

Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa

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Summary

1. Megaherbivores have been lost from most ecosystems world-wide, and current increases in poaching of rhino and elephant spp. threaten their status in the systems where they still occur. Although megaherbivores are said to be key drivers of ecosystem structure and functioning, empirical evidence is strongly biased to studies on African elephant. We urgently need a better understanding of the impact of other megaherbivore species to predict the consequences of megaherbivore loss.

2. We used a unique 'recolonization experiment' to test how a megagrazer, white rhinoceros, is affecting the structure of savanna grasslands in Kruger National Park (KNP).

3. With a 30-year record of rhinoceros distribution, we quantified how they recolonized KNP following their re-introduction. This allowed us to identify landscapes with high rhino densities and long time since recolonization versus landscapes with low rhino densities that were recolonized more recently but were otherwise biophysically similar. We recorded grassland heterogeneity on 40 transects covering a total of 30 km distributed across both landscapes. We used two proxies of grassland heterogeneity: % short grass cover and number of grazing lawn patches. Grazing lawns are patches with specific communities of prostrate-growing stoloniferous short grass species.

4. Short grass cover was clearly higher in the high rhino impact (17.5%) than low rhino impact landscape (10.7%). Moreover, we encountered ~20 times more grazing lawns in the high rhino impact landscape. The effect of rhino on number of lawns and on short grass cover was similar to the two dominant geologies in KNP, basalt-derived versus granite-derived soils.

5. Synthesis. We provide empirical evidence that white rhinoceros may have started to change the structure and composition of KNP's savanna grasslands. It remains to be tested if these changes lead to other ecological cascading effects. However, our results highlight that the current rhino poaching crisis may not only affect the species, but also threaten the potential key role of this megaherbivore as a driver of savanna functioning.

Key-words: *Ceratotherium simum*, consumer-resource feedbacks, grazing lawn, heterogeneity, megafaunal extinctions, megaherbivore, plant-herbivore interactions, rhino poaching, role of apex consumers in ecosystem functioning, top-down ecosystem control

Introduction

The importance of top-down control of ecosystem functioning is unambiguous (Hairston, Smith & Slobodkin 1960), and the loss of apex consumers has been recognized as possibly 'humankind's most pervasive influence on nature' (Estes *et al.* 2011). Due to a lack of top-down control by predators, apex consumers typically have a disproportionate impact on the environments in which they live and, as such, may also be

defined as keystone species (Paine 1995). Much of the current attention on apex consumers focusses on the role of large carnivores (e.g. Callan *et al.* 2013). Megaherbivores, however, are an equally strong example of apex consumers that have an especially large impact on the ecosystems they live in (Owen-Smith 1988). Moreover, similar to large carnivores, megaherbivores increasingly struggle to survive in a human-dominated world.

With a body mass of ≥ 1000 kgs, megaherbivore populations are mostly limited by food availability because their large body mass means they escape top-down control by

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predation (Owen-Smith 1988). As a result, megaherbivore population size is much closer to the limits imposed by vegetation than population sizes of smaller species. Therefore, megaherbivore vegetation impact is hypothesized to be disproportionately larger than that of animals that are also controlled by predation (Owen-Smith 1987). As a result, the Pleistocene extinctions of megaherbivores have been argued to drive major historic ecosystem change, including changing fire regimes, plant communities (Gill *et al.* 2009) and cascading extinctions of other taxa (Owen-Smith 1987). The potential legacies of the Pleistocene megafauna extinctions have recently been cited among the most fundamental questions in ecology (Sutherland *et al.* 2013). The same thinking underlies recent debates on introducing extant megaherbivores to ecosystems to restore the functional roles of their extinct relatives as in the rewilding philosophy (Donlan *et al.* 2006).

Empirical studies on the ecosystem impact of megaherbivores are strongly biased to one species of megabrowser, the African elephant *Loxodonta africana* (see Kerley *et al.* 2008 for a review). There is very little contemporary evidence for ecosystem-scale impacts by other megaherbivore species. Much of the literature on extinct megafauna discusses effects on grazing systems including effects on fire regimes (Gill *et al.* 2009) and biome shifts (Zimov *et al.* 1995). However, there is very little empirical data on extant megagrazer impacts on landscape to ecosystem scales. Among the very few exceptions is the pioneering work of Norman Owen-Smith on the ecology of white rhinoceros (rhino from here on) *Ceratotherium simum* in Hluhluwe-iMfolozi Park (HiP) in the late 1960s and early 1970s (Owen-Smith 1988) and work by Waldram, Bond & Stock (2008) showing how rhino influence grassland heterogeneity and fire regimes in the same reserve. However, HiP represents an area with very high rhino densities where conservation management has been focused on maintaining these densities. In addition, it is a relatively small fenced reserve, and its high rhino densities may be a classical example of a fence effect, where fencing maintains relatively high densities through limiting dispersal (as suggested by Owen-Smith 1988). Hence, the question is to what extent can HiP serve as a model system for megagrazer impact and do white rhino have similar ecological impacts in other systems where they were recently re-introduced after a long absence?

As Paine (1995) discussed, a robust way of testing potential ecosystem effects of keystone species is experimental manipulations of population numbers. Yet, carefully designed, controlled experiments with different levels of megaherbivore numbers are hard to accomplish practically and ethically. An alternative lies in finding well-documented natural experiments, such as re-introductions of megaherbivores. The unique, spatially explicit, long-term data set on the recolonization of Kruger National Park (KNP), South Africa, by white rhino gave us such an opportunity for studying the ecosystem impact of a returning megagrazer. White rhino went extinct in KNP in 1896, due to intense hunting, and were re-introduced during the 1960s (Pienaar 1970). Re-introduction of rhino to KNP has been very successful, and rhino numbers have increased

strongly to an estimated 10–11000 individuals in 2010 (Ferreira, Botha & Emmett 2012). However, rhino have not yet recolonized all parts of KNP to the same extent. As a result, the recolonization of KNP by rhino has created a natural experiment of rhino impact, with areas in KNP varying in the time since they were colonized by rhino, and in their local rhino density.

We used this natural experiment to see if, and how, rhino have started changing the structure of KNP's savanna grasslands. In doing so, we present some of the first empirical data on potential ecosystem-scale impacts of returning a megagrazer into the landscape. Our study is now especially relevant in the light of the current rhino poaching crisis in South Africa (Biggs *et al.* 2013). Current poaching rates may wipe out wild rhino populations within the next 20 years (Ferreira, Botha & Emmett 2012). Our results contribute to understanding the effects of their possible elimination.

Materials and methods

STUDY SITE

Kruger National Park is situated in the north-eastern corner of South Africa bordering Mozambique in the east and Zimbabwe in the north (24.01°S, 31.49°E). The KNP is 350 km long and ~60 km wide and was proclaimed as a national park in 1926 with some parts protected since 1898. Climate is subtropical and rainfall in the park ranges from 400–500 mm annually in the north to 500–700 mm in the southern sections (Venter, Scholes & Eckhardt 2003). The climate is strongly seasonal; most of the rain falls occur during the wet summer season from November to April. The ~19 000 km² of KNP are covered with arid to semi-arid savanna. The KNP is geologically divided into granite-derived soils in the west and basalt-derived soils in the east. This strongly influences the overall landscape and vegetation types with more open, productive, grasslands on the basalts and denser bushland savanna on the granites (Venter, Scholes & Eckhardt 2003).

White rhino went extinct in KNP in 1896. Between 1961 and 1972, a total of 336 rhino were successfully released into different sections of KNP (Pienaar, du Bothma & Theron 1992), 330 in the southern part of KNP and only six in northern Kruger (Pienaar 1970; Fig. 1a). No rhino have been released in the central area of KNP between the Sabie and Olifants rivers (D.J. Pienaar, unpubl. data). Although rhino were observed to have crossed the Sabie river as early as 1964 (Pienaar 1970), 30 years later in 1991, there were still only an estimated 197 rhino between these two rivers, <10% of the 2000 rhino that were estimated to live in the whole of KNP (Pienaar, du Bothma & Theron 1993). Of the 330 rhino released in southern Kruger, 315 were released on the granite-derived soils along the western border of the park, and only 15 on the basalt-derived soils in the east (Fig. 1a).

QUANTIFYING RHINO RECOLONIZATION AND DENSITY DISTRIBUTION PATTERNS

To design our study of rhino impact, we first mapped the rhino recolonization pattern and their density in more detail using data from two different aerial census counts: fixed-wing counts that census all ungulate species and helicopter counts that specifically target megaherbivore species. The fixed-wing counts were flown annually, conducted as total counts, from 1980 to 1993, covering the entire KNP except

for the most northern tip, on adjacent transects 800 m apart. Since this period, the fixed-wing counts are conducted as sample counts, still covering the full extent of KNP, but with transects further apart (3–4 km until 2001, 5–6 km from 2001). The helicopter counts have been performed annually for white rhino since 1989 and cover the whole park following a total count approach. For more detailed information on both methods, see Smit, Grant & Whyte (2007). We combined fixed-wing census data from 1980 to 1988 and megaherbivore count data from 1989 to 2010 to create a rhino recolonization map for the entire KNP except for the most northern sections. Using ESRI ArcGIS 10.0, we overlaid these data with a grid of 2 by 2-km cells. We determined colonization of all grid cells as the first year that a rhino was counted in a grid cell. This gave us a map with time since colonization by rhino for the entire KNP with a 4-km² resolution. We used this map as a proxy for *duration* of potential rhino impact. As a proxy for *intensity* of rhino impact over the past 20 years, we created a rhino density map for the entire KNP by estimating a quadratic kernel density (Silverman 1986) using all 1989–2010 white rhino helicopter counts. Using the spatial analyst tool in ArcGIS 10, we estimated a weighted kernel using rhino group size as a weight for each sighting. Kernel density in this case reflects the aggregated observation density (number of rhino observations from the helicopter between 1989 and 2010 for a given kernel pixel). Due to the current rhino poaching crisis, there is an embargo on publishing detailed spatial distribution data of white rhino in KNP. Hence, we cannot show any of the recolonization and kernel density results in detail and have to limit ourselves here to a general description. Both analyses showed that KNP can be divided in three areas that differ strongly in time

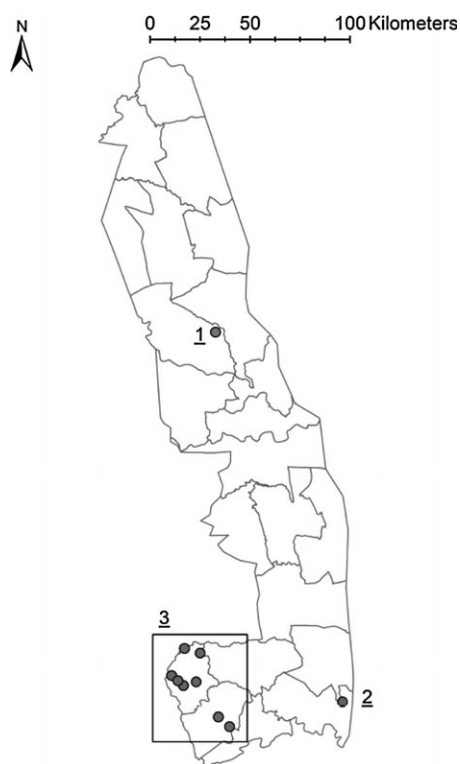


Fig. 1. Overview of the study area, Kruger National Park (KNP), showing original release sites, blue dots, of white rhino during the 1961–1972 re-introduction phase; 15 rhino were released in each of site 1 and 2, while 315 rhino were introduced in the sites within box 3 (Pienaar 1970, D.J. Pienaar, unpubl. data). Lines show KNP's management section boundaries.

since colonization by rhino and rhino density. These three areas are split by two main rivers that form strong recolonization barriers. By 1988, 80% of area A had already been colonized by white rhino, versus 30% of area B and only about 10% of area C (Fig. 2). In 2010, just before we performed our study, the whole of area A had been colonized by rhino versus 86% of the area B, and still only 40% of area C. Hence, there is about a 20 years' time lag in recolonization of area B versus area A and even slower recolonization of area C (Fig. 2). In addition to a difference in time since colonization, the areas also clearly differ in kernel density. Average rhino observation density was four times higher in the management sections in area A (8.6 observations per km² between 1989 and 2010 \pm 0.97 SE) than in area B (2.0 \pm 0.28 SE), and very low in area C (0.23 \pm 0.04 SE).

DESIGN OF A NATURAL EXPERIMENT

Based on the recolonization and kernel density patterns, we decided to treat areas A and B as two levels of a rhino impact factor, where we assume that area A with its longer history and higher density of rhino has experienced relatively higher rhino impact (from here on 'high rhino impact area') than area B which has been colonized more recently and still has much lower rhino densities ('low rhino impact area'). Hence, we use an approach similar to that of Landman & Kerley (2013), which assumes that longer presence, and higher mean densities, leads to higher impact. We did not include area C because we wanted to study rhino impact within areas with a generally similar landscape and abiotic setting to avoid an effect of confounding factors. We also included geology as a treatment since initial introductions were strongly biased towards the granite-derived soils. Hence, we focused on the following two landscapes in KNP: the *Combretum* spp. and mixed *Combretum* spp. *Terminalia* spp. woodland savanna on the granitic plains and the *Sclerocarya birrea* or *Acacia nigrescens* tree savanna on the basaltic plains. These landscapes are relatively homogenous in

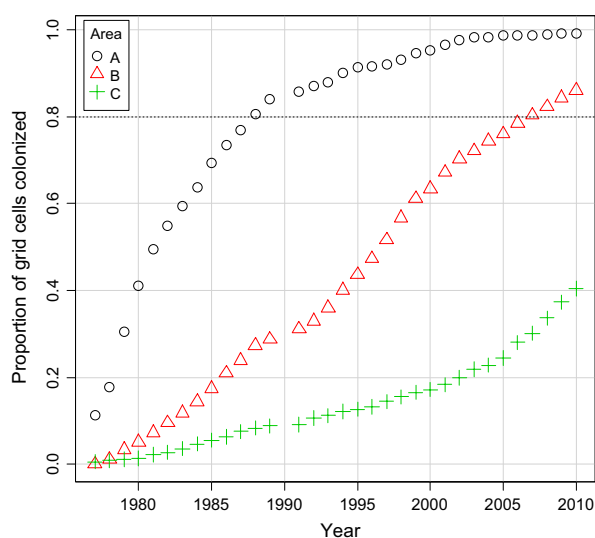


Fig. 2. Proportion of 2 by 2-km grid cells of three different sections of Kruger National Park (KNP) that were colonized by white rhino for each of the years 1977–2010. The three sections A, B, C represent three areas that together cover the whole of the KNP. Each area shows a distinctly different recolonization pattern, where most of area A was colonized by the mid-1980s, while only 20 years later most of area B had been colonized. Most of Area C still remains to be colonized.

geomorphology, climate, soil and vegetation (Gertenbach 1983). We chose these two landscapes because they are among the most common landscape types in areas A and B and, as such, representative. With the 'Rhino impact' and 'Geology' factors, we created a full-factorial design with four treatment combination blocks: an area with long history of colonization and high rhino density on granitic soils (high rhino impact on granite), an area with shorter history of colonization and lower rhino density on granites (low rhino impact on granite), an area with long history of colonization and high rhino density on basalts (high rhino impact on basalt) and an area with shorter history of colonization and lower rhino density on basalts (low rhino impact on basalt). In each treatment combination area, we quantified grassland heterogeneity on 10 transects of 750 m, totalling a number of 40 transects with a total length of 30 km.

Using available GIS layers, we distributed transects according to a stratified random sampling scheme to control for factors that likely also influence grassland heterogeneity, including rainfall, fire frequency, and tree cover. As a result, rainfall, fire frequency, and tree cover did not differ between high and low rhino transects (rainfall: $t_{38} = -0.70$, $P = 0.49$; fire: $t_{38} = -0.38$, $P = 0.71$; tree cover: $t_{38} = -0.28$, $P = 0.78$). To further reduce possible confounding effects, we placed all transects on and along the crests of catenas, especially to avoid measuring grassland heterogeneity created by typical catenal effects, for example, presence of sodic sites along footslopes (Grant & Scholes 2006). Hence, there was no difference in altitude between high and low rhino transects ($t_{38} = -0.32$, $P = 0.75$), with an average altitude of around 300 m. We also positioned transects at least 1 km away from artificial water points and main rivers and kept them 200 m away from roads. On the granites, we placed transects at least 1 km away from areas with a gabbro geology, which are basaltic intrusions into the granites. While controlling for all these environmental factors, we maintained a strong rhino presence contrast. Using the transects to extract our helicopter count kernel density estimates, we found that rhino observation density between 1989 and 2010 was about four times higher on high rhino (11.3 observations per km² ± 1.1 SE) than on low rhino (2.9 ± 0.4 SE) impact transects ($t_{38} = -10.67$, $P \ll 0.001$), reflecting the overall difference between area A and B that we described earlier.

QUANTIFYING GRASSLAND HETEROGENEITY

We quantified grassland characteristics during the January and February wet season months of 2011. Every 2 m along each 750-m transect, we recorded the following characteristics of the grassland: grass height using a disc pasture metre (DPM, Bransby & Tainton 1977), % cover of grass underneath the DPM disc, number of dung pellet groups per ungulate species and whether the 2-m plot was in a grazing lawn state (yes/no). We defined the 2-m plot as a grazing lawn state if >50% of the plot was covered with stoloniferous, prostrate-growing grass species, and the grass height was not higher than 4 cm (see Cromsigt & Kuijper 2011 for a more extensive definition). In addition to quantifying the number of grazing lawns, we also tested for an effect of rhino on the proportion of short grass in the system. We calculated this as the proportion of 2-m transect-fragments that were covered by short (but not necessarily stoloniferous) grass. Following Waldram, Bond & Stock (2008), we defined short grass as 2-m fragments with ≥50% grass cover and <7 cm in height. Hence, we test rhino impact on two measures of grassland heterogeneity: (i) number of grazing lawns per transect, (ii) proportion of transect covered by short grass, where (i) represents a subset of (ii).

DENSITY DISTRIBUTION OF OTHER GRAZERS ACROSS OUR TREATMENT COMBINATIONS

We controlled for variation in the most important environmental factors with our stratified design, but the effects of rhino on grassland heterogeneity could also be confounded by the presence of other large grazers. Although we counted dung to assess the distribution of other grazers, such counts are not always the best proxy for herbivore distribution and abundance. To account for this, we used the fixed-wing aerial count data, described above, as an additional data set to estimate densities of the five common large grazers (impala *Aepyceros melampus*, warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus*, African buffalo *Syncerus caffer* and plains zebra *Equus quagga*) and the two relevant megaherbivores (elephant and white rhino). We then estimated aggregated kernel observation density maps for each species using the same procedure as described above for the helicopter counts. We used fixed-wing data from 1980 to 2010, although the years 1994 to 1997 were left out because the whole park was not covered during these years and data for 2008 to 2009 was not available (resulting in a total of 25 years). After calculating kernel observation density maps for each species, we then created buffers around each of our 40 750-m transects, with a radius of 1 km (~5 km² buffers) and estimated the average kernel density per transect area. We compared the white rhino fixed-wing counts with the helicopter counts described above as an independent control of rhino density distribution patterns. The kernel density estimates from helicopter and fixed-wing counts for white rhino correlated very strongly ($r = 0.92$, $P < 0.001$).

DATA ANALYSIS

We performed a factorial analysis, not a gradient analysis. Hence, 'Rhino impact' took the form of a factor with two levels (high versus low) instead of a covariate. We went for this approach because the main contrast in rhino density and colonization occurred between our High and Low rhino area and not among transects within each area. We started our analyses with the full-factorial models, including the rhino impact and geology factors and their interaction term and the following response variables: number of lawns per transect, proportion short grass per transect and kernel densities of all herbivore species per transect. We used generalized linear models and included a Poisson family in the case of count and kernel density data and a binomial family in the case of proportion data. To correct for possible overdispersion, we used quasi-Poisson distributions (Crawley 2007). We used ANOVA tables to assess the significance of the different fixed factors (Table 1). We estimated effect sizes (odds ratios) for the most parsimonious models following backward selection where we used deviance ratio F -tests to assess whether a given parameter could be removed (Crawley 2007). All analyses were done in the statistical environment R version 3.0.2 (R Development Core Team 2012).

Results

NUMBER OF LAWNS AND PROPORTION OF SHORT GRASS ALONG RHINO AND GEOLOGY CONTRASTS

The rhino impact treatment influenced the number of lawns and the proportion of short grass in the landscape, and this effect did not depend on geology (Table 1, interaction NS). We were 20.9 times less likely to find grazing lawns in the low rhino impact than in the high rhino impact landscape

Table 1. ANOVA results for the fixed factors 'Rhino impact' ('Rhino' in table), 'Geology' and their interaction term used in generalized linear models for the different response variables (binomial regression in the case of % short grass, Poisson regression for other response variables)

Response variable	Predictor	d.f.	Deviance	Resid. d.f.	<i>F</i>	<i>P</i>
Lawns (<i>n</i>)	Rhino	1	67.1	38	20.2	<0.001***
	Geology	1	0.06	37	0.02	0.89
	Rhino:Geology	1	4.1	36	1.2	0.27
% Short grass	Rhino	1	144.7	38	†	<0.001***
	Geology	1	367.5	37	†	<0.001***
	Rhino:Geology	1	0.23	36	†	0.63
White rhino density	Rhino	1	109.0	38	68.6	<0.001***
	Geology	1	12.4	37	7.8	0.008**
	Rhino:Geology	1	0.4	36	0.24	0.63
Elephant density	Rhino	1	0.06	38	0.04	0.85
	Geology	1	0.05	37	0.03	0.87
	Rhino:Geology	1	0.4	36	0.23	0.63
Wildebeest density	Rhino	1	32.0	38	2.0	0.16
	Geology	1	384.1	37	24.0	<0.001***
	Rhino:Geology	1	0.0	36	0.0	0.99
Zebra density	Rhino	1	39.4	38	3.7	0.06
	Geology	1	377.5	37	35.2	<0.001***
	Rhino:Geology	1	8.0	36	0.7	0.39
Buffalo density	Rhino	1	3.3	38	0.5	0.50
	Geology	1	207.9	37	29.7	<0.001***
	Rhino:Geology	1	71.8	36	10.2	0.003**
Impala density	Rhino	1	1022.4	38	16.4	<0.001***
	Geology	1	8.3	37	0.13	0.72
	Rhino:Geology	1	1.6	36	0.03	0.87
Warthog density	Rhino	1	12.3	38	11.6	0.002**
	Geology	1	36.5	37	34.4	<0.001***
	Rhino:Geology	1	5.8	36	5.5	0.03*

The deviance is shown relative to the null model, which reflects the overall mean of the response variable. Predictor terms were added sequentially. *F*-tests were used for the quasi-Poisson regressions of lawn numbers and herbivore densities, while chi-square tests were used for the binomial regression of % short grass (Crawley 2007). **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

†Deviance values represent the chi-square values.

($t_{38} = -2.7$, $P = 0.0097$). We found on average 3.15 (± 0.94 SE) lawns on a 750-m transect in the high rhino impact area versus only 0.15 (± 0.11 SE) in the low impact area (Fig. 3a). Lawns had an average diameter of 4.0 m (± 0.34 SE).

The likelihood of finding short grass patches was 1.8 times lower in the low rhino impact than in the high rhino impact landscape ($z_{37} = -12.0$, $P < 0.001$), and this effect of rhino did not depend on geology (Table 1, interaction NS). In addition to an effect of rhino, the proportion of short grass also differed between the two geology types (Table 1). Short grass patches were 2.5 times more likely on granite-derived soils than on basalt-derived soils ($z_{37} = 18.5$, $P < 0.001$). On the granites, the percentage of short grass increased from an average 15.09% (± 1.96 SE) in the low rhino impact landscape to 23.89% (± 4.21 SE) on the high rhino impact landscape, while on the basalts, the percentage of short grass increased from 6.35% (± 1.60 SE) to 11.17% (± 3.14 SE) (Fig. 3b).

ABUNDANCE OF GRAZER SPECIES ALONG RHINO AND GEOLOGY CONTRASTS

We counted the following numbers of dung pellet groups per herbivore species other than rhino summed over all transects:

145 elephant, 83 white rhino, 15 impala/nyala-sized, 96 buffalo, 27 zebra, five warthog, eight black rhino, three duiker-sized, one bushpig, three hare, and 11 kudu/giraffe-sized. Coefficients of correlations between dung count and kernel density values for each transect were very low and not significant (Pearson $r \leq 0.17$, P -value ≥ 0.30). The only exception was the correlation between impala dung and kernel density ($r = 0.33$, P -value = 0.04), despite the very small number of pellet groups counted for this species. Based on these results, we decided not to use the dung counts to test for treatment effects on other grazer species but rather focus on the kernel density estimates (Fig. 4).

White rhino were observed 7.4 times more often in the high rhino impact area than in the low impact area between 1980 and 2010 ($t_{37} = 6.7$, $P < 0.001$), and they were observed 1.8 times more often on granites than on basalts ($t_{37} = 2.8$, $P = 0.009$); there was no interaction between geology and rhino impact areas on rhino densities (Table 1). Observed densities of elephants, the other megaherbivore in the ecosystem, were unrelated to either geology or rhino impact areas (Table 1). Among the other large grazers, observed wildebeest densities were unrelated to rhino impact areas (Table 1) and were 66.7 times greater on basalts than granites ($t_{38} = 4.2$, $P < 0.001$). Zebra densities tended to be

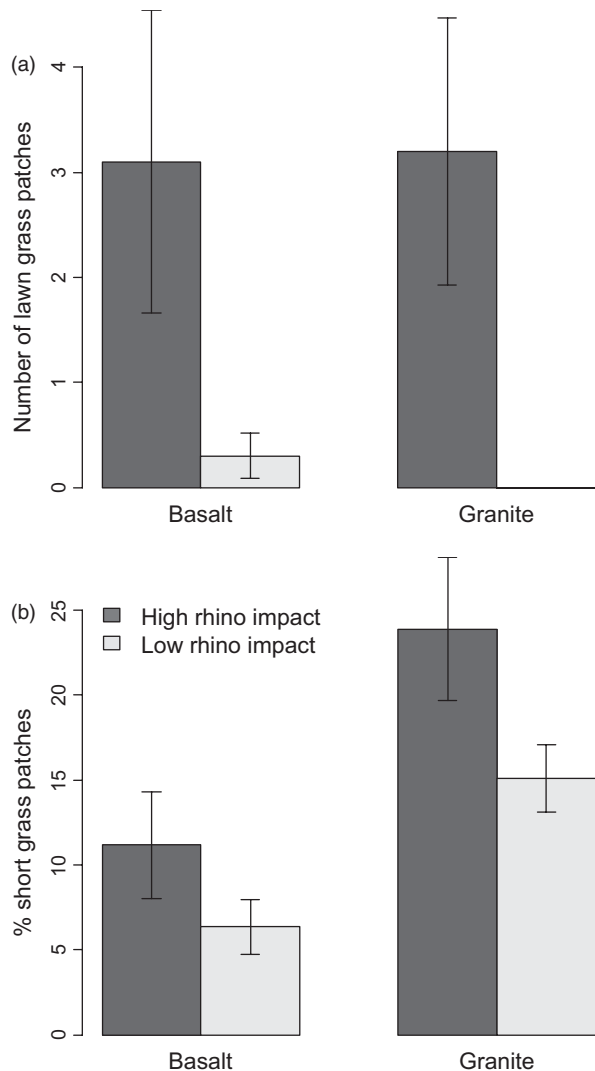


Fig. 3. (a) Average number of lawns per 750-m transects. We found no lawns in the low rhino area on granites. (b) Proportion of 750-m transects covered with short grass patches ($\geq 50\%$ grass cover and grass height < 7 cm). Bars show the mean values and whiskers the standard errors of the mean.

greater in low rhino impact areas ($t_{37} = 1.9$, $P = 0.06$) and their densities were 3.7 times greater on basalts than granites ($t_{37} = 5.4$, $P < 0.001$); there was no geology \times rhino impact interaction (Table 1). Buffalo densities were overall c. 10 times greater on basalts than granites ($t_{36} = 4.5$, $P < 0.001$), but when on granites, their densities were 5.5 times greater in low versus high rhino impact areas ($t_{36} = 2.9$, $P = 0.006$; significant geology \times rhino impact interaction, Table 1). Impala densities were 2.5 times greater in high versus low rhino impact areas ($t_{38} = 3.9$, $P < 0.001$) and were unrelated to geology. Warthog densities on basalts were 2.2 times greater in high versus low rhino impact areas ($t_{36} = 4.0$, $P < 0.001$) but conversely on granites they were slightly (1.05 times) greater in low versus high rhino impact areas ($t_{36} = 2.3$, $P = 0.03$; significant geology \times rhino impact interaction, Table 1).

Discussion

We present some of the first data of landscape-level impacts of a reintroduced megagrazer. The number of grazing lawns and proportion of short grass were clearly higher in landscapes in KNP that white rhino colonized early on and where they occur in higher densities. Grazing lawns were close to absent in the low rhino impact landscape and the proportion of short grass 60–80% lower than in the high rhino impact landscape. These results confirm those of Waldram, Bond & Stock (2008) who used the rhino removal programme in HiP, South Africa, as a natural experiment. In this programme, rhino are removed from predefined areas to re-introduce them in other reserves. Waldram, Bond & Stock (2008) showed that the percentage of short grass cover around wallows was lower in areas where rhino had been removed than around wallows in control areas. Our results suggest that the return of this megagrazer to KNP is indeed increasing grassland heterogeneity in similar ways as in HiP.

Since our study is not a strictly manipulated experiment, there is a risk that the rhino density gradient in KNP is confounded with other landscape gradients. However, we specifically controlled for other factors that could strongly influence the proportion of short grass in the system. In addition to grazing, rainfall and fire frequency are arguably two of the most important factors driving heterogeneity in tall and short grasslands (Archibald 2008). We positioned transects such that high versus low rhino impact areas did not differ in average annual rainfall and fire frequency and transects were at least 1 km away from areas that typically increase the proportion of short grass, such as artificial water points and main rivers. Another potential confounding factor is the presence of other megaherbivores in our study area. KNP is well known for its large elephant population, with potentially large effects on ecosystem structure and functioning (Kerley *et al.* 2008). However, the presence of elephants in our study site does not confound our results. Firstly, elephant kernel density did not differ between low and high rhino treatment areas (Fig. 4). Secondly, elephants affect the woody components of ecosystems, such as tree-fall rates, tree height (e.g. Asner & Levick 2012) and woody species composition (O'Connor, Goodman & Clegg 2007). They are unlikely to create short grass patches because elephants pluck grass tufts with their trunk, in contrast to the cropping behaviour of white rhino (Owen-Smith 1988). While cropping 'mows' grasslands short, plucking does not. Hence, resource interactions between elephant and white rhino are less obvious than for elephant and black rhino *Diceros bicornis*, where elephant may affect browse availability for black rhino (Landman & Kerley 2013). Hippopotamus, *Hippopotamus amphibius*, another megagrazer occurring in KNP, is known to create grazing lawns (Lock 1972). However, their effects are limited to the edges of water bodies, away from the crests that we studied. Therefore, we are confident in concluding that our results are not confounded by the impact of other megaherbivore species.

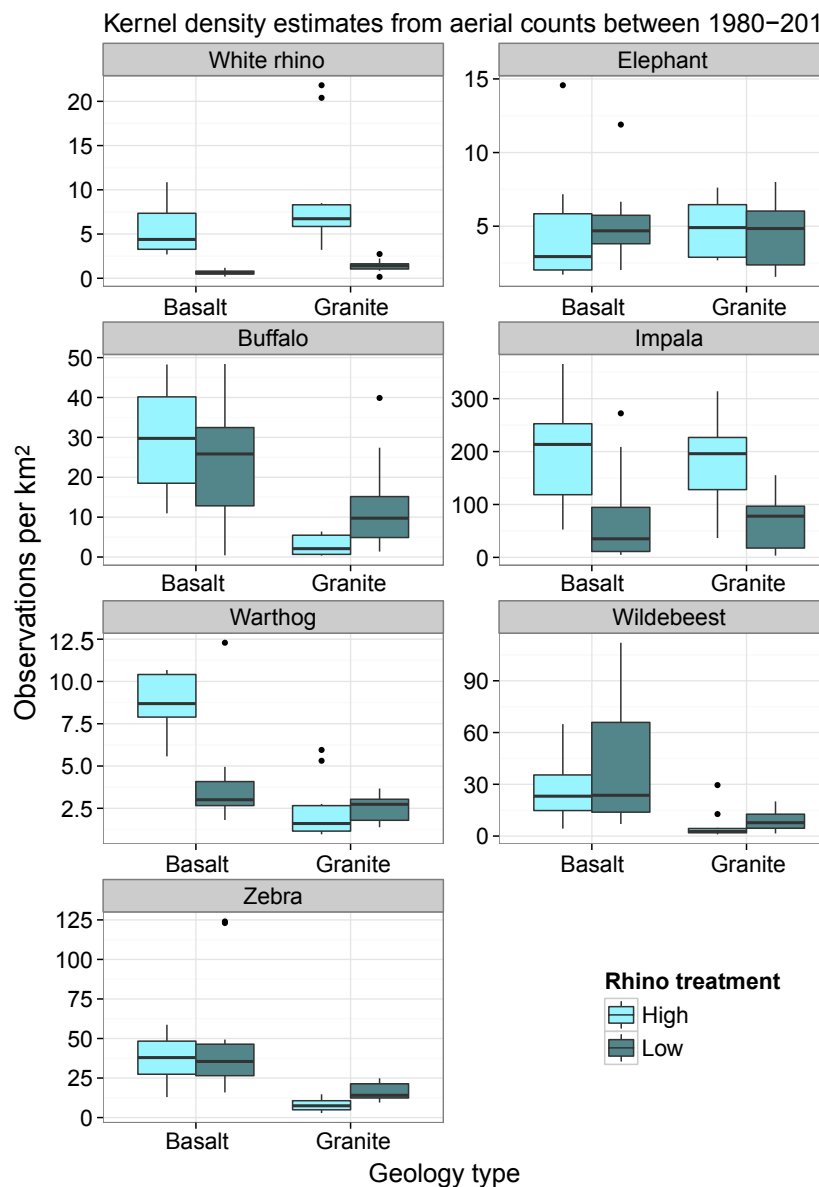


Fig. 4. Box and whisker plot for kernel density estimates for seven common large grazer species per each of four combinations of the Rhino presence and Geology treatments. Kernel density estimates reflect the aggregated number of observations between 1980 and 2010 from a fixed-wing aircraft per km² within a ~5 km² buffer area surrounding each 750 m transect. The thick black line represents the median, the box corresponds to the interquartile range (IQR, distance between 25th and 75th percentile), the whiskers cover the 1.5*IQR range and the points represent outliers.

The situation of the smaller grazers is more complex. Zebra, buffalo, and wildebeest densities did not differ or were lower in our high than low rhino treatment area. This excludes the role of these species in increasing the prevalence of lawns and short grass. This is especially relevant for wildebeest, which are known to be able to create grazing lawns (McNaughton 1984). Impala and warthog densities were higher in the high rhino than low rhino area, although in the case of warthog only on basalts (Fig. 4). Hence, their effects possibly confounded our rhino effect. However, we think it is unlikely that small species such as impala and warthog strongly increase the number of grazing lawns and short grass patches on a landscape scale. Their small body mass does not allow them to intensively crop tall grass similar to a white rhino, because of their relatively low tolerance of low-quality food (Owen-Smith 1988). Hagenah, Prins & Olff (2009), in a nested enclosure experiment, showed that grass height only

dropped below 10 centimetres when excluding white rhino and not when excluding any of the smaller-bodied grazers. Territorial males of some smaller-bodied grazers, such as blesbok and springbok, are known to create small lawns (Novellie & Gaylard 2013). However, these lawns are very recognizable by being covered by dung pellets. In our case, 54 out of 66 lawns had no dung, six had dung of white rhino, one had dung of white rhino and elephant, and only one lawn patch had one impala dung pellet group. In conclusion, we believe white rhino grazing, and not smaller grazers, was responsible for the increases in grassland heterogeneity that we found. But why are impala and warthog densities higher in the high rhino impact area? Earlier work has shown that these species do use grazing lawns extensively (Cromsigt, Prins & Olff 2009) and may play a role in maintaining lawns that are created by rhino (Cromsigt & Olff 2008; Waldram, Bond & Stock 2008), that is, higher densities in the high

rhino area may indicate that white rhino exerts a facilitative effect on these species. This is, however, speculation and the correlated presence of rhino, impala and, on the basalts, wart-hog, needs to be looked at in more detail.

We focused on impact of rhino on grassland heterogeneity on the crests of catenas. The understanding of catenal effects on savanna structure is well-developed (Venter, Scholes & Eckhardt 2003). The transport of nutrients down the slope of a catena creates intensively grazed nutrient hot spots along its foot slopes (so-called sodic sites) and relatively nutrient-poor taller grasslands on the crests (Venter, Scholes & Eckhardt 2003; Grant & Scholes 2006). By specifically focusing on the crests we avoided confounding our results with these abiotically driven catenal effects on grassland heterogeneity. Moreover, our results suggest that white rhino might play an important role as a biotic driver of grassland heterogeneity along the crests that would otherwise be much more homogeneous. In this light, it is essential to get a better understanding of how and why rhino use the different parts of the catena. We suspect that termites play an important role in this. Many of the lawn patches we observed on the granites were linked to large *Macrotermes* spp. mounds (personal observations), representing intensively grazed circles of ~4–5 m in diameter around these mounds covered with prostrate-growing grass species such as *Cynodon dactylon* and *Urochloa mosambicensis* (Fig. 5). We suggest that large termite mounds are an essential resource patch for white rhino on the relatively nutrient-poor granitic crests. Gosling *et al.* (2012) recently confirmed that *Macrotermes* spp. mound soil had increased levels of macro and micro nutrients and facilitated grazing lawn cover. Interestingly, the lawns on the basalts seem to be functionally different from those on granites. On the basalts, lawns were similar in size but not as clearly related to termite mounds (personal observations). These lawns were dominated by *Tragus berteronianus* and *Urochloa mosambicensis* and generally had a higher cover of leguminous forbs than the



Fig. 5. Typical white rhino grazing lawn surrounding a *Macrotermes* spp. termite mound on granitic crests in the high rhino impact area with relatively high rhino density and long time since colonization by rhino. We did not find such clear lawns around *Macrotermes* spp. mounds in the low rhino impact area.

granitic lawns (personal observations). Unfortunately, we did not methodologically record the association between termite mounds and grazing lawns in our study. Hence, the ideas put forward here, though based on observations, remain speculative and need further testing.

If rhino indeed increase grassland heterogeneity on the catenal crests of KNP, what does this mean for the functioning of KNP's savanna ecosystem? An increase in short grass cover may lead to a wide range of cascading effects, including creating habitat for certain species (birds, Krook, Bond & Hockey 2007; grasshoppers, Joern 2005; small mammals, Engle *et al.* 2008; and ungulates, Verweij *et al.* 2006), changing fire regimes (Owen-Smith 1988), and influencing tree-grass dynamics (Bond 2008). But do our results give reason to believe that rhino impact has such cascading effects in KNP? With an average of ~3 lawns per 750 m transect and average lawn diameter of 4 m, grazing lawns only covered ~1–2% (mean of $1.7 \pm 0.46\%$ SE) of transects in the high rhino impact area. In HiP, where rhino densities have been high for many decades, areas with >10% grazing lawn cover are not uncommon and lawns are often much larger than a few square metres (Archibald *et al.* 2005; Cromsigt 2006). This suggests that the current effect of rhino on grazing lawn prevalence in KNP is still rather small and likely does not result in major ecological cascading effects. In terms of short grass cover the story might be slightly different. Short grass cover was clearly higher in the high rhino impact area: an 83% (11% vs. 6%) increase on basalts and 60% (24% vs. 15%) increase on granites. In HiP short grass cover was ~140% lower in rhino removal areas in the mesic northern part of the park (14% vs. 34% in control areas) but only ~24% in the semi-arid south (45% vs. 56% in control areas; Waldram, Bond & Stock 2008). In both cases, the reduction in short grass cover coincided with changes in the fire regime, where fire extent was larger and less patchy in rhino removal areas. Considering that they looked at areas immediately surrounding wallows where impact is especially high, they likely overestimated short grass cover compared with our estimates from random tracts of grassland. Hence, we think it is not unreasonable to assume that the changes in short grass cover we found would affect the fire regime in these parts of KNP. However, it remains to be tested whether the impact of rhino on grassland heterogeneity in KNP indeed affects fire or leads to other ecological cascading effects.

To put our results into perspective, it is relevant to know how current densities of rhino in KNP compare with those in HiP. The average density in HiP varied between 1.7 and 2.5 rhino per km² during the past 20 years (D. Druce, Ezemvelo KZN Wildlife, unpubl. data). This is similar to the density of 2.1 rhino per km² reported for the early 1970s by Owen-Smith (1988). During the 2010 KNP helicopter counts, 64% of rhino were observed in the high rhino impact area. Multiplying this proportion with the 2010 park-wide estimate of rhino numbers (~10 500, Ferreira, Botha & Emmett 2012), we get an average density for 2010 of ~1.8 rhino per km² in the high rhino impact area. Using the same method, we find that the density in the low rhino impact area is still much

lower, only ~0.5 rhino per km² (and only 0.09 rhino per km² in area C, Fig. 2). This means that the current density in the high rhino impact area in KNP is in fact similar to the density in HiP. This is, however, only a very recent phenomenon, because the rhino population in KNP increased exponentially during the last decade. Using population estimates from Ferreira, Botha & Emmett (2012), we estimate that rhino density in the high impact area was 1.4 rhino per km² in 2005 and only 0.6 rhino per km² in 2000. By contrast, as discussed above, rhino density in HiP has been around 2 rhino km² for 40 years. Hence, in KNP, we have only very recently entered the era that rhino reached a density that their impact will become significant. However, the current rhino poaching crisis has made their future in the wild look dismal. If current trends in poaching continue, rhino will go extinct in the near future (Ferreira, Botha & Emmett 2012). Our study stresses the severe indirect effects of this crisis. Not only is rhino poaching threatening the species conservation status, but also the potentially key role of this apex consumer for savanna ecosystem dynamics and functioning.

Acknowledgements

We thank Izak Smit, Rina Grant, Danie Pienaar, Sam Ferreira and Atle Mysterud for valuable discussions during the design phase of the study. Danie Pienaar provided unpublished data on re-introduction of white rhino. We thank SANParks for granting permission for this project (registered as CROJPGM802) and sharing aerial census and background GIS data. Great thanks go towards the helicopter pilots, the Kruger's section rangers and numerous observers that assisted in aerial surveys during the past 3–4 decades. We are grateful for efficient handling of data requests by Sandra Mac Fadyen and Judith Kruger-Botha. The rhino surveys presented in this study were funded by SANParks. J.P.G.M.C. was supported by a Marie Curie Intra-European fellowship (PIEFGA-2008-220947), a Marie Curie Career Integration Grant (PCIG10-GA-2011-304128) and the Swedish thematic research programme Wildlife & Forestry. M.t.B. acknowledges support from Stellenbosch University (Sub Committee B to KJ Esler). Comments by Norman Owen-Smith, the Associate Editor and an anonymous referee strongly improved the manuscript.

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Received 25 September 2013; accepted 16 January 2014

Handling Editor: Peter Bellingham