

Ecological Engineering by a Mega-Grazer: White Rhino Impacts on a South African Savanna

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ABSTRACT

Herbivory can change the structure and spatial heterogeneity of vegetation. We ask whether all species of grazers in a savanna ecosystem can have this effect or whether megaherbivores (>1000 kg) have a 'special' role that cannot be replicated by other species of grazers. We performed a replicated landscape scale experiment that examined the effects of White Rhino on the grass sward, on other species of grazing mammals and on the movement of fire through the landscape. White Rhino maintained short grass ('lawn') patches in mesic areas (~750 mm pa) with increases in grass sward height when they were removed. Other species of grazers were unable to maintain short grass communities when White Rhino were removed. In semi-arid areas (~600 mm pa) other, smaller grazers were able to maintain short grass communities in the absence of White Rhino and sward height did not

increase. White Rhino removals affected fire by increasing fuel loads and fuel continuity. This resulted in larger, less patchy fires. We propose that the White Rhino acts as an influential ecosystem engineer, creating and maintaining short grass swards, which alter habitat for other grazers and change the fire regime. These results indicate the existence of context-dependent facilitation between White Rhino and other grazers in mesic, but not in semi-arid, savannas. Such top down effects on the ecosystem may have been much more widespread before the extinction of large grazers in the Pleistocene.

Key words: megaherbivores; White Rhino; savanna; grazing; fire; facilitation; keystone species; ecosystem engineers; Pleistocene extinctions.

INTRODUCTION

Fire and mammal grazers both consume grass and both are important modifiers of ecosystems, especially in savannas where these two agents are often acting together. In principle, grazers could have marked indirect effects on their habitat by altering the fire regime. If grasses are grazed short enough, grazers could create biologically induced barriers to the spread of fire potentially altering the size, spa-

tial distribution and frequency of fires in a landscape. Grazer species capable of altering fire regimes in this manner could be considered 'ecosystem engineers' (Jones and others 1994). Their addition or extirpation from a landscape might have significant non-trophic impacts on ecosystem structure, function and biodiversity.

Owen-Smith (1988) coined the term megaherbivores for very large herbivores with an adult bodyweight greater than 1000 kg. He noted that large body size renders them largely immune to (non-human) predation while their bulk feeding allows them to tolerate food of a lower quality than

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that required by smaller herbivores. He suggested that megaherbivores would therefore be less affected by predation or environmental fluctuations (for example, drought) than mesoherbivores (herbivores <1000 kg) and their populations would be maintained at high density causing heavy sustained impacts upon their environment. This led Owen-Smith to suggest that megaherbivores are likely to act as keystone species.

There has been considerable debate on the concept of keystone species (Power and others 1996; Hurlbert 1997; Polis and others 2000; Bond 2001). Owen-Smith's hypothesis of keystone megaherbivores is consistent with the definition of a keystone species as one whose ecosystem effects are disproportionately large relative to its abundance (Power and others 1996). To date most of the literature discussing vegetation impacts of megaherbivores has focused on the impacts of browsing species, such as the African Elephant (*Loxodonta africana*) (Van de Koppel and Prins 1998; Fritz and others 2002), but grazing megaherbivores could have equally large impacts. The only extant megaherbivores that exist on a diet of grass are the White Rhinoceros (*Ceratotherium simum*), the Hippo (*Hippopotamus amphibius*) and to some extent the Indian Rhinoceros (*Rhinoceros unicornis*). Of these the Indian Rhinoceros, although principally a grazer, also consumes seasonal browse and fruit in its diet (Laurie 1982; Dinerstein 2003) and Hippo are limited to areas within a few kilometers of water. This leaves the White Rhinoceros (hereafter just Rhino) as the sole extant analogue for an extinct suite of terrestrial grazing megaherbivores. Both Rhino and Hippo prefer to feed in areas of short grass (Lock 1972; Olivier and Laurie 1974; Owen-Smith 1975), a habit to which they are suited by their wide mouths and low slung head, and help create and maintain short grass patches (Eltringham 1970; Arsenault and Owen-Smith 2002; Verweij and others 2006). Grazed patches initially consist of cropped bunch grasses (a structural change), but under continued heavy grazing sward composition changes through the invasion of grazing resistant grass species with stoloniferous habits (Archibald and Bond 2004). Vesey-Fitzgerald (1965) used the term 'grazing lawn' to refer to the latter communities noting that they are maintained in a nutritious and productive juvenile growth form through repeated grazing. McNaughton (1984) suggested that the grass species comprising lawns are likely to have co-evolved with grazing mammals. In contrast to bunch grasses, which burn readily when dry, lawns seldom carry fire as they do not have enough biomass to burn.

Grazing lawns have been studied in East Africa (McNaughton 1979, 1984, 1985; Augustine and McNaughton 1998) but have received little attention elsewhere in the tropics. Lawns have previously been noted as being maintained by hippo (Eltringham 1970; Lock 1972; Verweij and others 2006) but also by large herds of migratory Wildebeest (*Connochaetes taurinus*, McNaughton 1984, 1985) and it is unclear whether they are an example of the keystone facilitation described by Owen-Smith, that is, requiring the presence of megaherbivores, or whether large herds of mesoherbivores can perform an equivalent function.

Depending on the magnitude of grazer/fire interactions, changes in the grazer assemblage could have cascading effects on an ecosystem by releasing, or suppressing, fires. Flannery (1994), for example, suggested that the extinction of the Australian grazing megafauna resulted in increased fuel loads, leading to more frequent/extreme fire events with cascading community effects and, ultimately, to the eventual dominance of pyrophilic vegetation communities in much of Australia (Bradstock and Gill 2002). Implicit in this hypothesis is the idea that grazing megaherbivores act as ecosystem engineers, with large non-trophic impacts on the ecosystem (Jones and others 1994). The fire release hypothesis has received some support from recent paleo-ecological studies (Burney and others 2003; Robinson and others 2005) but the effects of extant grazing megaherbivores upon their environment remains untested in the field.

Whilst the fire release hypothesis was first proposed for Australia, the hypothesized effects of grazing megaherbivores are likely to have been global as recently as the Pleistocene when a full complement of grazing (and browsing) megaherbivores occurred worldwide. The causes of the Pleistocene extinctions (Martin and Wright 1967) have been debated in the recent literature (Choquenot and Bowman 1998; Brook and Bowman 2002; Johnson and Prideaux 2004; Burney and Flannery 2005; Miller and others 2005), but the ecological repercussions of the extinctions have received less attention (Owen-Smith 1987, 1989). Post-Pleistocene megafaunal communities remain intact only in Africa and parts of tropical Asia, making them the only places where it is possible to test the ideas of Flannery and Owen-Smith about the effect of megafaunal grazers on vegetation, on animal communities and on fire regimes.

Evidence for keystone influences in terrestrial ecosystems has been scarce, partly because the experimental manipulations needed to test them

are rarely possible for practical, ethical or conservation reasons. Many studies use historic reconstructions to infer trophic relationships (for example McLaren and Peterson 1994; Ripple and Beschta 2004). Here we report the results of a replicated landscape scale experiment in which individual Rhinos were removed as part of a conservation management exercise allowing us to test the keystone megaherbivore and fire release hypotheses of Owen-Smith and Flannery. The removals took place at both ends of a rainfall gradient allowing us to locate possible keystone influences along a productivity gradient. We ask whether Rhino not only consume large amounts of grass, but also act as ecosystem engineers by creating and maintaining grazing lawn communities, an ecosystem function that cannot be replicated by mesoherbivores. Where grass productivity is high we expect the influence of Rhino to be large because this species may be the only grazer capable of grazing grasses short enough to prevent lawn species being overtopped by bunch grasses during the growing season (compare Verweij and others 2006 for hippo lawns in West Africa). We also tested the response of other species of mammalian grazers to Rhino removals to determine whether Rhino facilitate, or compete with, smaller species of grazers using lawns. Finally we tested the idea that lawns form grazer maintained firebreaks so that, with removal of White Rhinos, fires will spread more readily over larger areas because of increased fuel loads and fuel continuity.

MATERIALS AND METHODS

The study was conducted in Hluhluwe iMfolozi Park (HiP) in sub-tropical KwaZulu Natal, South Africa. HiP has an area of 90,000 ha, is located between S 28.0000–28.4300, E 31.7160–32.0150 and has an altitude range of 20–580 m above sea level. Rainfall in the park increases with altitude (Balfour and Howison 2001). The rainfall in Hluhluwe (the northern portion of the park) supports a mesic savanna with an average of approximately 750 mm of rain per annum increasing to approximately 1000 mm/pa on the higher hilltops some of which support closed forest. iMfolozi (the southern portion) supports a semi-arid savanna with rainfall of approximately 600 mm/pa. The vegetation of the park varies from grasslands to *Acacia* woodlands and denser thickets dominated by broad leaf species such as *Euclea* and *Maytenus* with a turnover of tree species from Hluhluwe to iMfolozi (Whateley and Porter 1983 give a detailed description). The grass sward consists mostly of fire-

prone bunch grasslands (including *Themeda triandra*, *Sporobolus pyramidalis*, *Hyparrhenia filipendula*). Grazing lawns, characterized by grazing-tolerant short and/or stoloniferous grasses (for example, *Digitaria longiflora*, *Digitaria argyrograpta*, *Urochloa mossambicensis*, *Panicum coloratum*, *Sporobolus nitens*), occur as patches in the taller bunch-grass matrix. Short grass patches (lawns, and heavily grazed forb/grass mixtures) currently occupy less than 10% of the grassy areas of the park and are most common in the semi-arid region (Archibald and others 2005). Most lawn patches are small with approximately 1.5% of the total exceeding 8 ha in extent (Krook and others 2007).

Mammal populations in HiP have fluctuated greatly through the last century due to the effects of disease, culling operations to control disease, and other management interventions. By the beginning of the 20th century HiP had become a last refuge for Rhino and the range of the southern sub-species had become restricted to the park boundaries. This led to protection, population recovery and, from 1961, translocation to other areas (Player 1967, 1972). The park also supports a full compliment of predators, browsers and other grazers (see Brooks and Macdonald 1983). Herbivore biomass is high (~12,500 kg/km²) in comparison with other African conservation areas with Rhino presently accounting for 25% of the animal biomass in the park (~1700 individuals in 2004). The major grazing species, their body mass and density in the two parks are listed in Table 1.

Rhino in iMfolozi occupy core ranges estimated as 0.7–2.6 km² in the 1960s (Owen-Smith 1975, 1988) and 5 km² in the 2000s (White and others 2007) which dominant males defend against each other whilst tolerating adult females, juveniles and submissive males (Owen-Smith 1975, 1988). Rhino are captured and removed from HiP for sale and translocation. We used animal census/mortality data and game capture records to define areas from which one or more Rhino had been removed (removed treatments) and compared these with control areas without removals. Field observations suggest that Rhino are slow to disperse into new areas (>3 years in one instance) allowing us to make use of the temporary reduction in Rhino numbers to measure ecosystem responses. Because remaining Rhinos are free to move into a vacated area, our tests of ecosystem effects of Rhino removal are very conservative and biased against finding treatment effects. Rhino removal information was first collated into a GIS database and displayed on a 1 km² grid (Figure 1), a scale that is similar to the home range size of Rhino. Control

Table 1. Mammal Grazers in Hluhluwe-iMfolozi

Species	Body mass (kg)	ME	Hluhluwe mesic		iMfolozi semi-arid		
			N	MBD (kg ^{0.75} km ⁻²)	N	MBD (kg ^{0.75} km ⁻²)	
White Rhino	<i>Ceratotherium simum</i>	1900	1.0	562	601	1169	536
Buffalo	<i>Syncerus caffer</i>	600	2.4	1113	501	2039	394
Zebra	<i>Equus burchelli</i>	235	4.8	846	189	2543	243
Waterbuck	<i>Kobus ellipsiprymnus</i>	210	5.2	212	43	495	44
Wildebeest	<i>Connochaetes taurinus</i>	200	5.4	717	142	2365	200
Nyala	<i>Tragelaphus angasi</i>	85	10.3	3448	359	4042	180
Warthog	<i>Phacochoerus africanus</i>	70	11.9	742	67	2442	94
Impala	<i>Aepyceros melampus</i>	52.5	14.8	4354	315	20117	625

Body mass ex Owen-Smith (1988). ME is the number of individuals metabolically equivalent to a White Rhino (where metabolic body weight = $M^{0.75}$, Owen-Smith 1988). N is population size and MBD is metabolic biomass density for the 2004 census (KZN wildlife 2004, unpublished data).

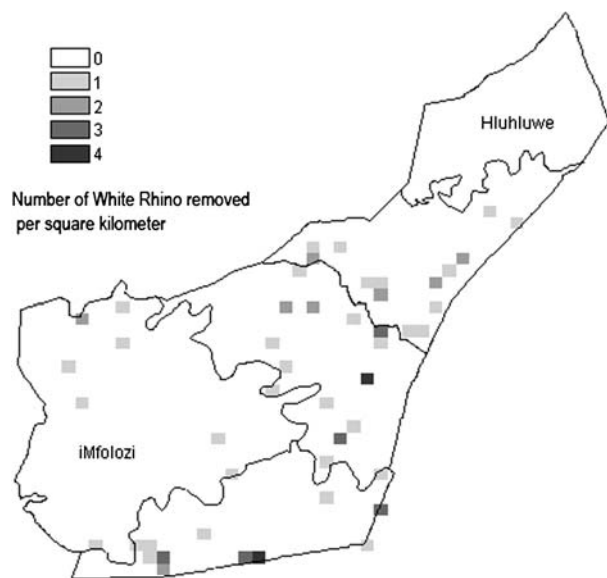


Figure 1. Rhino removals in Hluhluwe iMfolozi Park during 2003. Grid squares are 1 km².

and removed areas were manually selected and, because multiple removals were very rare at this scale, grouped into a binary 'removed vs. control' treatment. Grid squares of both treatments were located in both Hluhluwe (mesic) and iMfolozi (semi-arid) to examine the effects of Rhino grazing along a rainfall gradient.

Grass and Grazer Response to Rhino Removal

We used wallows as focal points within the 1 km² treatment areas around which sampling for grass and grazers responses were centered. Wallows are depressions that fill with water during rains, usually created by the actions of the animals that use them. Their distribution in the landscape is not

restricted to any specific topography. Sampling was by means of eight radially arranged transects of 60 m in length around each wallow. To measure grass sward height we used a Disk Pasture Meter (DPM), a metal disk (diameter 45 cm, weight 1500 g) dropped from a standard height (Bransby and Tainton 1977). DPM settling height was calibrated to biomass at sites within the park (grass biomass in g/m² = 12.6 + 26.1 DPM, $R^2 = 0.73$, $N = 1745$). Visual sward height is not a good measure of biomass because sward density varies. Our DPM height units are compressed relative to visual estimates, so we report biomass equivalents to facilitate comparison with other methods. Readings were taken every 5 m along each transect. To estimate the relative abundance of other grazers using the area, we also recorded the presence of fresh dung piles in a 1 m strip on either side of the transect between DPM readings. We consider dung counts a reliable relative measure of habitat use by grazers because none dung in territorial middens (Barnes 2001). The White Rhino, in contrast, does remove dung to middens and habitat use by this species cannot be evaluated by this method.

We calculated the mean grass height along transects around wallows in removed and control areas (Figure 2). Because Rhinos are thought to be important in creating and maintaining grazing lawns, we also estimated Rhino effects on the extent of short grass patches by calculating the proportion of short grass (<7 cm DPM) around each wallow. We tested the effects of park, Rhino removal treatment and elevation (which correlates with rainfall, Balfour and Howison 2001) on the proportion of short grass using a standard least squares regression model with nominal variables replaced by dummy variables to fit separate coefficients for each level (JMP version 5.0.1.2). Park

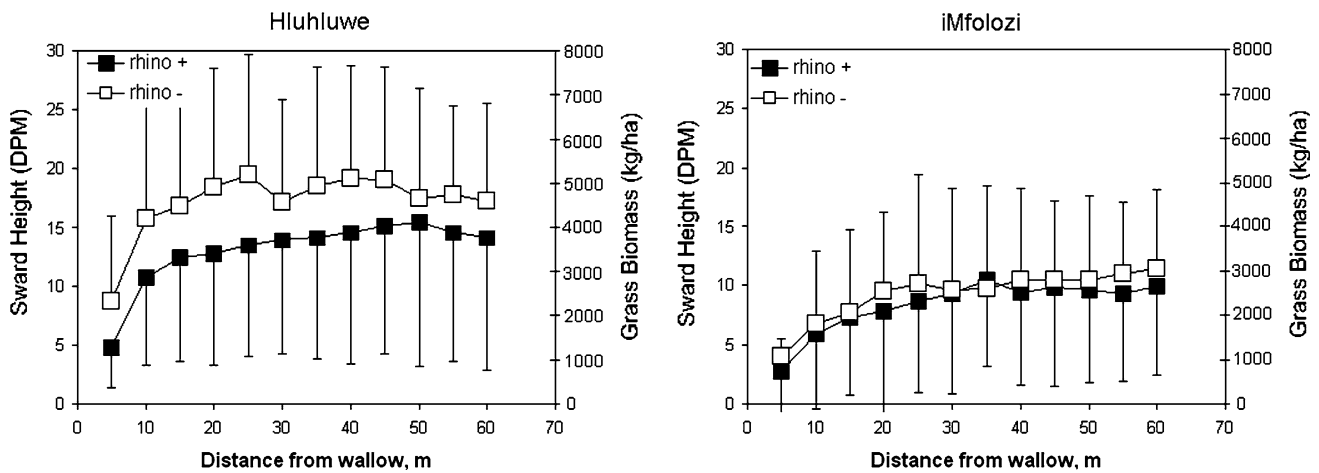


Figure 2. Mean grass height (measured in centimeters with a disk pasture meter) along transects radiating out from wallows (eight transects per wallow). Transects are grouped into Rhino removal and control treatments in both Hluhluwe (mesic) and iMfolozi (semi-arid savannas). Bars represent standard deviation. The equivalent aboveground biomass (kg ha^{-1}) is also indicated. Averaged grass biomass around wallows in removed areas in Hluhluwe was significantly greater than that around control wallows (Mann–Whitney U Test, $P = 0.05$). There was no significant difference in iMfolozi.

and treatment were crossed to determine possible interactions. Subsequently, a reduced model was constructed including only variables with significant effects. We estimated relative mesoherbivore abundance by summing the amount of dung around each wallow and testing for Rhino removal effects using a non-parametric post-hoc Wilcoxon rank sum test (JMP version 5.0.1.2). Fieldwork around wallows occurred at the end of the wet season in June 2004.

Fire Response to Rhino Removal

To test the effects of Rhino removal on the ability of fire to spread through the park, we developed maps of burn scars in HiP for the years 2001, 2002 and 2004 using the Enhanced Thematic Mapper (ETM) onboard the Landsat 7 satellite and the supervised classification technique in ERDAS IMAGINE v.8.7. Burn scar classifications were developed using methods similar to those described by Hudak and Brockett (2004b). Spectral signatures were extracted from visually identified burn scars of various ages in the original image. The individual signatures were then merged to create a single spectral signature, which was then applied to the whole image using a parallelepiped classification technique. This classification was then visually inspected against the original image for errors of omission and commission (Congalton 2001) before being either accepted or further modified. Separate classifications were performed for different years and for Hluhluwe and iMfolozi before merging to give a final image. The classification technique was

validated by comparing the 2004 burn scar image to reference data collected on the ground during the 2004 fire season. The 2004 image was not used to analyze burn scars as the image was disrupted by a malfunction in the scanner onboard Landsat 7 (see Anon 2003). The reference and classified maps were compared using 200 randomly selected points to calculate an error matrix and the KHAT statistic (Congalton 2001).

Burn scar images from 2001 and 2002 were overlaid onto Rhino removal data using GIS software and labelled as belonging to the removed treatment if they occurred in the same square kilometer as a Rhino removal. Burn scars not overlaid by a Rhino removal were labelled as belonging to the control group. We then used the spatial pattern analysis program FRAGSTATS V3.3 (McGarigal and others 2002) to calculate numerical parameters describing the size and shape of burnt patches in HiP. We calculated the following metrics for each burnt patch identified in the images:

- Area, calculated in hectares, describes the size of burnt patches in the landscape. We expect this value to be larger in removed treatments as grass fuel load increases in the absence of Rhino.
- Shape measures the complexity of the outline of burnt patches, but removes the size bias inherent in the perimeter–area ratio. It is calculated as the patch perimeter divided by the perimeter of a maximally compact shape of the same area and hence has no units. A value of 1 indicates a maximally compact shape with higher values representing more complex shapes.

- The Contiguity metric is calculated as the number of like (that is, burnt) pixels surrounding a central burnt pixel. It is expressed as a unitless value in the range of 0 (for an entirely isolated burnt pixel) to 1 (for a burnt pixel completely surrounded by other burnt pixels). The value for a patch is calculated as the average contiguity value for all pixels in a patch. Like the Shape metric, Contiguity measures burnt patch shape, but also the patchiness of a burn. We expect both metrics to be less complex (that is, nearer to 1) in removed areas due to a more continuous grass layer (that is, less unburnt short grass patches).
- The Core Area Index is calculated as the size of a core area within a burnt patch, defined as being 3 pixels (90 m) from the edge. This is divided by the total area of the burnt patch and is expressed as a percentage. The CAI measures the patchiness of a burnt patch, as unburnt patches contained within the perimeter of a burn will lower the CAI. Hence we expect the CAI to be higher in Rhino removal areas.

More detailed descriptions of the metrics used can be found in the documentation for FRAG-STATS (McGarigal and others 2002). The resulting data set of metrics for burnt patches in control and removed areas was statistically analyzed using non-parametric statistical methods because the data were not normally distributed (Mladenoff and others 1993). The two-tailed Wilcoxon test in JMP version 5.0.1.2 was used to test for significant differences. A potential bias in our data set is that fires may be larger in removed areas because removals often occur, for logistical reasons, from open grassy sites. We tested for this bias using a vegetation map of the park (Meyer 2001, unpublished thesis) and looked at the proportion of vegetation types within removed grid squares in relation to the proportion of vegetation types in the rest of the park.

RESULTS

Grass and Grazer Response to Rhino Removal

Eighty-six Rhino were removed from the park in 2003/2004 prior to the wallow study (Figure 1). Using the removal data we identified 52 wallows in the park, 23 in removed areas and 29 in control areas. Figure 2 illustrates the grass biomass profile around wallows in removed and control treatments in Hluhluwe and iMfolozi. Grass sward height was greater in Hluhluwe than in iMfolozi, and in both parks sward height increased following Rhino removal. The increase was greater in Hluhluwe than

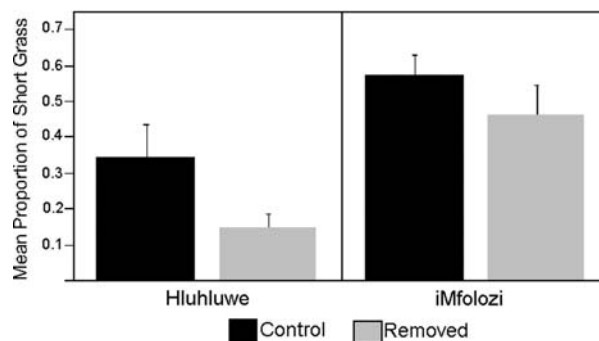


Figure 3. The proportion of short grass (<7 cm DPM reading) around removed and control wallows in both Hluhluwe and iMfolozi. Bars represent the mean and whiskers the standard error.

in iMfolozi, an average of 4.5 cm compared to 1.4 cm DPM, respectively (equating to fuel load increases of 1300 and 490 kg ha⁻¹). The proportion of short grass around wallows also decreased with the removal of White Rhino (Figure 3), more so in mesic Hluhluwe than in semi-arid iMfolozi, which had larger amounts of short grass around wallows in general. The regression model (Table 2) explained a relatively low amount of the variation in the occurrence of short grass patches around wallows ($R^2 = 0.29$). Both park ($P < 0.01$) and Rhino removal treatment ($P < 0.05$) significantly affected the proportion of short grass around wallows. The elevation of wallows and the park/treatment interaction term were non-significant and excluded from the final model.

We recorded 844 dung piles along transects around wallows. Figure 4 shows the data for the four most common grazing species. In Hluhluwe, significantly more Impala, Zebra and Wildebeest dung was recorded around control wallows than around Rhino removal wallows. In iMfolozi, there was no significant difference in the amount of dung counted around control or removal wallows. Buffalo showed no significant difference in the amount of dung around wallows at either end of the park.

Fire Response to Rhino Removal

Classified images of burn scars are shown in Figure 5. The 2004 data were found to match the reference data collected on the ground with an overall accuracy of 91.8% and a KHAT value of 83.5. Because KHAT values greater than 80 indicate a strong agreement between classified and reference data (Congalton 2001), we conclude that our method of classifying burn scars from satellite imagery was accurate. We identified 335 burnt patches ranging in size from 0.1 to 3217 ha in the

Table 2. Regression Model for Proportion of Short Grass around Wallows

Variable	Estimate	Std error	<i>t</i> Ratio	Prob > <i>t</i>	Sum of squares	DF
Intercept	0.383	0.036	10.74	<0.0001		
Treatment	0.073	0.035	2.08	0.0425	0.271	1
Park	-0.134	0.036	-3.77	0.0004	0.886	1

$R^2 = 0.29$
 Prob > $F = 0.0003$

Parameters of the reduced least squares regression model (only significant parameters included) for proportion of short grass (<7 cm DPM) around wallows. R^2 gives total amount of variation in dataset explained by model, and Prob > F overall significance of model. Estimate gives size of effect, standard error of predictor variable, *t* ratio = computed test statistic for variables, Prob > *t* = chance of statistic being exceeded by chance alone, DF = degrees of freedom. Sum of squares = amount of variation in the dataset explained by each variable.

burn scar classifications from 2001 and 2002. Of these, 54 occurred in Rhino removal areas. Metrics for burnt patches in the two treatments and results of the Wilcoxon test are given in Figure 6. All metrics showed significant differences ($P < 0.001$) with a consistent direction of effect between control and Rhino removal treatments in both mesic and semi-arid savannas. Burnt patches were larger, less patchy and had more complex shapes when they occurred in areas from which Rhino had been removed.

The test for bias in the amount of open vegetation in Rhino removal areas found there to be no difference between removed and control areas. A line fitted to a graph of percentage occurrence of vegetation types in removal grid squares plotted against the percentage of the park occupied by those vegetation types had a slope of 1.01 and an R^2 of 0.99, indicating that removals were not biased to open areas. We also tested whether the different scales at which Rhino removals and burnt patches were mapped might have biased the burn scar analysis, with large burns being more likely to occur in removal treatments. We excluded burn scars from the analysis, starting with the largest and gradually excluding progressively smaller burn scars down to a scale of 1 km². Because this did not affect the statistical outcome of the analysis, we concluded that this potential bias was not affecting our conclusions.

DISCUSSION

As Rhino removals are likely to cause, at most, a temporary reduction rather than a complete removal of grazing pressure, our analysis is a very conservative test of the importance of megagrazers in this ecosystem. Nevertheless, we found significant effects of Rhino removals on average grass sward height, the proportion of short grass patches, the abundance of grazer species near wallows and

in the size and pattern of fires. The regression model explained only 29% of the variation in short grass but was highly statistically significant (Table 2). Of the predictor variables we considered, park accounted for most of the variation with much larger short grass patches in semi-arid iMfolozi than mesic Hluhluwe. Rhino removal caused a significant reduction in short grass patches in both parks with more than 50% reduction in the mesic savanna compared to less than 20% reduction in the semi-arid savanna (Figure 3). From this we conclude that although there are many factors influencing the grass sward, megaherbivore grazing has a distinct and predictable effect. This is consistent with current understanding of savanna ecology; savannas are highly heterogeneous landscapes with many factors influencing the vegetation community structure. Rhino removal had a greater effect in Hluhluwe than in iMfolozi, consistent with our prediction of greater changes in grass sward height in the more mesic areas of HiP.

The loss of short grass patches with Rhino removal had a measurable effect on other grazers in the ecosystem. Patch use by Impala, Wildebeest and Zebra declined where Rhino had been removed in comparison to controls in Hluhluwe but not in iMfolozi. Impala and Wildebeest are known to prefer short grass swards, whereas Zebra are typically generalists. In contrast, Buffalo, which prefer to graze taller grass swards (Perrin and Brereton-Stiles 1999), showed no significant decrease following Rhino removal in either part of HiP. We interpret these results as indicating that Rhinos facilitate short grass grazer use around wallows in the mesic savanna. Without Rhinos to maintain them, the grass sward in Hluhluwe grew too tall for short grass specialists.

We suggest that the different treatment responses of grass swards and grazers in the two parks reflect differences in grass productivity. Grass growth in mesic Hluhluwe was too rapid for mes-

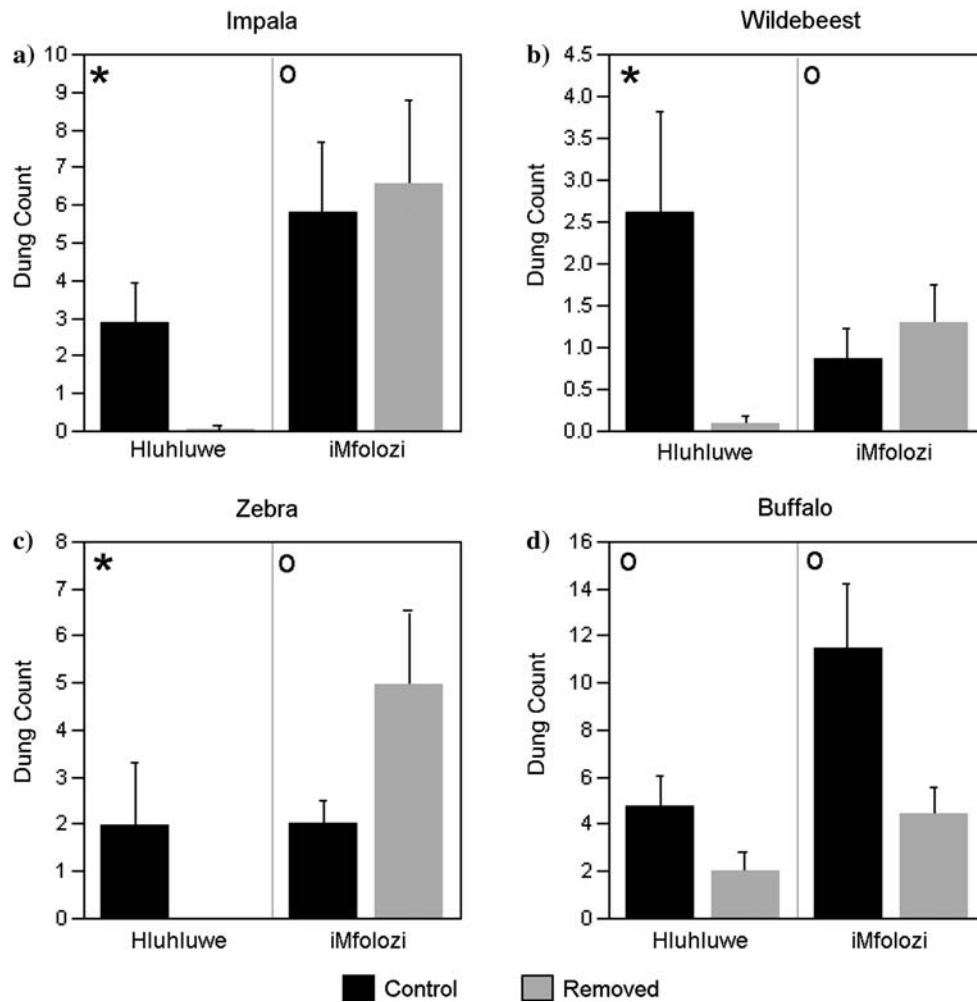


Figure 4. The relative herbivore pressure, measured by the number of dung piles, around control (*dark grey*) and Rhino removal (*light grey*) wallows in a mesic (Hluhluwe) and a semi-arid (iMfolozi) savanna for (A) Impala, (B) Wildebeest, (C) Zebra and (D) Buffalo. Bars give the mean amount of dung and whiskers give standard error. Wilcoxon test result is indicated in the upper left corner, with significant results ($P < 0.05$) marked with an *, and non-significant results marked with an O.

herbivores to crop short where Rhinos had been removed. In semi-arid iMfolozi, where grass productivity is lower, short grass grazers were able to maintain short grass swards in removal areas and their abundance increased, although not significantly (Figure 4). Thus Rhino facilitate short grass grazers in mesic savannas but likely compete with them in semi-arid savannas. Because the effect of Rhino grazing varies with rainfall, its ecosystem function is context dependent (Power and others 1996).

This study was conducted during the wet season. During the dry season, as lawns become less productive, competition among grazer species may occur in Hluhluwe as well as iMfolozi. The net effect of wet and dry season availability of fodder on herbivore populations is not yet known (Arsenault and Owen-Smith 2002) and it is not possible to

estimate the demographic effect of Rhinos on populations of smaller grazers. However, our results support other studies on the behavioral relationships between grazers in which larger bodied herbivores facilitate smaller ones (Bell 1971; Verweij and others 2006), as well as lending some support to the keystone megaherbivore hypothesis.

Burnt areas increased in size in response to Rhino removal in both Hluhluwe and iMfolozi. Differences between burn scars in removed and control areas were larger in mesic Hluhluwe than semi-arid iMfolozi but were also statistically significant in the latter. This was unexpected as the response of the grass layer to Rhino removal was much smaller in iMfolozi. The probable mechanism by which Rhino removal leads to an increase in burnt areas is not just an increase in fuel loads, but a reduction in the number, size and distribution of



Figure 5. Burn scar classifications of Landsat 7 remote sensing imagery: (A) 2001 image acquired 15/09/2001, (B) 2002 image acquired on 11/10/2002. Burn scar classification accuracy = 91.8%.

short grass patches acting as grazer-maintained firebreaks. Experimental burns in 40×40 m enclosures in the park (W.J. Bond, unpublished manuscript) have shown that fires never spread through treatments with greater than 40% of the area covered by short grass, a threshold consistent with percolation theory (Turner and others 2001). Hence, Rhino do not need to directly influence large areas to exclude fire, but only need to create enough short grass patches to halt the spread of fire into larger areas.

Our study provides some support for Flannery's fire release hypothesis predicting that removal of megafauna results in larger, more intense fires. The release of fire has important indirect effects on the ecosystem. Large fires homogenize the grass sward by dispersing grazers away from grazed patches and

onto post-burn regrowth (Archibald and Bond 2004; Archibald and others 2005). This reduces concentrated grazing in patches, inhibiting the development of grazer-maintained fire breaks and thereby increasing the chances of more large fires, a positive feedback that leads to a fire-dominated landscape. Grazing lawns are also maintained by positive feedback. Areas that have been grazed are more likely to be re-grazed. That both fire and grazing driven systems appear to be self-sustaining supports the suggestion that the savannas of Hluhluwe iMfolozi can exist in alternate fire- or herbivore-driven states (Bond and others 2001; Bond 2005). Fire-dominated systems are more likely to prevail where rainfall is higher and grazer-dominated systems where rainfall is lower. Areas of intermediate rainfall can support both types of systems and it has been suggested that Hluhluwe has undergone a transition from a grazing to a fire-dominated system during the 20th century (Bond and others 2001). Yet, small fires can also concentrate grazing (Fuhlendorf and Engle 2001, 2004; Vermiere and others 2004) and we suggest that Rhinos may contribute to shifting mesic savannas towards being grazer dominated by limiting the size of fires as well as directly maintaining grazing lawns.

The effects we observed on short grass patches, patch use by other grazers and fire were produced by a very small reduction in the Rhino population ($\sim 4\%$ of the total population in the park) with the remaining population free to move into the removal areas. Rhinos are a very influential species in this ecosystem with disproportionately large effects relative to their abundance (compare Power and others 1996). This has not been widely recognized by managers who have set Rhino capture levels to ensure sustainability of Rhino populations rather than on their wider ecosystem effects. However, although ecosystem effects of a single Rhino are large, they may not be disproportionate to the forage eaten relative to mesoherbivores. The reduction in stocking rate, even from removal of a small number of individuals, may be equivalent to removing a large number of mesoherbivores. We estimated the effect of the removals on grass consumption by calculating the metabolic biomass density (Owen-Smith 1988) of the herbivore populations. Metabolic mass ($= \text{Mass}^{0.75}$) scales body mass across species such that, to a first approximation, daily food intake per unit metabolic mass is equal. Hence, daily grass consumption by a species whose population density is known can be compared or summed with others using metabolic biomass density (Table 1). The Rhino population of

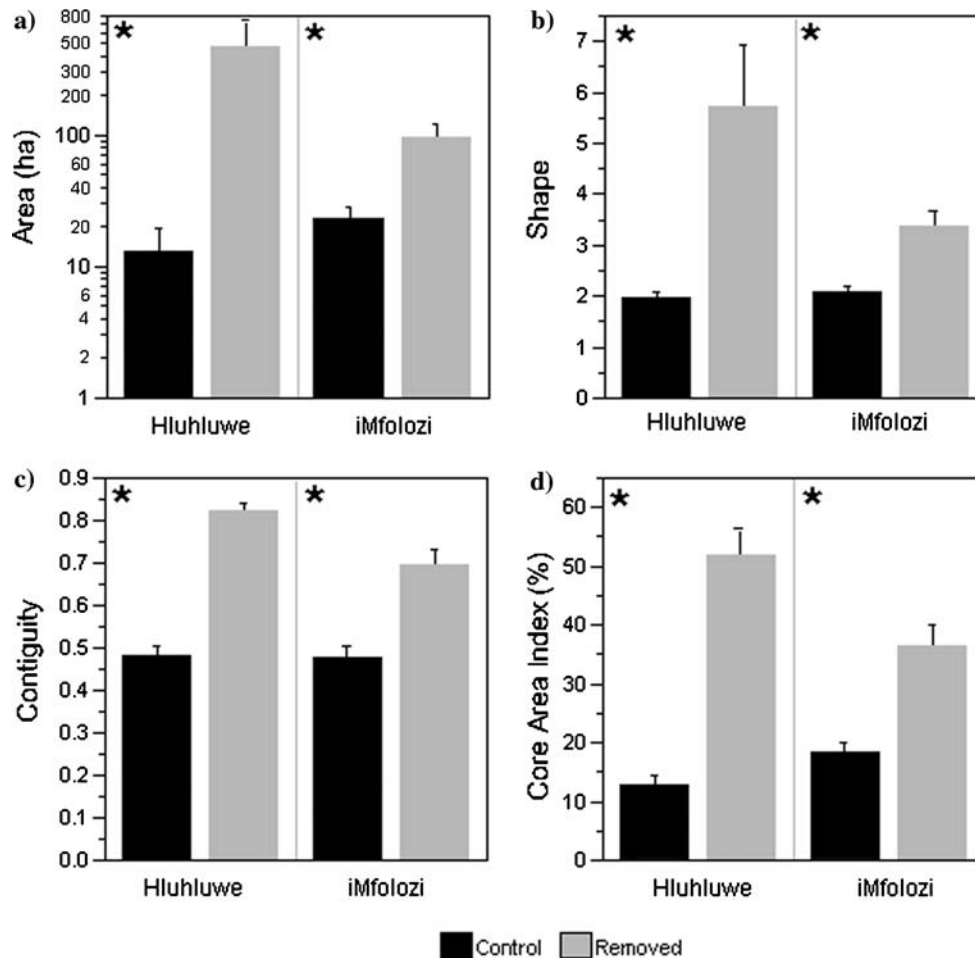


Figure 6. Patch metrics for burn scars in control (*dark grey*) and Rhino removal (*light grey*) treatments in mesic (Hluhluwe) and semi-arid (iMfolozi) savanna of HiP; **(A)** burn scar area (ha, given on a log scale), **(B)** burn scar shape, **(C)** contiguity and **(D)** core area index (%). Whiskers represent mean value for the patch metrics and lines give the standard error. Data from 2001 and 2002 are combined. Significant results of Wilcoxon signed rank test ($P < 0.001$) indicated with an *. Details of patch metric calculations are given in the text.

Hluhluwe and iMfolozi was estimated to comprise 27 and 23% of the total metabolic grazer biomass density respectively, a grazing effect greatly disproportionate to their abundance (<5% of the number of large mammal grazers, Table 1). In 2003, prior to our study, 22 Rhinos were removed from Hluhluwe and 64 from iMfolozi. This would have reduced metabolic biomass density by only about 1 and 1.25%, respectively. Thus the removals themselves would have had a trivial effect on total grass consumption from the parks.

At the scale of the core range of a Rhino, removal of an adult would reduce metabolic biomass density of grazers by 12.5% for very small core ranges (1 km²) and 2.5% for the current mean core range of 5 km² for both males and females (White and others 2007). Mesoherbivores were free to move into areas from which Rhinos had been removed. Table 1 lists the number of individuals of common

grazing species metabolically equivalent to a Rhino in terms of forage consumption. For example, approximately 15 Impala, or 2.4 Buffalo or 4.8 Zebra would need to move into the range of a Rhino to graze the equivalent forage. In HiP, the populations of these species alone numbered approximately 24,000, 3100 and 3400 so that local movement of mesoherbivores into vacated Rhino ranges would readily compensate for Rhino removal within the time scale of our study. In the mesic savanna, Wildebeest and Impala abandoned areas from which Rhinos had been removed, whereas in the semi-arid savanna they did not. In mesic Hluhluwe, Rhinos appear to be irreplaceable ecosystem engineers, maintaining lawns by their 'lawn-mower' feeding mode, an ecosystem function that could not be replaced by smaller grazing species. This effect facilitated other short-grass specialist grazers. In semi-arid iMfolozi, local

movement of these grazers onto wallow sites from which Rhinos were removed apparently compensated for the grazing impact of Rhino.

African savanna parks, which have been continually inhabited by grazing megafauna, are among the last relics of Pleistocene grazing ecosystems. Our study in HiP provides a glimpse into the ecology of how ecosystems may once have functioned before the majority of mega-grazers were extirpated in the Pleistocene. Although the White Rhino has been translocated from this park into many others in Africa, HiP is the only area where the species has persisted at high densities for several decades and therefore likely to have had maximum impact on the rest of the ecosystem. We predict that other parks in Africa will show similar ecosystem responses as re-introduced Rhino populations grow to their ecological limits. Grazing lawn areas should expand, favoring short-grass grazers, with a reduction in the size, and frequency, of fires. The addition or expansion of short grass areas may add to the biodiversity of an ecosystem, as has been shown for birds in HiP (Krook and others 2007). These ecosystem effects should be most pronounced at intermediate rainfall, as in the Hluhluwe savanna, where the role of the Rhino in engineering greater heterogeneity in the grass sward could not be replaced by mesoherbivores.

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