore reconsideration in interaction webs

As I discussed in this thesis, herbivores can be potential initiators of interaction chains and interaction modifications. Despite recognition that indirect effects initiated by large herbivores are likely to have profound impacts on ecological community structure and function (Danell *et al.* 2006), the existing literature on indirect effects focuses largely on the role of predators (Pringle *et al.* 2007). The first studies assessing the role of indirect effects in

food webs focused on the paramount role of predators (Hairston *et al.* 1960, Paine 1966), and this perhaps paved the way for the following studies on indirect effects which remained largely top-down and predator-centric (Kagata and Ohgushi 2006). This emphasis was not without justification, with empirical studies demonstrating spectacular ecological modifications in the absence of top predators (Terborgh *et al.* 2001, Estes *et al.* 2011, Ripple *et al.* 2014).

While such a top-down control in which a higher trophic level dominates populations and/or communities of lower trophic levels has been widely accepted, lower trophic levels can also propagate upward to nonadjacent higher trophic levels (“cascading upward” Hunter and Price 1992). Hunter and Price (1992) suggested a model that synthesized the top-down and bottom-up concepts for terrestrial food webs. They suggested that species at any trophic level can dominate other trophic levels due to feedback loops of top-down and bottom-up cascading effects (Hunter and Price 1992). Paine, whose work was critical in establishing the concepts of keystone predation and trophic cascades, predicted that mammalian herbivores would be found to exert “rampant indirect effects” and urged ecologists to test for them (Paine 2000). Interaction chains and interaction modifications have however been underutilized, and non-trophic interactions could therefore be more fully incorporated into ecology by simply loosening the predator-centric view of HSS (Pearson 2010). Pringle *et al.* (2007) in their study endorsed this view and observed herbivore-initiated interaction cascades on plants, arthropods and insectivorous lizards representing several trophic levels. These authors indicated that large herbivore declines can have cascading ramifications comparable with those observed in other systems after the loss of predators and thus, that large-bodied herbivores, where they still exist, might be equally critical to ecosystem function. Although remaining rare, studies of the indirect effects of herbivores on other species gain in importance (Côté *et al.* 2004, Goheen *et al.* 2004, Vázquez and Simberloff 2004, McCauley *et al.* 2006, Schmitz 2008, Fig. 5) and these indirect effects are increasingly recognized to exert powerful influences on communities and ecosystems (Foster *et al.* 2014, Daskin and Pringle 2016).

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« Tout a une fin, sauf la banane qui en a deux, »
Proverbe africain



Fin.