COMMUNITY ECOLOGY

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Megaherbivores influence trophic guilds structure in African ungulate communities

Abstract We used a data set of ungulate censuses from 31 natural ecosystems from East and Southern Africa to test two hypotheses: (1) megaherbivores should dominate ungulate communities in ecosystems with high rain-fall and low soil nutrient status because of their ability to survive on poor quality food resources, and (2) the abundance of megaherbivores affects the abundance of the mesoherbivores, distinguishing the different feeding guilds: mesograzers, mesobrowsers and mesomixed feeders. Two axes of a multivariate analysis (77% of the variance) discriminated the sites well, the first separating sites dominated by megaherbivores from those dominated by mesoherbivores, and the second representing a gradient between mesograzers and mesobrowsers. Our analysis shows (1) that megaherbivores can be considered to be a separate trophic guild and (2) that mesograzers and mesobrowsers respond differently to variation in their trophic environments. The metabolic biomass density of megaherbivores increased with annual rainfall, but was not related to soil nutrient status, and as predicted, megaherbivores comprised a larger proportion of the biomass of ungulate communities in ecosystems with high rainfall and low nutrient soils. The metabolic bio-mass density of mesoherbivores increased with rainfall and soil nutrient status. Within the mesoherbivores, the metabolic biomass density of mesograzers showed the same trend, and seemed unaffected by megaherbivores. Conversely, mesobrowsers and mesomixed feeders appeared to be unaffected by rainfall or soil nutrient status, but mesomixed feeders declined when megaherbivores

were abundant. This suggests that megaherbivores may compete with the mesomixed-feeder species for food or they may alter the vegetation communities unfavourably. A similar analysis using elephants alone instead of megaherbivores as a group showed that both mesobrowsers and mesomixed feeders were affected significantly by elephant, which is consistent with the fact that most of the effect of megaherbivores on browse resources or woodland habitat is due to elephants. This study shows that the different trophic guilds within African ungulate communities react differently to environmental factors (rain and soil), and that megaherbivores, and particularly elephants, appear to compete with mesomixed feeders and mesobrowsers. These results are relevant for the understanding of the functioning of African ungulate communities and call for further testing with longitudinal data.

Keywords Browsers • Grazers • Herbivory • Mesoherbivores • Savannas

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Introduction

Understanding the patterns of variation in abundance and structure of communities and the consequences for species diversity has been a focal point in ecology for many decades (Hutchinson 1959). Africa has ungulate communities of unique diversity: their species richness is at least twice that of ungulate communities in the other bio-geographic regions, even allowing for the Pleistocene extinctions (Sinclair 1983). A striking feature of these communities is their spatial variability (McNaughton and Georgiadis 1986): for example, the biomass density of the ungulate communities in different national parks varies across two orders of magnitude, 10^2 to 10^4 kg/km² (e.g. Fritz and Duncan 1994).

Previous work suggests that African herbivore abundance and community structure are primarily determined by rainfall and the nutrient status of the soil, via their effects on the quantity and quality of the primary production.

Coe et al. (1976) proposed a model describing the variation in biomass of the ungulate communities based on annual rainfall, a good predictor of primary production across the globe (Lieth 1975a; Lauenroth 1979), and specifically in sub-Saharan Africa (Le Houérou and Hoste 1977; Desmukh 1984). The model explained a large proportion of the variance in ungulate biomass, but it has been criticised for the small data set used, the limited range of annual rainfall covered (100-700 mm) and the fact that it does not take into account the soil nutrient status (Bell 1982) and other factors which influence the quantity and quality of plant resources, such as the grazing process itself (McNaughton and Georgiadis 1986). Soil nutrient status influences both plant production and quality (Die and Spear 1982) and consequently the nutrition of herbivores: for example, the nitrogen content of grass leaves on nutrient rich soils is 1.5 times that on nutrient poor soils in the Nylsvlei savanna (Scholes and Walker 1993). The level of nitrogen in grasses also de-clines more slowly in the dry season on richer soils (Scholes and Walker 1993; Prins and Olff 1998). Further, the nitrogen level in grasses on nutrient rich soils never falls below the 1% value regarded as the minimum for the maintenance of rumen micro-organisms, whereas it does on poor soils (Scholes and Walker 1993).

Fritz and Duncan (1994) extended this regional approach to a larger number of sites and included the effect of soil nutrient status: 87% of the variance in the bio-mass of wild and domestic ungulate communities is ac-counted for by variations in annual rainfall and soil nutrient status. This implies that ungulate communities in semi-arid ecosystems in Africa are generally resource limited, which is supported by the few long-term studies on African ungulate populations (e.g. Owen-Smith 1990; Mduma et al. 1999). Competition is therefore likely to play a key role in shaping these communities (though there are notable cases where the abundance of ungulates is controlled by predation and disease, e.g. Gasaway et al. 1996; see also Sinclair 1985; Fritz 1997).

The African megafauna (species whose individuals may weigh over 10^3 kg, comprising elephants *(Loxodonta africana),* the rhinos *(Diceros bicornis)* and *(Ceratotherium simum),* hippos *(Hippopotamus amphibus)* and giraffes *(Giraffa camelopardalis),* is of particular interest as these animals are relatively unselective feeders which remove large quantities of vegetation and have powerful effects on plant dynamics (Owen-Smith 1988), and hence on the biodiversity of savanna ecosystems (e.g. birds and bats in Miombo woodlands, Herremans 1995; Cumming et al. 1997). Their large body size leads to large food requirements and tolerance of low quality food (Demment and van Soest 1985; Illius and Gordon 1992). Bell (1982) first formulated the hypothesis that megaherbivores should dominate ecosystems with high plant biomass but low quality vegetation, such as dystrophic savanna wood-lands. This hypothesis has not been tested statistically. The impact of these megaherbivores, particularly elephants, on plant communities could be detrimental (competition) or beneficial (facilitation) for small- and medium-sized species, the mesoherbivores [ranging from 4 kg, dik-dik *Madoqua kirkii,* to 450 kg, buffalo *Syncerus caffer* (Coe et al 1976)]. Owen-Smith (1988) pointed out that though megaherbivores may compete with other species (because they remove large quantities of resources, or cover, see Jachman and Bell 1985; Kabigumila 1993), it is possible that feeding and trampling by megaherbivores induces regrowth of new shoots of higher quality in both the herb- and the shrub-layer, thus facilitating smaller and more selective species. A comparison between West Africa and East and southern Africa, for example, showed that in the former the medium-sized ungulates appear to have partially compensated in terms of biomass for the absence of megaherbivores (Fritz 1997), suggesting that megaherbivores (primarily elephants) have a competitive effect on mesoherbivores.

Large mammalian herbivores separate on the basis of their diet selection into grazers (consuming primarily graminoids) and browsers (consuming primarily dicoty-ledons), with mixed feeders using both resources (Hoff-man and Stewart 1972). The abundance and distribution of grass and browse vary across rainfall gradients (Lieth 1975b), so the response of the three herbivore dietary guilds to environmental gradients may differ strongly, and they need to be studied separately. We also hypothesise that mesoherbivores of different dietary guilds respond differently to the presence or absence of high bio-mass densities of megaherbivores. The direction of the influence of megaherbivores on these trophic groups cannot be predicted from theory, since both facilitation and competition can occur. However, since megaherbivores are dominated by elephant in most sites, we may hypothesise that the pattern at the regional level will reflect the fact that high biomass densities of elephants reduce browse and increase grass (e.g. Laws 1970; Dublin et al. 1990). Megaherbivores could therefore have a competitive effect on mesobrowsers and a facilitating effect on mesograzers. Mesomixed feeders are likely to respond in a similar way to mesobrowsers because they both rely on browse resources during the dry season (e.g. Jarman and Sinclair 1979).

In this paper we present results of (1) a statistical test of Bell's hypothesis that megaherbivores contribute a greater proportion of ungulate communities in ecosystems with high rainfall and low soil nutrient status, and (2) an investigation of the influence of the abundance of megaherbivores on that of the medium-sized and small species of the three trophic guilds: the mesograzers, mesobrowsers and mesomixed feeders.

Materials and methods

We use a data set of wild ungulate censuses from 31 natural eco-systems from East and southern Africa (Fritz and Duncan 1994; Fritz 1997), considering only the sites where there were no live-stock present. As discussed in Fritz and Duncan (1994), these data suffer from the well-known errors of bias and precision (Caughley 1977); however such errors will mask rather than create statistical relationships, we therefore consider that principles which emerge from this study are robust. The information collated in our data set

is from ecosystems large enough to allow seasonal movements (over 1,000 km² except for four smaller sites, all of which have been used in all previous analyses, e.g. Coe et al. 1976). They were divided in three classes of soil types (SOIL): high, medium, and low nutrient status (Bell 1982; East 1984).

The abundance of ungulates was measured as the metabolic biomass ($W^{0.75}$ kg/km²) and species were categorised into four groups on the basis of body size and diet type: the megaherbivores (MEG) and the mesoherbivores of three feeding guilds, mesograzers (MESOG), mesobrowsers (MESOB) and mesomixed feeders (MESOM, based on Owen-Smith 1982). We calculated the pro-portion of the total ungulate biomass that comprised each of the four categories of herbivores in each site. We then performed a principal component analysis (PCA) on the proportions to de-scribe variations in community composition, regardless of their overall ungulate biomass. This analysis was done at the trophic group (rather than species) level because the guilds in East and southern Africa contain different species which occupy similar niches (e.g. springbok *Antidorcas marsupialis* and Thomson's gazelle *Gazella thomsoni).*

The residuals of the regression of the metabolic biomass density of megaherbivores on rainfall (RESMEG), with soil nutrient status as a factor, were used as an index of the relative abundance of megaherbivores in the different sites (as in Rosenzweig et al. 1984 for desert rodents). We included this index as an explanatory variable with RAIN and SOIL in the ANCOVA on mesoherbivores to test for an effect of megaherbivores on the smaller species. A similar approach was used for elephant alone (RESELE).

The statistical analyses were performed with SAS Software (SAS 1990). Analyses of covariance and multiple regressions were conducted using the backwards procedure. When parametric analyses were performed on proportions, the data were first arcsine square root-transformed (Sokal and Rohlf 1995).

Results

Multivariate analysis of community structure

The first axis of the PCA explained 45% of the variance, and described a gradient from megaherbivores to meso-herbivores, with mesograzers and mesomixed feeders farther from megaherbivores than mesobrowsers (Fig. 1). This shows that there is a strong contrast between sites
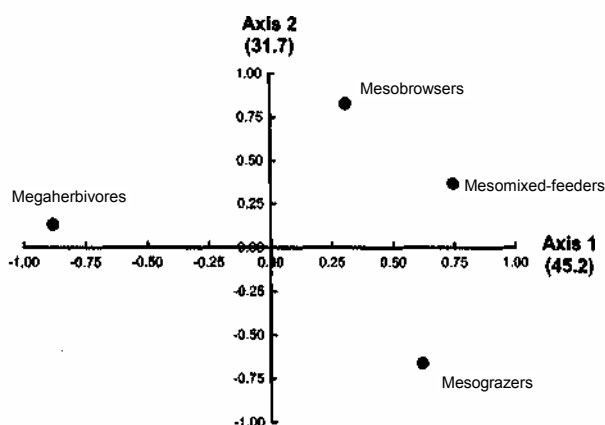
Fig. 1 Principal component analysis of the structure of the ungulate communities (% of each of the categories of herbivores) in each site. Axis 1 discriminates megaherbivores from mesoherbivores, and axis 2 describes a browser-grazer continuum. The figures in brackets for each axis are the percentage of the variance explained

Table 1 Results of the analysis of covariance with the proportion of the biomass of large herbivores represented by megaherbivores (%, arcsin transformed, PCMEG) as the dependent variable, soil nutrient (SOIL) as a factor and annual rainfall (RAIN) as a covariate. The interaction SOILxRAIN was not significant ($P>0.2$); the table shows the result of the analysis without the interaction. The model adjusted R^2 is 0.42 (all variables are Log_{10}-transformed)

Source	SS	df	Variance explained	F-ratio	P
RAIN	1.74	1	15%	6.42	0.02
SOIL	3.19	2	27%	5.90	0.01

dominated by megaherbivores, and the others. The second axis (32%) expresses a gradient from grazers to browsers within the mesoherbivores, which may reflect differences in resource availability between sites (e.g. grasslands vs shrublands). The ordination using both axes suggests that mixed feeders are closer to browsers than to grazers in the way they respond to spatial variations in the availability of plant resources.

Abundance of megaherbivores

The biomass of megaherbivores responded to rainfall only ($F_{1,29}=22.61$; $P<0.001$; $R^2=0.42$, $Log_{10}MEG= 2.99Log_{10}RAIN-6.22$). Soil nutrient status had no significant effect ($F_{1,29}=0.60$; $P>0.9$), which is consistent with the fact that these large ungulates are relatively insensitive to low forage quality (Owen-Smith 1988; Illius and Gordon 1992). We tested the first prediction that mega-herbivores contribute a relatively large proportion of the ungulate biomass when rainfall is high and soil nutrient status is poor: this is so, as rainfall and soil nutrient status make significant contributions to the ANCOVA, with soil nutrient status explaining a greater share of the variance (Table 1). The interaction SOILxRAIN was not significant ($F_{2,24}=1.53$; $P>0.2$). The proportion of the ungulate biomass represented by megaherbivores increases with rainfall for all soils, and was consistently greater on poorer soils (Fig. 2).

Megaherbivores and the abundance of mesoherbivores

On average mesograzers represented 81±15% (SD) of the metabolic biomass of the mesoherbivore community, mesomixed feeders 15±14% and mesobrowsers 4±6%. Total mesoherbivore biomass responded to rainfall ($F_{1,27}=15.75$, $P<0.001$) and soil nutrient status ($F_{2,27}= 10.81$, $P<0.001$), with the mesoherbivore biomass in-creasing with soil quality for a given rainfall (Fig. 3). There was no significant interaction between SOIL and RAIN ($F_{1,25}=1.63$, $P>0.2$).

To test for the influence of the quantity and quality of the primary production, and of the abundance of mega-herbivores on the biomass densities of the three trophic groups of mesoherbivores, we performed covariance an-
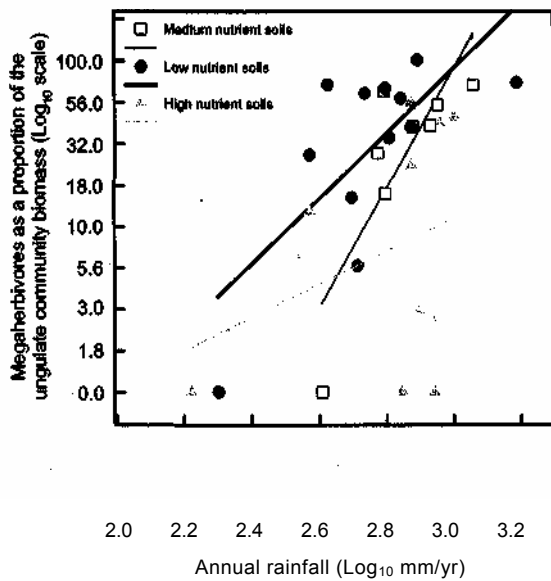
Fig. 2 Proportion of the ungulate biomass represented by megaherbivores in relation to rainfall and soil nutrient status. The equations are, for low nutrients: $Log_{10}PCMEG=0.90xLog_{10}RAIN-0.93$, for medium nutrients: $Log_{10}PCMEG=3.60xLog_{10}RAIN-8.87$ for high nutrients: $Log_{10}PCMEG=1.01xLog_{10}RAIN-1.96$

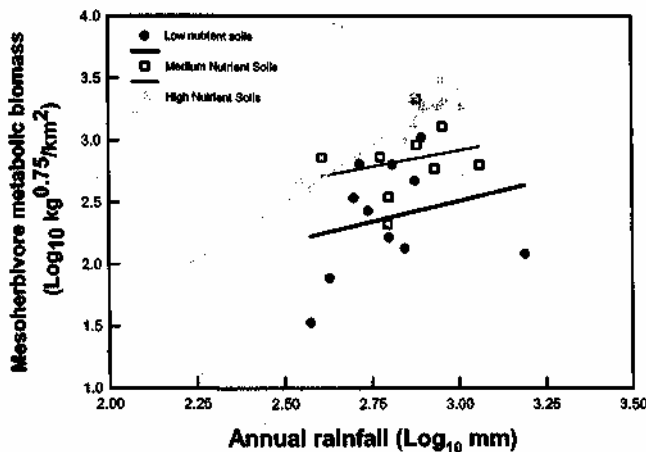

Fig. 3 Metabolic biomass densities of mesoherbivores in relation to annual rainfall and soil nutrient status. The equations are, for low nutrients: $Log_{10}MESO=0.67xLog_{10}RAIN+0.50$, for medium nutrients: $Log_{10}MESO=1.34xLog_{10}RAIN+0.52$ for high nutrients: $Log_{10}MESO=1.83xLog_{10}RAIN-2.08$

alyses with rainfall, soil nutrient status and the relative abundance of megaherbivores as explanatory variables. For mesograzers, only rainfall and soil nutrient status had a significant effect (Table 2). In contrast, for meso-browsers, there was no significant effect of rainfall ($F_{1,25}=0.87$, P>0.3), soil nutrient status ($F_{1,25}=2.12$, P>0.1) or megaherbivores ($F_{1,25}=0.70$, P>0.4). For mesomixed feeders, rainfall and soil nutrients had no effect on their abundance ($F_{1,25}=0.73$, P>0.4 and $F_{1,25}=1.64$, P>0.2, respectively), whereas RESMEG had a significant negative effect on their metabolic bio-mass ($F_{1,25}=5.23$, P=0.03). The equation of this rela-tionship was: $Log_{10}MESOM=0.55xLog_{10}RESMEG+1.53$ ($F_{1,28}=4.97$, P=0.03, $R^2=0.15$). Competition may there-

Table 2 Results of the covariance analysis with the biomass of mesograzers (MESOG) as the dependent variable, soil nutrient as a factor (SOIL), annual rainfall (RAIN), and the relative abundance of megaherbivores (RESMEG) as covariates. The interaction SOILxRAIN was not significant (P>0.3); the table shows the result of the analysis without the interaction. The adjusted R^2 is 0.69. (RAIN is Log_{10}-transformed)

Source	SS	df	Mean-square	F-ratio	P
RAIN	2.73	1	2.73	23.10	<0.001
SOIL	1.99	2	1.99	14.28	<0.001
RESMEG	0.01	1	0.01	0.07	0.79

fore occur between megaherbivores and mesomixed feeders. When we grouped the mesomixed feeders and mesobrowsers, MESOMB, as suggested in the PCA, we obtained a similar result, with a stronger relationship:

$$Log_{10}MESOMB = -0.62 \times Log_{10}RESMEG$$
$$+1.77(F_{1,28} = 9.29, P<0.01, R^2=0.26). (1)$$

Most of the effect of megaherbivores on browse resources and woodland habitats is due to elephants alone, so we carried out the same analysis with RESELE. The results showed that RESELE had a significant effect on both mesomixed feeders ($Log_{10}MESOM = -0.33xLog_{10}RESELE + 1.51$ $F_{1,28}=5.39$, P=0.03, $R^2=0.16$) and mesobrowsers ($Log_{10}MESOB=-0.21xLog_{10}RESELE+0.85$; $F_{1,28}=4.17$, P=0.05, $R^2=0.13$) whereas RAIN and SOIL remained non-significant (All P>0.10). RESELE had no significant effect on mesograzers (P>0.3).

Discussion

The results of this analysis confirm earlier suggestions, that there is a clear contrast between sites dominated by megaherbivores and those dominated by mesoherbivores. By using the proportion of the biomass represent-ed by each trophic guild rather than just the biomass, we focus on the way these guilds partition the primary production in a given ecosystem. This is equivalent to the 'dominance index' used by Cumming (1982) to assess the contribution of large herbivore species in the community biomass, and the possible effect on vegetation of their abundance. The fact that in some sites megaherbivores make up a greater share of the ungulate community than in others may not only be due to their ability to tolerate low quality food, but also be due to their ability to monopolise resources, i.e. a competitive effect.

Our results support the first prediction that megaherbivores constitute a greater part of the ungulate community biomass in sites with high rainfall and soils with poor nutrient status. The fact that the biomass of mega-herbivores seems to respond to rainfall only is consistent with the fact that these animals are primarily limited by food quantity, and not quality. If there is a competitive effect of megaherbivores, it may be stronger in ecosystems with poor nutrient status,

since their proportion of the biomass is greater than on nutrient rich soils.

Overall, the abundance of mesoherbivores was positively related to annual rainfall and soil nutrients, as previously found for the whole community (Fritz and Dun-can 1994), with almost an order of magnitude difference between their biomass on soils with high nutrient status and that on soils with low nutrient status, for a given rainfall. However, the different trophic groups within the mesoherbivores showed different patterns of response. The mesograzers responded positively to rainfall and soil nutrient status. This is consistent with the fact that grass production and peak standing crop are correlated with rainfall (Desmukh 1984), and that nitrogen content is greater on nutrient rich than on nutrient poor soils (Scholes and Walker 1993). Megaherbivores do not affect mesograzers, which is consistent with the argument that small grazing herbivores are competitively dominant over large herbivores on shorter and scarcer grass re-sources (Illius and Gordon 1987).

Mesomixed feeders and mesobrowsers did not respond to variations in rainfall and soil nutrients, which may reflect the fact that browse resources are less abundant and more heterogeneously distributed, and also that the relationship between the abundance of browse (shrubs or trees) and rainfall is not a simple one: e.g. polynomial rather than linear [see (Lieth 1975b) for data from North America], It is also possible than the absence of a relationship with these two environmental factors may be due to the height distribution of resources: the distribution of accessible plant biomass is more important for browsers than the absolute amount of plant bio-mass produced by the system (see also Du Toit 1990). The fact that mesobrowsers represented less than 5% of the mesoherbivore community metabolic biomass makes it difficult to detect patterns for this trophic guild. For mesomixed feeders, however, we found a negative relationship with the relative abundance of megaherbivores. This suggests that the megaherbivores outcompete the mesomixed feeder species for food, or else that they alter the vegetation communities to make them unfavourable for these animals, either as food resources or as cover from predators. Most of the effects of megaherbivores on mesomixed feeders or mesobrowsers should in fact be elephant effects, since only elephants have a major impact on browse resources as well as on woodland habitats. This may also explain why mesobrowsers did not respond to the relative abundance of megaherbivores as a whole. In fact both mesomixed feeders and mesobrowsers were negatively affected by the abundance of elephants, which confirms their major role in savanna eco-system, particularly those dominated by woodlands and bushlands (Bell 1982; Cumming 1982; Owen-Smith 1988). The absence of relationship with rainfall and/or soil nutrient status, for both mesomixed feeders and mesobrowsers, could thus also be due to their limitation by the competitive effect of elephants. This pattern could not result from confounded effects of soil quality and megaherbivore abundance since the soil nutrient status

of sites with relatively high and low biomass of mega-herbivores are not different ($P>0.9$; for elephants also $P>0.9$). Mesomixed feeders and mesobrowsers being smaller and more cryptically coloured are more subject to counting errors, particularly in bushed and treed habitats. Given the complex non-linear relations between woody cover, rainfall and megaherbivore abundance, it is unlikely that the negative relationship between mega-herbivores and mesomixed feeders and mesobrowsers arise from counting bias.

This study shows that the different trophic guilds in African ungulate communities react differently to variations in the abundance and quality of plants, and that megaherbivores may compete with mesomixed feeders and perhaps mesobrowsers. The difference between mesograzers and mesobrowsers (including mesomixed feeders) in their competitive relationship with megaherbivores may be a reflection of the profound differences in the grazing and browsing processes. When grazing, the larger herbivores remove large quantities of vegetation, regard-less of the quality. There is, however, still some food for a small herbivore to feed on. Hence megaherbivores may in fact facilitate mesograzers by creating favourable feeding patches (Owen-Smith 1988). In browsing, what is left by very large browsers is of such low quality (large twigs) that it is not edible for small browsers: in the case of elephants whole branches are often removed. There re-mains a theoretical possibility that elephants could facilitate mesobrowsers: recent studies in southern Africa show that elephant browsing on trees and shrubs can in-crease the density of edible shoots available to mesobrowsers (Skarpe et al. 2000). Nevertheless, the patterns shown here at the regional level strongly suggest a competitive relationship, though certainly mediated by habitat preference of each specific ungulate taxon (e.g. Green-acre and Vrba 1984). One species of particular interest among the megaherbivores is the giraffe, which could suffer from competition from elephants (N. Owen-Smith and H. Prins, personal communication); however this was not reflected in our data set ($P>0.2$).

These results are relevant for the understanding of the functioning of African ungulate communities and provide useful information for the debate on the management and regulation of overabundant herbivore populations, particularly elephants (Cumming 1981), both inside (Van Aarde et al. 1999) and outside protected areas (Hoare and Du Toit 1999). However, our conclusions call for further investigations, as competition is known to be difficult to detect from co-occurence data (Rosenzweig et al. 1985). This could be done using long-term longitudinal data on sites where the abundance of megaherbivores such as elephants has undergone major changes over time.

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