Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe

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Abstract: This study investigates whether increases in elephant populations may influence the structure of African savannas, and consequently may affect other herbivores through changes in habitats. Two contrasting periods in terms of elephant population densities were compared in Hwange National Park, Zimbabwe: the early 1980s and the late 1990s. Elephant population density and other ungulate population densities were estimated for a *c.* 400-km^2 area from road counts. Vegetation structure at the landscape scale was assessed using aerial photographs for the same area. All browsers and grazers declined between the early 1980s and the late 1990s, whereas elephants experienced a 16-fold increase. At the landscape scale, vegetation structure changed little with no evidence of an opening of the habitats. These results do not support any kind of medium-term facilitation between elephants and other herbivores. They rather suggest a negative effect of elephants on other herbivore species when elephants are present at high densities. This study rules out a scenario where the decrease of the different herbivore populations was caused by large changes in vegetation structure due to elephant activity.

Key words: aerial photographs, Africa, browsers, community, grazers, line transect, megaherbivores, road counts, savanna, transition matrix

INTRODUCTION

Many field studies (Ben-Shahar 1993, Buechner & Dawkins 1961, de Beer *et al.* 2006, Eckhardt *et al.* 2000, Guy 1989, Laws 1970) and some modelling studies (Baxter & Getz 2005, Dublin *et al.* 1990) have shown that elephants can play an important role in the dynamics of the structure and composition of African savannas. One of the most obvious features of elephant impact on vegetation structure is the destruction and uprooting of trees and bushes that can ultimately lead to a diminution in the area of woodland and bushland (Mosugelo *et al.* 2002). Hence, elephants are organisms that can indirectly affect the availability of resources (food and shelter) for other species by causing structural changes in woody vegetation, and can thus be considered as ecosystem engineers (Jones *et al.* 1994).

Some concerns have recently arisen that elephants, when present at high density, may influence the structure and abundance of African ungulate community. On the one hand, Fritz *et al.* (2002) have shown that there is a negative correlation between the elephant biomass and the browser biomass across ecosystems, and other studies have shown that in ecosystems where elephant numbers have increased, browser numbers have decreased (Owen-Smith 1989, Parker 1983). Browsers being herbivores that feed mainly on woody dicotyledonous vegetation (Gordon & Illius 1994, Hofmann & Stewart 1972), they consequently inhabit woodlands and bushlands. Thus, it has been suggested that one possible explanation for their decline in areas where elephant numbers have increased can be linked to elephant-induced vegetation changes that can deplete resources or alter habitats for browsers. On the other hand, in Chobe National Park, the increase in the elephant population has been correlated to an increase in some herbivore populations

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(Skarpe *et al.* 2004). This was, for example, the case of the impala population for which medium-term facilitation has been suggested, as elephants may contribute to generating more food resources for browsers (Rutina 2004, Rutina *et al.* 2005, Skarpe *et al.* 2000, 2004). Little is known about the influence of high densities of elephants on ungulate community structure and few studies have simultaneously considered vegetation structure at the landscape scale and ungulate community structure in contrasting situations in terms of elephant densities.

In this study, we used data from Hwange National Park, Zimbabwe, which provided the opportunity to use historical data to assess the evolution of both the ungulate community and the woody vegetation structure between two contrasting periods in terms of elephant abundance. Indeed, the elephant population was managed through culling and held stable up to 1986 but has increased since then, reaching one of the highest densities of the African continent (Blanc *et al.* 2005). We used data from road counts to estimate the densities of the elephant population, and of other ungulate populations (browsers as well as grazers) in the early 1980s and in the late 1990s. We also used aerial photographs that were available for the same periods to evaluate the changes in the woody vegetation structure at the landscape scale. This comparative approach aims at investigating whether an increasing elephant population induced structural vegetation changes at the landscape scale and whether this in turn affected the structure of ungulate communities.

METHODS

Study area

The study area covers $378\,km^2$ of semi-arid savanna on Kalahari sands in the northern part of Hwange National Park, Zimbabwe (19°00′S, 26°30′E) (Figure 1). The long-term mean annual rainfall is 606 mm. The vegetation community in the study area is dominated by *Baikiaea plurijuga* Harms, *Terminalia sericea* Burch. ex DC., *Combretum* spp., *Acacia* spp. and *Burkea africana* Hook.

Herbivore abundance

The abundance of herbivores in this area has been monitored with road counts following principles from the Line Transect method and the Distance Sampling theory (Buckland *et al.* 1993). Although we acknowledge that we are at the limit of the application of the Distance Sampling theory (Buckland *et al.* 1993), which requires use of straight random lines as transects, the use of roads as transects is now a standard way of monitoring animal

abundance (Pollard *et al.* 2002) and it is now admitted that straight lines are not an absolute requirement (Hiby & Krishna 2001). Hence, the densities presented here should not be considered as absolute densities but as reliable indices of absolute densities.

The same transect, i.e. the same road (Figure 1), has been regularly monitored at the end of the dry season, i.e. from August to October, during two periods: 1979–1984 (except 1983), i.e. during culling, and 1999–2005, i.e. 13 y after culling stopped. The mean annual rainfall was 586.4 mm for the 1979–1984 period and 634.4 mm for the 1999–2005 period. The fact that densities have been calculated for the same transect with the same observation and analysis techniques allows comparison of the densities for the two study periods. During the 1979–1984 period, the sampling effort was 4067 km, and during the 1999–2005 period, it was 1424 km. The difference in sampling effort was due to a difference in the number of repetitions of the transect. To be able to compare the two periods, we selected at random some repetitions from the 1979–1984 period in order to reach a similar sampling effort of 1424 km.

We calculated densities of herbivore populations for the two periods using Distance Sampling software, version 3.5, which follows the principles of the Distance Sampling theory (Buckland *et al.* 1993). To estimate densities we used the most likely detection probability function model selected using the Akaike Information Criterion (Burnham & Anderson 2002). We also based our model selection on the χ^2 goodness-of-fit test. We then expressed herbivore abundances in biomass by using the unit mass published in Cumming & Cumming (2003) to investigate the changes in the composition of the biomass density of the herbivore community.

We studied the densities of the elephant *Loxodonta africana* (Blumenbach) population and of 13 other herbivore species populations: five dry-season browsers (common duiker *Sylvicapra grimmia* (Linnaeus), giraffe *Giraffa camelopardalis* Linnaeus, impala *Aepyceros melampus* (Lichtenstein), greater kudu *Tragelaphus strepsiceros* (Pallas) and steenbok *Raphicerus campestris* (Thunberg)), and eight grazers (African buffalo *Syncerus caffer* (Sparrman), reedbuck *Redunca arundinum* (Boddaert), roan antelope *Hippotragus equinus* Desmarest, sable antelope *Hippotragus niger* Harris, warthog *Phacochoerus africanus* (Pallas), waterbuck *Kobus ellipsiprymnus* (Ogilby), blue wildebeest *Connochaetes taurinus* (Burchell) and Burchell's zebra *Equus quagga* Boddaert).

Vegetation structure

The structure of the vegetation in the study area was determined from aerial photographs. We used two sets of eight black-and-white aerial photographs available from the Surveyor General of Zimbabwe, one from 1982
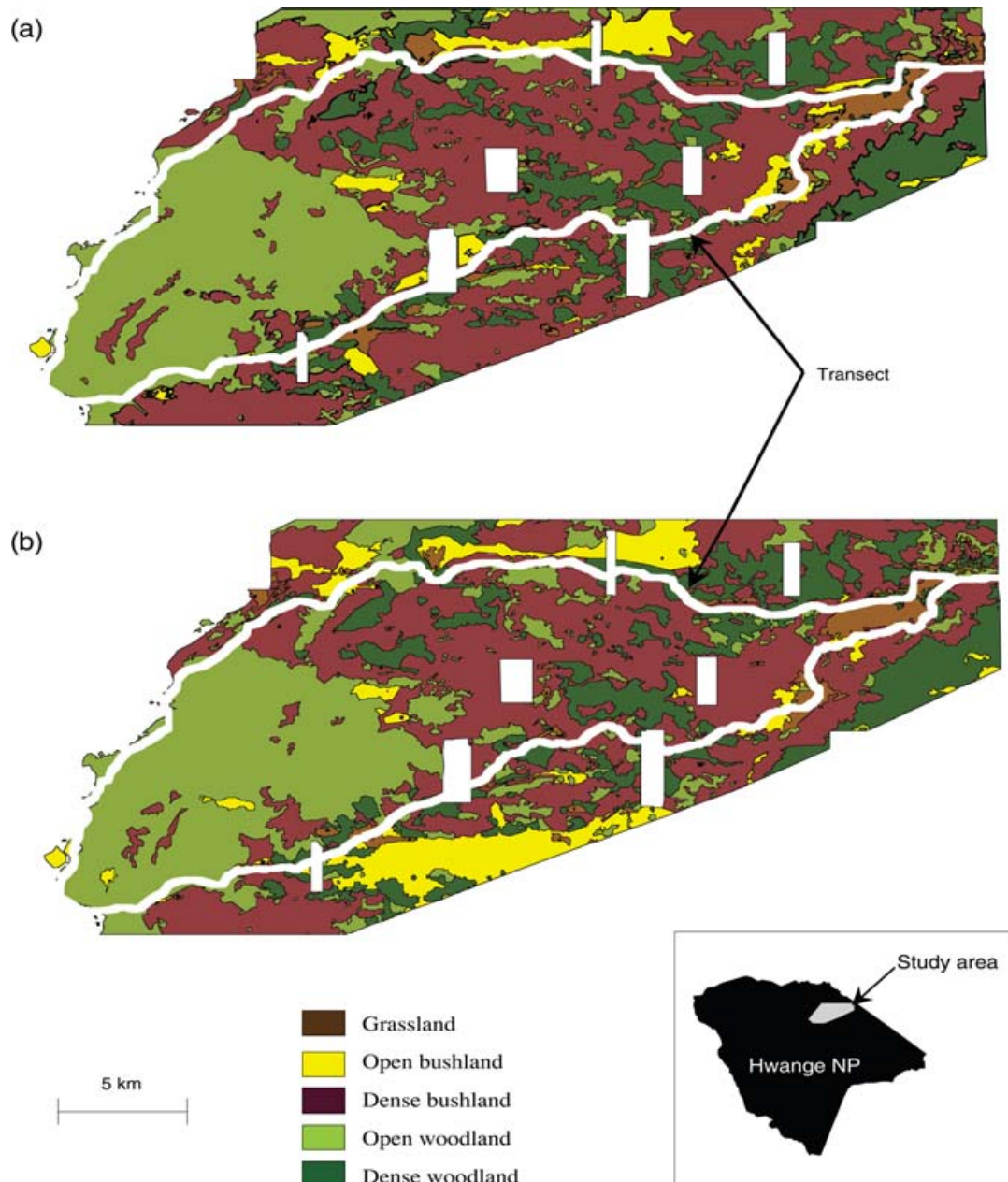
Figure 1. Maps showing the spatial distribution of the landscape units (vegetation structure) in the study area for (a) the 1979–1984 period and (b) the 1999–2005 period.

(scale: 1:80000) and one from 1998 (scale: 1:56000). After being geo-referenced, all the aerial photographs were incorporated into a Geographic Information System. A visual photographical interpretation based on grey contrasts and texture from the plane view photographs was performed by the same observer (S.D.). We discriminated five landscape units: dense woodland, open woodland, dense bushland, open bushland and grassland. The landscape unit polygons were digitized in the GIS application ArcView 3.2 (Environmental Systems Research Institute Inc., Redlands, USA) on vector format.

First, we checked that the study transect sampled the main vegetation structure classes in proportion to their abundance (in the early 1980s: $\chi^2 = 7.22$; df = 4; P = 0.125; in the late 1990s: $\chi^2 = 4.83$; df = 4; P = 0.305). Then, we calculated for 1982 and for 1998 the total area covered by each landscape unit (vegetation structure). We also studied the changes in the vegetation structure using a transition matrix. Each cell represents the proportion of the landscape that was in a particular state in 1982 (landscape unit represented by the row of the matrix) and that was in another particular state in 1998

Table 1. Comparison of herbivore population density (mean $\pm$ SD) between the periods 1979–1984 and 1999–2005. Species are grouped by feeding type. Results are from Distance Sampling analyses. Only species for which enough observations allowed reliable estimates are presented. ESW indicates the Effective Strip Width. The difference in densities between the two periods are tested by a Student's t-test (*indicates significance at a probability level of 0.05).

Species	1979–1984		1999–2005		Student's t
	Density (indiv. km^{-2})	ESW (m)	Density (indiv. km^{-2})	ESW (m)	
Elephant	0.19 ± 0.06	92	3.05 ± 0.53	156	80.0*
Browsers					
Duiker	0.24 ± 0.07	34	0.06 ± 0.02	70	12.6*
Giraffe	1.96 ± 0.53	44	1.49 ± 0.27	120	8.8*
Impala	3.94 ± 1.19	47	1.11 ± 0.31	102	22.4*
Kudu	3.78 ± 0.72	44	1.66 ± 0.27	75	32.2*
Steenbok	2.88 ± 0.37	27	0.99 ± 0.18	40	60.1*
Grazers					
Buffalo	2.07 ± 1.25	75	0.92 ± 0.53	157	2.9*
Roan	0.15 ± 0.07	78	–	–	–
Sable	0.25 ± 0.14	68	0.14 ± 0.07	174	2.8*
Warthog	0.79 ± 0.29	50	0.25 ± 0.08	115	11.7*
Zebra	1.34 ± 0.54	58	0.53 ± 0.16	203	10.0*

(landscape unit represented by the column of the matrix) (Lepart & Escarré 1983). Assuming a fixed number of possible landscape units, the transition to and from every state can be described by a single matrix.

RESULTS

Herbivore population abundance

Elephant population density has been multiplied by 16 in two decades in the study area. It increased from 0.19 ± 0.06 individual km^{-2} in the 1979–1984 period to 3.04 ± 0.53 individuals km^{-2} in the 1999–2005 period (Table 1). The numbers of observations were too low to calculate reliable densities for some species (reedbuck, waterbuck and wildebeest). For other species, all browser and grazer populations decreased significantly, and sometimes sharply, in the past 20 y (Table 1).

Effective strip widths differed between the two study periods: these were shorter for the 1979–1984 period. Hence, we also ran the Distance Sampling analyses for the 1999–2005 data with a fixed cut-off point corresponding to the effective strip width from the 1979–1984 period. The densities estimates and Student's t-test results were similar to those from the analyses without fixed cut-off points (Table 1) and are therefore not presented.

Herbivore community structure

The biomass density of the whole herbivore community nearly doubled between the early 1980s and the late 1990s: from 3865 kg km^{-2} in the 1979–1984 period, it reached 7211 kg km^{-2} in the 1999–2005 period.

Moreover, the relative importance of the species in the herbivore community changed significantly. Elephants that represented only 8% of biomass in the early 1980s (with 328 kg km^{-2}) now represent 73% (with 5253 kg km^{-2}). Browsers that represented 57% of biomass (with 2187 kg km^{-2}) now represent only 19% (with 1397 kg km^{-2}). If we exclude the giraffe, browsers dropped from 18% to 4% of biomass. The relative contribution of grazers also declined from 35% (with 1350 kg km^{-2}) to 8% (with 561 kg km^{-2}). If we exclude the biomass from megaherbivores (elephants and giraffes), the ratio of biomasses (browsers/grazers) remained rather stable (0.53 in the early 1980s versus 0.50 in the late 1990s).

Vegetation structure

Vegetation structure maps are presented for the 1979–1984 period (Figure 1a) and for the 1999–2005 period (Figure 1b). Vegetation structure did not change drastically between the early 1980s and the late 1990s. This was confirmed when comparing the global structural composition of the vegetation between the two periods (Table 2). However, the landscape itself somehow changed as the transition matrix indicates that 70.6% of the vegetation surfaces had a stable structure, while 14.6% of the vegetation surfaces became woodier, and 14.7% of the vegetation surfaces became more open (Table 2).

DISCUSSION

This study has provided a comprehensive description of the changes in species abundance and in the ungulate

Table 2. Transition matrix between 1982 and 1998. Values indicated in the matrix are percentages. The values on the diagonal indicate the proportions of the vegetation types that remained constant; values above the diagonal indicate an increase in woodiness and values below the diagonal an increase in openness.

		Vegetation 1998					
		Grassland	Open bushland	Dense bushland	Open woodland	Dense woodland	Total
	Grassland	2.1	0.4	0.6	0.2	0.4	3.7
	Open bushland	0.2	3.0	1.9	0.2	0.2	5.5
Vegetation 1982	Dense bushland	0.4	4.4	30.5	5.4	4.2	45.0
	Open woodland	0.1	0.5	3.5	23.5	1.2	28.8
	Dense woodland	0.3	0.4	3.6	1.2	11.5	17.0
	Total	3.1	8.8	40.1	30.5	17.5	100.0

community structure in the northern part of Hwange National Park, Zimbabwe, over the past 20 y. We have shown that the elephant population has increased drastically, while all other ungulate species have decreased. It is important to note that in addition to the sharp decline in browser populations, our study has also shown a decrease in grazer populations. These results do not support any kind of medium-term facilitation between elephants and other herbivores. They call for an urgent investigation of the mechanisms involved in the decline of ungulate populations.

The analysis of the two sets of aerial photographs has proven that the savanna has not become drastically more open over the past 20 y. Although the impact of elephants on mature trees is beyond question in Hwange National Park (Holdo 2003), the influence of elephants on the dynamics of the savanna at the landscape level in this ecosystem may be much more limited. Areas can be more-or-less sensitive to vegetation changes in a woodland system with increasing elephant densities depending on many factors, such as floristic composition (Nelleman *et al.* 2002). In our case, one of the dominating tree species is *Baikiaea plurijuga*, and elephant damage to *Baikiaea* woodlands is small because of its low palatability (Childes & Walker 1987). However, our results corroborate the findings from the modelling approach of Ben-Shahar (1996), which showed no substantial evidence that elephants reduce the biomass of *Colophospermum mopane* (Kirk ex Benth.) J. Léonard woodlands on a regional scale, in spite of a high susceptibility of *Colophospermum mopane* to elephant browsing and activities.

If our correlative approach suggests that elephants, when present at high density, may have a negative impact on the abundance of other herbivore species, we cannot reject more general hypotheses such as changes in dry-season rainfall, which have been advocated to explain some herbivore declines in semi-arid savannas (Dunham *et al.* 2004, Ogutu & Owen-Smith 2003). For elephant-based scenarios, our results do not support hypotheses whereby elephants would influence vegetation structure at large scale and consequently change habitats for other species over large areas. In the future, other mecha-

nisms need to be investigated. A study from Chobe National Park, a nearby and similar ecosystem, showed that elephant diet has small overlap with the diet of other browsers (Makhabu 2005). This suggests that an increasing elephant population is unlikely to deplete food resources for other browsers in such ecosystems. Consistently, our results showed that if elephant biomass increased, this was parallel to an increase of the global herbivore biomass, i.e. not entirely to the detriment of other species, suggesting that elephant diet did not overlap totally with those of other species. However, all browser species decreased, questioning the effect elephants may have on the small part of vegetation they share with other species. A small overlap in diet between elephants and other browsers may still mean a severe depletion of resources for the smaller herbivores, as the plant biomass harvested by elephants is an order of magnitude greater. We therefore feel that it would be premature to exclude this hypothesis. As elephants aggregate around waterholes in the dry season, there exists a vegetation utilization gradient, decreasing with the distance to water (de Beer *et al.* 2006, van Rooyen *et al.* 1994). We therefore suggest for future research that the spatial heterogeneity of the impacts of elephants on vegetation be carefully studied. Indeed, it is possible that elephants modify habitats of other ungulate species only in areas close to water sources. It is also possible that elephant-induced vegetation structure changes play a role either in terms of influencing plant species composition, or at a finer scale in terms of visibility as suggested by the higher visibility in the late 1990s. This last mechanism could be consistent with the fact that the species that experienced the sharpest decline were some of the smallest herbivores (duiker, impala, warthog, steenbok) more prone to predation (Sinclair *et al.* 2003), hence more vulnerable to changes in visibility. In addition, it is conceivable that the influence of elephants on other species can operate through competition for surface-water, which is a scarce resource in the Hwange ecosystem. The present work showing a correlation between the increase in an elephant population and a decline in all other ungulate populations, but with no correlation to changes

in vegetation structure at the landscape scale, underlines the need for a better understanding of the relations between elephants and other ungulates.

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