

The role of browsers in maintaining the openness of savanna grazing lawns

*Michael D. Voysey^{1,2}, Sally Archibald², William J. Bond³, Jason E. Donaldson², A. Carla Staver⁴, Michelle Greve¹

¹Department of Plant and Soil Sciences, University of Pretoria, Pretoria, South Africa.

²Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa.

³Biological Sciences, University of Cape Town, Rondebosch, South Africa

⁴Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut

*Correspondence author: mick.voysey@gmail.com; Tel: +27 (0)82 304 3510

Accepted by Journal of Ecology

Abstract

1. In savannas, ruminant herbivores can have divergent impacts on tree recruitment and subsequent woody cover. Whereas heavy grazing by cattle results in woody thickening, intensive grazing by wildlife instead tends to be associated with lower woody cover.
2. To disentangle why woody cover is low in areas heavily grazed by wildlife, we investigated (I) whether grazing lawns attract indigenous mammalian browsers, and if a preference for short-grass habitat decreases with browser body mass as predator susceptibility decreases; and (II) whether browser attraction to grazing lawns translates into the suppression of woody plants, including seedlings and saplings, thus maintaining the openness of heavily grazed short-grass areas.
3. In Kruger National Park, South Africa, we contrasted browser abundance (using dung counts) on grazing lawns and on low-herbivory sites characterised by tall grass. Additionally, a herbivore enclosure experiment was set up to investigate the combined impact of browser removal and grass height habitat type on seedling survival and sapling growth of a dominant woody plant species. Finally, in Hluhluwe-iMfolozi Park, we examined the long-term (10

year) impact of browser removal on the growth rates of a range of woody species, monitored across ten sites along a gradient of herbivory ranging from grazing lawn to tall grass.

4. Steenbok and impala selected short- over tall-grass as preferred browsing sites, while elephant preferred tall grass. Browser abundance on short grass decreased with browser body mass, indicating that predator avoidance might be a key factor driving mesoherbivores to utilise grazing lawns.
5. Seedling survival was lowest on grazing lawns when browsers were present, with mortality occurring in two out of every three seedlings. Similarly, sapling growth was lowest on grazing lawns, although browser removal had no significant effect. Evidence for increased browser impact on grazing lawns was clearest from our long-term herbivore enclosure experiment in HiP, which demonstrated that browsers strongly modify the growth rates of woody plants in short-grass habitats.
6. *Synthesis*. These results provide support for the hypothesis that browsers, particularly browsing mesoherbivores and mixed feeders, are attracted to short-grass habitats, and that they help maintain grazing lawn openness by suppressing seedling survival and woody plant growth where grass is kept short by grazers.

Key-words: African savannas, browsing and grazing, bush encroachment, grass height, grazing lawn, predation, seedlings and saplings, woody recruitment

1 Introduction

In African savannas, large mammal grazers create grazing lawns through frequent defoliation of the grass sward (McNaughton, 1984; Hempson et al., 2015). This repeated herbivory in turn increases grass foliar nitrogen by promoting grass species that allocate more resources to nitrogen-rich leaves, instead of carbon-dense stems (Stock, Bond, & van de Vijver, 2010; Coetsee, Stock, & Craine, 2011), upregulates grass primary productivity by stimulating grass regrowth (McNaughton, 1983; Anderson et al., 2013), and redistributes nutrients enriching grazing lawn soils (Augustine, McNaughton, & Frank, 2003; Mayengo, Armbruster, & Treydte,

2020). Accordingly, grazing lawns are a highly productive grassland state which support large grazer populations of a wide variety that maintain grazing lawns as a persistent alternative to tall, bunch grasslands (Verweij, Verrelst, Loth, Heitkönig, & Brunsting, 2006; Yoganand & Owen-Smith, 2014).

Curiously, grazing lawns in wildlife areas are also typified by sparse woody cover relative to wooded tall-grass areas (Riginos & Young, 2007; Riginos & Grace, 2008; Staver, Bond, Stock, van Rensburg, & Waldram, 2009; Stevens, Erasmus, Archibald, & Bond, 2016). However, surprisingly little is known about why short-grass states in wildlife areas have lower woody densities than adjacent tall-grass states (Riginos & Young, 2007; Riginos & Grace, 2008; Staver et al., 2009), how mammalian browsers utilise grazing lawns, or what role browsers play in maintaining the open physiognomy of grazing lawn environments (see Porensky & Veblen, 2012), since grazing lawns can only persist if they remain open and accessible to grazers (Hempson et al., 2015).

The question is particularly pertinent since, in African rangelands, heavy grazing by cattle in the absence of browsers leads to increases in woody cover (Skarpe, 1990; Roques, O'Connor & Watkinson, 2001; Tobler, Cochard, & Edwards, 2003). Indeed, overgrazing is recognised as one of the primary regional drivers of bush encroachment (O'Connor, Puttick, & Hoffman, 2014). Mechanistically, depletion of the grass sward decreases above- and below-ground grass biomass, reducing competition between grasses and woody plants and also suppressing fire, thus benefiting trees (van Langevelde et al., 2003; Case & Staver, 2016).

Since low grass fuel loads on grazing lawns mostly exclude fire (Archibald, Bond, Stock, & Fairbanks, 2005), which is otherwise a major suppressor of woody plants in savannas (van Langevelde et al., 2003; Higgins et al., 2007; Gignoux, Lahoreau, Julliard, & Barot, 2009; Smit et al., 2010; Case & Staver, 2016), an alternative explanation is required for low woody cover on grazing lawns in wildlife areas. In conjunction with fire, browsers maintain the codominance of trees and grasses in African savannas by preventing establishment of seedlings (O'Kane, Duffy, Page, & Macdonald, 2012; Morrison, Holdo, Rugemalila, Nzunda, & Anderson, 2018), and by limiting the recruitment of young trees to adult size classes (a browse trap – Scholes

& Archer, 1997; Higgins, Bond, & Trollope, 2000; Staver et al., 2009; Sankaran, Augustine, & Ratnam, 2013; Staver & Bond, 2014). Successful seedling establishment and the transition of saplings to adult size classes represent two important demographic bottlenecks that woody plants need to overcome to reach maturity and contribute to woody layer expansion (Midgley & Bond, 2001; Augustine & McNaughton, 2004; Holdo, Holt, & Fryxwell, 2009; Staver & Bond, 2014).

Therefore, explaining why grazing lawns remain open in a wildlife context would benefit from a better understanding of how browsers utilise short- versus tall-grass habitats, and how this in turn impacts on the performance of woody plants from young demographic stages, namely seedlings and saplings, which are thought to be impacted most by browsing (Roques et al., 2001).

In this study, we focus on the hypothesis that grazing lawns in wildlife environments have lower tree cover because some browser species prefer foraging in short- compared to tall-grass habitats, and thus contribute to keeping grazing lawns open by suppressing woody recruitment. There are several reasons why short-grass habitats might be attractive to browsers. Short-grass areas might improve the apparency of seedlings and saplings to browsers (e.g. black rhino: Bond, Smythe, & Balfour, 2001; other herbivores: Riginos & Young, 2007), while the unique forb flora found on grazing lawns might further encourage browsers to forage in short grass. Open, short-grass areas might also improve the ability of browsers to detect and avoid predators (Valeix et al., 2009). Mesoherbivores in particular, which are most susceptible to predation, should benefit from increased detectability, enabling them to spend more time foraging and less on predator-avoidance behaviour (Underwood, 1982; Sinclair, Mduma, & Brashares, 2003; Riginos, 2015). Furthermore, if grazing lawns attract mixed feeders for the improved grass quality, they would be expected to browse while foraging if tree seedlings are available (O’Kane et al., 2012).

In addition to herbivory, short- and tall-grass systems differ in the resource environment for seedlings and saplings (Bond et al., 2017). For example, increased compaction and high evaporation rates on grazing lawns (Veldhuis, Howison, Fokkema, Tielens, & Olf, 2014),

leading to low soil water availability (van der Waal et al., 2011), has been suggested as an important limiting factor to seedling establishment on grazing lawns (Walters, Midgley, & Somers, 2004). Conversely, high soil nutrient availability, which is typical of grazing lawns, has shown to confer grasses with a competitive advantage over seedlings (Kraaij & Ward, 2006; van der Waal et al., 2011; Porensky & Veblen, 2012; February, Higgins, Bond, & Swemmer, 2013; Morrison et al., 2018). Consequently, the impact of consumers and resources need to be understood to best elucidate the role of browsers in keeping grazing lawns open.

Here we take several approaches to assess the role of browsers (i.e. consumers) in keeping woody plants out of grazing lawns. First, we assessed how grassland structure affects browser presence in a savanna with extant wild herbivores. To complement this correlative analysis, we used combined results from a short-term herbivore exclosure experiment with a long-standing herbivore exclusion experiment to assess whether seedling establishment or sapling growth and recruitment limited woody presence on grazing lawns, and whether this was driven by differences in browsing pressure, or other abiotic factors. Specifically, we investigated the following:

- (I) Do grazing lawns attract indigenous mammalian browsers, and does a preference for short-grass habitat decrease with browser body mass, i.e. as predator susceptibility decreases?
- (II) Does browser attraction to grazing lawns translate into the suppression of woody plants, including seedlings and saplings, thus maintaining the openness of short-grass areas?

2 Methods and Materials

2.1 Study Sites

Three different datasets were used to answer the research questions outlined above. Data were collected from two savanna systems in South Africa, namely Kruger National Park (KNP)

and Hluhluwe-iMfolozi Park (HiP) (du Toit, Rogers, & Biggs, 2003; Cromsigt, Archibald, & Owen-Smith, 2017).

In Satara, KNP, an existing short- and tall-grass mosaic (details in Donaldson et al., 2017) was used to test whether grazing lawns have higher browser abundances than tall-grass habitats, and whether grazing lawns show lower survival and growth of seedlings and saplings. In HiP, data from a long-term (10 year) herbivore exclosure experiment (details in Staver et al., 2009) was used to test the effect of browser removal on the growth rates of a range of woody species monitored along a gradient of herbivory ranging from grazing lawn to tall grass.

Kruger National Park (Satara: 24.40° S, 31.77° E) and Hluhluwe-iMfolozi Park (28°00" - 28°26" S; 31°43" - 32°09" E) are climatically similar savanna ecosystems: summer temperatures are hot (regularly exceeding 35°C) while winters are mild and frost free (Venter, Scholes, & Eckhardt, 2003; Howison, Olf, Owen-Smith, Cromsigt, & Archibald, 2017). Both regions receive most of their rainfall during the austral summer (November to April) which constitutes the main growing season. Mean annual rainfall at study sites in KNP (Satara: 544 mm) are lower than study sites in HiP (~590-780 mm).

The Satara landscape is dominated by nutrient-rich clay soils derived from basalt (Venter et al., 2003). The Satara basalts are dominated by the tree species *Acacia (Senegalia) nigrescens*, *Dichrostachys cinerea*, *Dalbergia melanoxylon* and *Sclerocarya birrea*. Soils in HiP are also closely linked to the underlying geology, comprising mostly Ecca shales and sandstones but also basalts (Howison et al., 2017). Common tree species in HiP include *A. nigrescens*, *Acacia (Vachellia) nilotica*, *Acacia (Vachellia) tortilis*, *D. cinerea*, *Euclea divinorum*, *Gymnosporia heterophylla* and *Gymnosporia senegalensis* (Whateley & Porter, 1983).

KNP and HiP are host to a full suite of indigenous large-mammal herbivores. Among them are short-grass grazers, whose concentrated grazing activity help to establish and maintain grazing lawns. Hippopotamus *Hippopotamus amphibius* and white rhino *Ceratotherium simum*, which occur at high densities in HiP, are especially important for

facilitating grazing lawn establishment by transforming tall-grass swards into short-grass patches. However, frequent and concentrated herbivory by mesoherbivores (e.g. blue wildebeest *Connochaetes taurinus*, warthog *Phacochoerus africanus* and impala *Aepyceros melampus*), also create grazing lawns (Verweij et al., 2006). These often more abundant herbivore species are particularly important for maintaining a lawn-grass state (Waldram, Bond, & Stock, 2008; Hempson et al., 2015).

In addition to grazers, browsers and mixed-feeders consume varying quantities of available plant material, but of interest here is the contribution of woody plant material to their diet. Present in both study areas are the megaherbivore browsers African elephant *Loxodonta africana* and giraffe *Giraffa giraffa*, which have important top-down effects on tree cover in African savannas (Bond & Loffell, 2001; Guldmond & van Aarde, 2008). However, mesoherbivores, including mixed feeders such as impala, the most plentiful ungulate herbivore in both study systems, also play a major role in suppressing woody plant recruitment and growth (O’Kane et al., 2012; Staver & Bond, 2014). Other common browser species considered in this study include steenbok *Raphicerus campestris*, kudu *Tragelaphus strepsiceros* and common duiker *Sylvicapra grimmia*. All these species were present at all study sites.

2.2 Grass height and habitat preference of browsers

2.2.1 Experimental design

The experiment in Satara was designed to test how different fire sizes, ignited during different seasons, affect resource quality and the landscape of fear, and how this in turn influences site selection by grazers. Results from this experiment have shown that grazers are attracted to the flush of nutrient-rich grass that follows after fire (Donaldson et al., 2017). Because the burns were small, grazing activity was concentrated, and consequently grass remained short, palatable and attractive to grazers. Accordingly, the study site, which was initially a homogenous tall-grass landscape, was characterised by experimental plots where grass was kept short (consistently below 10 cm), initially by fire but maintained by herbivores (Donaldson

et al., 2017). In contrast, in control plots that were not burned, grass height was statistically taller (consistently above 30 cm), and equivalent to the surrounding tall-grass landscape. Before the start of the experiment, the proportion of area covered by short grass (grass height less than 10 cm) across the short- and tall-grass sites was 0.91 (SE = 0.03) and 0.08 (SE = 0.04) respectively (Donaldson et al., 2017). Therefore, the outcome of experimental treatments provided a unique opportunity to examine browser preference for short-grass habitats (grazing lawns) and adjacent tall-grass habitats, and to determine whether browser preference for grazing lawn sites correlates with reduced seedling survival and sapling growth, which could provide initial support for the role of browsers in maintaining the open physiognomy of lawn-grass ecosystems.

The experimental design included a control, where the absence of fire and limited grazing kept grass tall, and a late season burn treatment where grass was kept short by repeated herbivory (Fig. 1; Donaldson et al., 2017). Grazing lawn sites in Satara had only recently (in the last 3 years) developed from a site that was previously a uniform tall-grass landscape. Ancillary data indicate that although the sward structure has changed considerably, and the grass species composition significantly, there has not yet been significant feedbacks to soil nutrients.

Fire season treatments were replicated across three different fire sizes: 0.25 ha, 5 ha and 25 ha burn plots. Eight replicates of each treatment were included in the study and all plots were located within a management area covering approximately 6600 ha. Distance between plots of the same size and treatment ranged between 1.5 and 17 km, and the maximum distance between any two plots was 19 km. Sampling occurred on sub-plots measuring 50 m x 50 m with sampling effort (i.e. number of sub-plots) being larger on the larger plots. For details see Donaldson et al. (2017).



Fig. 1. Experimental set-up in the short- and tall-grass mosaic of Satara, KNP: a) experimental plots were characterised by a short-grass treatment (top right of picture), initiated by fire but maintained by herbivores, and control plots where grass height remained distinctly taller (left of picture). To test whether browser abundance was higher on grazing lawns, and how browsing in turn impacted seedling survival and sapling growth, herbivore exclosures were set up over *A. nigrescens* b) seedlings and c) saplings, in both short and tall grass. For every fenced seedling and sapling, another remained unfenced, and was thus susceptible to d) browsers.

Dung counts were used as a proxy for herbivore habitat use and subsequently used to test whether the individual browser species select grazing lawns over tall-grass habitats. Dung counts were conducted along two 4 x 50 m belt transects within each sampling subplot. Counts occurred monthly from June 2015 to April 2016 and dung was identified to species level. A single dung pile from an individual of a species was considered a dung deposition event. After counting, all dung piles were squashed to prevent recounts. Total dung counted along both

transects in each subplot was summed for each browser species and divided by the number of days between sampling events to account for variability in time during which dung accumulated (which could range between 25 and 35 days). From this, a value that represented dung deposition per day for each species in each subplot for each month was obtained. Values of dung deposition per day were averaged across all months to obtain an average dung deposition value for each browser species in each subplot for the duration of the study period.

Dung counts as a measure of herbivore presence over time can be confounded by different decay rates at different times of year, and comparisons in the amount of dung between species can be confounded by differences in the way animals deposit dung. However, in this study we were comparing the average dung found for individual species between two sites within a single season. Therefore, differences in dung counts between sites should be a reliable measure of differences in animal presence (Marques et al., 2001; Sensenig, Demment, & Laca, 2010).

2.2.2 Statistical analyses

A generalized linear mixed effect model (GLMM) was run for each browser species to test whether dung deposition rate was higher on grazing lawns than tall-grass habitats (Bolker et al., 2008). Since several subplots were situated within the same plot, subplots could not be considered independent; therefore, plot identity was included as a random effect in each model (Bolker et al., 2008). Additionally, because dung deposition data for all browser species was zero-inflated, each GLMM was run using a Tweedie distribution and log-link function (Bonat, Jørgensen, Kokonendji, Hinde, & Demetrio, 2018). The Tweedie distributions are a versatile family of distributions which account for non-negative, count data that are zero-inflated (Bonat et al., 2018). In our use of the Tweedie distributions, the Poisson–Gamma distribution (power = 1.2 for giraffe, power = 1.3 for impala, duiker, kudu and elephant, and power = 1.4 for steenbok) was the best fit for our data.

For each subplot and browser species, we also calculated a grass height preference index as the ratio of dung in short grass divided by the combined total of dung in short plus

tall grass (Sensenig et al., 2010). The preference index ranges from 0 to 1, where 0 indicates absolute avoidance of short-grass habitat and 1 indicates complete preference for short-grass habitat. A preference index has the advantage of minimizing the effects of seasonality, accounts for regional variability in herbivore abundance, and allows comparisons to be made between species (Sensenig et al., 2010). Grass height preference index values were plotted against the body mass (log-scale) of each browser species. Body mass values were calculated as the average of the male and female mass reported in Skinner and Smithers (1990).

2.3 Seedling and Sapling Experiment

2.3.1 Experimental design

To test whether survival of seedlings and growth of saplings (i.e. height gain) was lower on grazing lawns than tall-grass habitats, an enclosure experiment was conducted on the Satara short- and tall-grass mosaic. Five matching tall-grass (control) and short-grass (late burn) sites were chosen. At each site, six randomly selected *A. nigrescens* saplings were identified on the short- and six on the tall-grass treatment. Saplings ranged in size from 9 to 76 cm at the start of the experiment. *Acacia nigrescens* was selected because it is the most abundant woody plant in the study area and is palatable to browsers. On each treatment and at each site, three of the six saplings were randomly allocated to the enclosure treatment and thereafter fitted with a wire-mesh enclosure (dimensions: 1 m wide and 1.5 m high), while three saplings remained open (Fig. 1). Each enclosed sapling was positioned at the centre of the enclosure. Sapling height, taken as the height from ground to highest living plant material, was measured upon commencement of the experiment in October 2016 and then again at the end of the experiment in June 2017. In total, 60 *A. nigrescens* saplings were included in the experiment, with 15 saplings allocated to each treatment combination.

The same experimental set-up was used to test whether seedling survival was lower on grazing lawns with herbivores present (Fig. 1). The seedling enclosure experiment included three of the five matching short- and tall-grass sites used in the Satara sapling experiment. The seedling experiment utilised the same wire-mesh enclosure set-up for the saplings; in

each enclosure seedlings were planted near the periphery. Three seedlings were planted in each enclosure and three seedlings were planted three meters away from the enclosure within the same treatment (tall grass or short grass). No burns were applied during the seedling or sapling studies.

Seedlings were grown from seeds collected near Orpen, KNP and germinated in early September 2016 in black plastic bags at Wits Rural Facility, Mpumalanga. After germination, seedlings grew for ~2 months before being planted at the study site in early December 2016, just as the rains started. In total, 72 *A. nigrescens* seedlings were planted, with 18 seedlings allocated to each treatment combination. Seedling survival was recorded one week after planting to account for transplant mortality. Thereafter, seedling survival was recorded at the end of the experiment in June 2017. In addition, because grass inside enclosures on the short-grass treatment was not accessible to herbivores, grass was clipped monthly to retain the short-grass treatment.

2.3.2 Statistical analyses

Two GLMMs were run to test whether survival of seedlings and growth of saplings was lower on grazing lawns than tall-grass habitats. A two-way interaction term between grass height and enclosure status was included in each model to test whether seedling survival and sapling growth would be lowest on a combined short-grass, non-fenced treatment.

Furthermore, to control for the effect of sapling height recorded at the beginning of the experiment on growth, the initial height of each sapling was included as a predictor variable in the sapling growth GLMM. For both GLMMs, site was included as a random effect (Bolker et al., 2008). In addition, enclosure identity was included as a random effect in the seedling model (with enclosure nested within site) to account for variation in seedling survival between different enclosures (Bolker et al., 2008). The seedling survival GLMM was fitted with a binomial distribution and logit-link function and the sapling growth GLMM was fitted with a Gaussian distribution and identity-link function.

2.4 Long-term tree growth rates along a gradient of grass height

2.4.1 Experimental design

To assess whether browser pressure, and therefore tree growth rates, differ between grazing lawn and tall-grass sites, data from a long-term (2000 - 2009) herbivore exclosure experiment in Hluhluwe-iMfolozi Park were used (details in Staver et al., 2009). In 2000, ten sites were selected with the aim of contrasting short-grass (grazing lawn) vs. tall-grass habitat across a gradient of herbivore pressure in the park (Staver et al., 2009). Sites were located on predominantly dolerite-derived soils but there were sandstone- and shale-derived soils. At each site, an exclosure plot (40 x 40 m), which excluded all large herbivores using fencing, was set up, and a control accessible to all herbivore species was demarcated. To validate the effectiveness of the herbivore exclusion treatment, the number of dung piles in each plot was counted during each month of the experiment.

At the beginning of the experiment, all trees (any woody individual, regardless of size or life stage) in each plot were mapped onto a 2 x 2 m grid that covered half of each plot (40 x 20 m) and their heights measured. Thereafter, following each growing season until the end of 2009, the height of already-mapped trees was re-measured. New individuals were also recorded during each census and monitored thereafter.

To obtain a relative measure of grass sward height, a disk pasture meter (DPM) was used, which is a metal disk (diameter 45 cm, weight 1500 g) dropped from a standard height (Bransby & Tainton, 1977). DPM readings were taken in each 2 x 2 m grid, at the end of the rainy season (in June of each year), which usually represents peak grass biomass. The extent of short-grass habitat at each site was calculated by dividing the number of DPM drops recorded to fall below 10 cm, by the total number of DPM drops (ranging from 170 to 210 drops at each site), then averaged across years (2000 - 2003), and reported as the mean proportion of grass height below 10 cm.

All sites burned every two years beginning in 2000 after the tree census was complete (i.e. in 2000, 2002, 2004 and 2008). The application of fire coincided with management burns, to ensure that small burned patches did not attract herbivores. Although fire was applied to all

sites and treatments, only those with adequate grass biomass provided enough fuel to burn the entire plot. Fire often did not actually spread in heavily grazed plots (i.e. where dung counts were high) (Staver et al., 2009).

2.4.2 Statistical analysis

Linear mixed effect models (LMMs) were run to test the effect of browser removal on the growth rates of a range of woody species monitored along a gradient of herbivory ranging from grazing lawn to tall grass. Tree growth rates were analysed separately for the two most abundant woody species recorded in experimental plots, namely *D. cinerea* (1686 individuals) and *A. nilotica* (546 individuals), and for two woody plant functional types, namely fine-leaved (6 species: *A. nigrescens*, *A. gerrardii*, *A. karroo*, *A. nilotica*, *A. tortilis* and *D. cinerea*, totalling 3480 individuals) and broad-leaved (3 species: *E. divinorum*, *M. heterophylla* and *M. senegalensis*, totalling 433 individuals). Fine-leaved species are considered to be more palatable to browsers than broad-leaved species (Owen-Smith & Cooper, 1989). Each species included in our analyses comprised at least 130 individuals of both small (<0.5 m) and medium (0.5 – 2.0 m) size classes. Trees of all sizes (ranging from 10 cm to 10 m) were included in the analyses, with 96% of trees falling within the 0.0 – 2.0 m size range. Only trees with at least five years of continuous record were included in the analyses. Tree growth rates (in cm/year) were calculated by dividing the total growth of an individual tree during the tracked period by the number of years the tree was monitored.

In each LMM, the proportion of grass height below 10 cm and enclosure status (fenced vs. unfenced) were included as fixed effects. In the same model, the significance of a two-way interaction term between short grass proportion and enclosure status was also tested; we expected grazing lawns to be more challenging than tall-grass habitat for saplings to transition into larger size classes (due to increased browsing pressure), and therefore, we expected that the growth rate of unfenced saplings would decrease as short grass area increased, whereas the growth rate of fenced saplings would be unaffected by grass height (i.e. the response is explained by browsing, not other environmental differences between short and tall grass).

Furthermore, we expected that the response of woody plants to short grass proportion and exclosure status might differ with woody plant functional type. For fine-leaved species, which are more palatable, our abovementioned prediction remained, whereas for broad-leaved species, we expected that tree growth rate would be less well predicted by grass height and exclosure status because of the lower palatability of broad-leaved species (Owen-Smith & Cooper, 1989).

With the same dataset used in this study, Staver et al. (2009) demonstrated that woody plant growth in HiP is not related to initial sapling size, and thus sapling size was not included as a predictor variable in the models. To account for differences between the sites in Hluhluwe and iMfolozi Game Reserve, Game Reserve identity was included as a random effect in all LMMs.

2.4.3 Statistical software

All analyses were conducted in R, version 3.5.0 (R Core Team 2018) using the 'lme4' (Bates, Maechler, Bolker, & Walker, 2015) and 'glmmADMB' packages (Bolker et al., 2008).

3 Results

3.1 Grass height habitat preference of browsers

Grass height habitat type significantly predicted dung deposition for steenbok, impala and elephant (Table 1). Steenbok and impala selected grazing lawns over tall-grass habitats, whereas elephant selected tall-grass over grazing lawns. Grass height habitat type did not significantly explain abundance of the three remaining browser species, namely duiker, kudu and giraffe.

The short-grass preference index quantified for five out of six browser species decreased with browser body mass (Fig. 2, $R^2 = 0.834$, $df = 4$, $p = 0.011$) as expected, steadily changing from preference to avoidance at ~800-900 kg.

Table 1. Results from general linear mixed-effects models testing the effect of grass height habitat type (short vs. tall) on dung deposition of six browser species in Satara, KNP. Significant effects are shown in bold ($p < 0.05$).

Browser species	Level	Estimate	SE	t value	p-value	n
Steenbok	Short > Tall	1.52	0.62	2.44	0.02	112
Duiker	ns	0.91	0.71	1.28	0.20	21
Impala	Short > Tall	1.08	0.22	5.03	<0.01	2697
Kudu	ns	-0.25	0.33	-0.75	0.45	172
Giraffe	ns	0.41	0.23	1.78	0.08	215
Elephant	Short < Tall	-1.17	0.45	-2.58	0.01	170

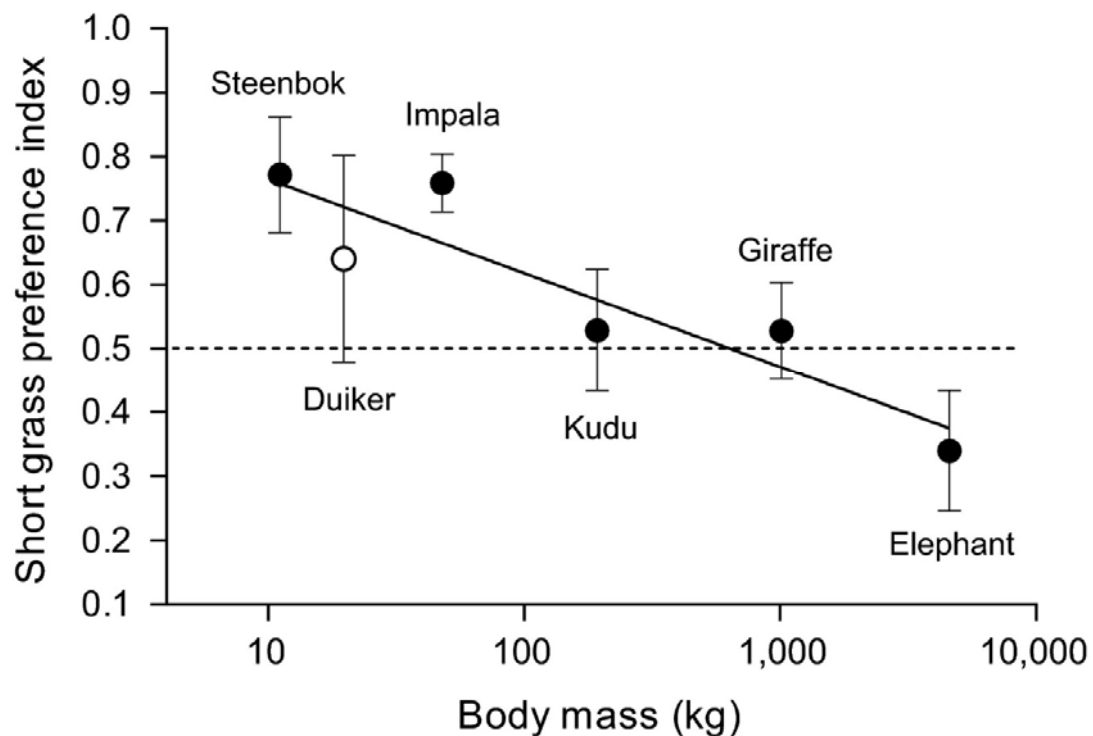


Fig. 2. Short grass preference (mean \pm SE) vs. body mass (log-scale) of six browser species. Short grass preferences were calculated as the ratio of dung in short grass divided by the combined total of dung in short plus tall grass for each species (Sensenig et al., 2010). The index ranges from 0 to 1, where 0 indicates absolute avoidance of short grass habitat and 1 indicates complete preference. Duiker (hollow symbol) was excluded from regression analysis due to small sample size (data only available for seven out of 20 subplots); its inclusion does not alter the trend of significance of the relationship ($R^2 = 0.834$, p -value = 0.01, $df = 4$).

3.2 Sapling and seedling experiment

Seedling survival was 25% greater when herbivores were removed compared to when they were present (Table 2). In the absence of herbivores, seedling survival was consistently above 70% regardless of grass height and decreased only slightly in tall-grass habitat when herbivores were present (Fig. 3). Conversely, on grazing lawns, herbivore presence resulted in the death of two out of every three seedlings. Overall, seedling survival was lowest on grazing lawns with browsers.

Table 2. Results from generalized linear mixed models testing the effect of grass height habitat type (short vs. tall), exclosure status and, for saplings, initial sapling height on seedling survival (n = 72) and sapling growth (n = 60) in Satara, KNP. Significant effects are shown in bold.

	Fixed effect	Estimate	SE	z value	p-value
Seedling survival	Grass height	-0.48	0.97	-0.50	0.62
	Exclosure	-2.28	0.90	-2.55	0.01
	Grass height: Exclosure	2.00	1.21	1.66	0.09
Sapling growth	Grass height	17.86	5.75	3.11	<0.01
	Exclosure	-7.43	5.51	-1.35	0.19
	Initial sapling height	-0.48	0.19	-2.51	0.02
	Grass height: Exclosure	-10.72	7.67	-1.40	0.17

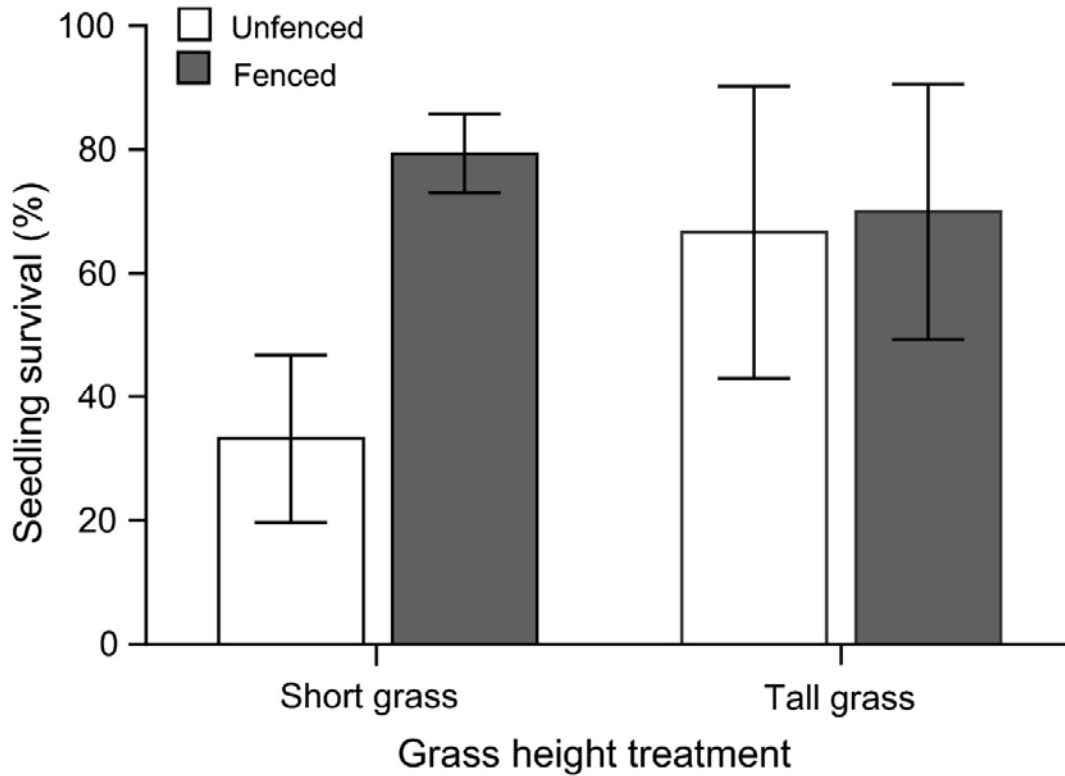


Fig. 3. Survival of *Acacia nigrescens* seedlings (mean \pm SD) over one growing season in Satara, KNP. We predicted that browsing pressure would be highest in short-grass environments. In support of our expectation, seedling survival was lowest in short grass when browsers were present (Table 2).

Grass height and initial sapling height were both significant predictors of sapling growth (Table 2). On average, sapling growth was 22% lower on grazing lawns than in tall-grass habitats (Fig. 4) and decreased with an increase in initial sapling height. Interestingly, exclosure status was not a significant predictor of sapling growth, even though sapling growth was on average 43% lower when herbivores were present.

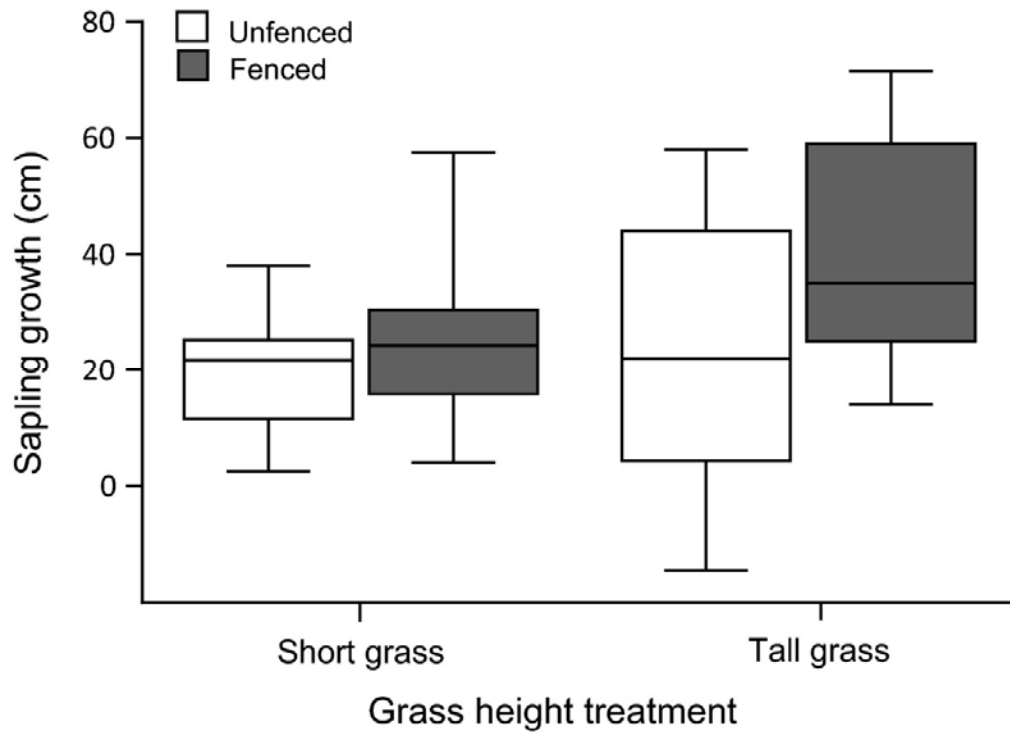


Fig. 4. Growth of *Acacia nigrescens* saplings over one season in Satara, KNP. We predicted that sapling growth would be impacted most by browsers in short-grass environments. However, our results demonstrate that, although sapling growth was significantly lower on the short-grass treatment, this could not be attributed to herbivory, since the combined effect of grass height and enclosure status was not significant (Table 2).

3.3 Long-term growth rates of woody plants

In the HiP experiment, an interaction between proportion short grass and enclosure status was significant in LMMs of both dominant tree species (*D. cinerea* and *A. nilotica*) and of both functional types (fine-leaved and broad-leaved species) (Table 3): for both species and functional types an increase in proportion short grass marked a significant decrease in tree growth rates for unfenced trees. In contrast, this trend was not true for fenced individuals, which either showed no relationship or increased growth as proportion short grass increased (Fig. S2).

Table 3. Results from general linear models testing the effect of grass height (proportion of grass height below 10 cm) and enclosure status on sapling growth rate (cm/year) for the two most common woody plant species in HiP (*D. cinerea* and *A. nilotica*) and for two woody plant functional types (fine-leaved and broad-leaved FT). Significant effects are shown in bold.

Species/FT	Fixed effect	Estimate	SE	t value	p-value
<i>Dichrostachys cinerea</i>	Exclosure	-1.35	0.63	-2.15	0.03
	Grass height	-0.08	0.01	-7.25	<0.01
	Exclosure: Grass height	0.15	0.02	9.93	<0.01
<i>Vachellia nilotica</i>	Exclosure	-0.81	1.36	-0.60	0.55
	Grass height	-0.08	0.03	-3.17	<0.01
	Exclosure: Grass height	0.21	0.04	5.87	<0.01
Fine-leaved	Exclosure	0.07	0.49	0.15	0.88
	Grass height	-0.05	0.01	-6.55	<0.01
	Exclosure: Grass height	0.12	0.01	11.02	<0.01
Broad-leaved	Exclosure	-1.97	1.03	-1.91	0.06
	Grass height	-0.04	0.02	-2.52	0.01
	Exclosure: Grass height	0.07	0.03	2.78	0.01

At our tall-grass sites, where there was a low proportion of short grass, differences between growth rates of fenced and unfenced woody plants were also low, i.e. the fenced treatment only improved woody growth rates by 18% on average because of limited browsing (Fig. 5). However, as grass height decreased, the difference between growth rates of fenced and unfenced individuals decreased significantly (Fig. 5), with the fenced treatment improving woody growth rates by 82% on average, demonstrating that browsing by large mammals was suppressing woody plant growth at sites with a high proportion of short grass. This trend was particularly evident for *D. cinerea* (Fig. 5a), the most common woody species in HiP, although, while showing the same trend, insignificant for *A. nilotica* (Fig. 5b), the second most common species (possibly because of its limited distribution across the 10 sites). Interestingly, a similar trend was demonstrated for both fine-leaved (Fig. 5c) and broad-leaved (Fig. 5d) functional types, despite our expectation that the less palatable, broad-leaved species would not be as susceptible to being browsed.

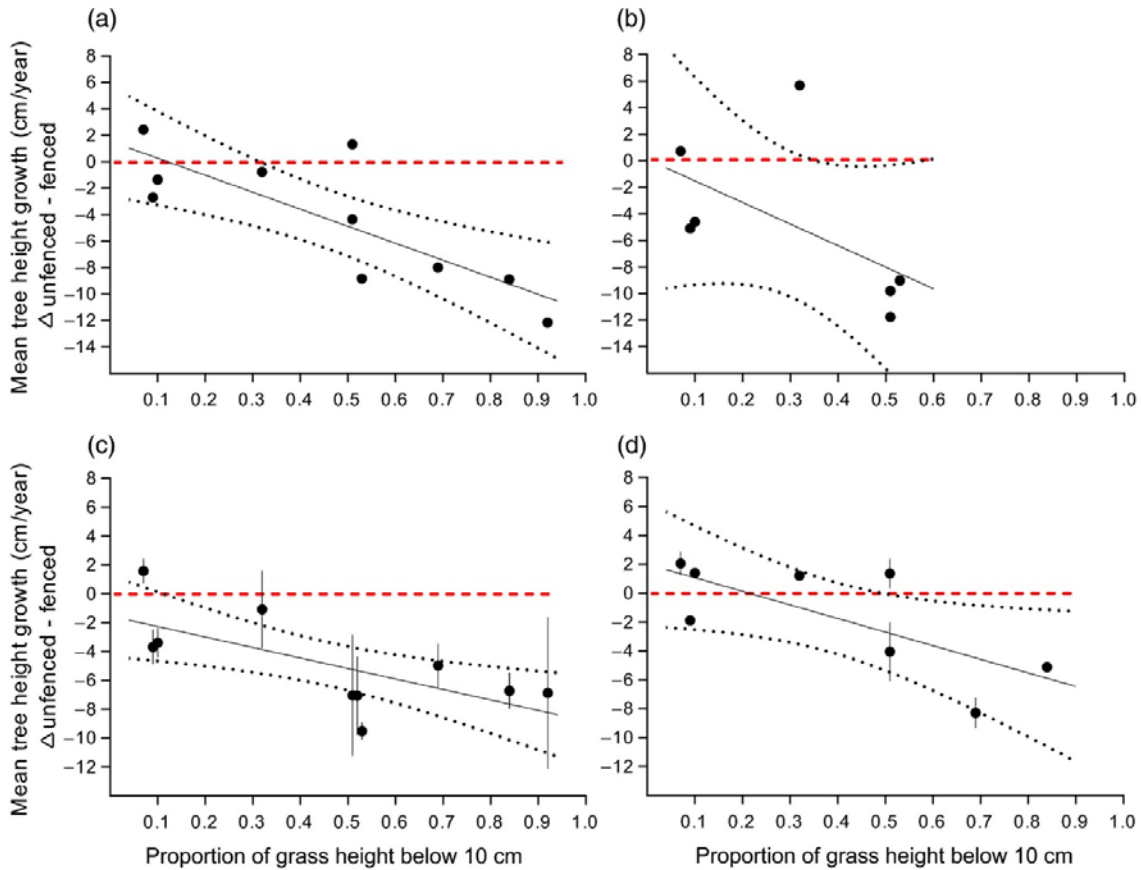


Fig. 5. The impact of grass height on differences in tree height gain between the browser present and browser removal treatment in HiP. Browsing impact on tree height gain was higher in areas with short grass i.e. browsers utilised trees more in short- than tall-grass ecosystems. The y-axis represents the difference in tree height gain (mean \pm SE) between the unfenced and fenced treatment at a range of sites which differ in their grass structural characteristics. We present the difference to control for other factors, such as soil nutrients and soil type, that might influence tree growth rates across the different sites. Linear regression analyses are shown for two dominant woody plant species: a) *D. cinerea* ($R^2 = 0.65$, p-value = 0.01) and b) *A. nilotica* ($R^2 = 0.32$, p-value = 0.19), and for two woody plant functional types: c) fine-leaved ($R^2 = 0.46$, p-value = 0.03) and d) broad-leaved ($R^2 = 0.52$, p-value = 0.04), across 10 sites in Hluhluwe-iMfolozi Park for the period 2000-2009. The dotted red line indicates where the net effect of herbivory switches from positive to negative.

4 Discussion

Here, we found (1) that some browser species actively select grazing lawn habitats and (2) they were predominantly mesoherbivores and therefore likely to have a greater impact on seedlings and saplings than on large trees. Also, (3) seedling survival was poorer without protection from browsing in grazing lawns, but not in tall grass, and (4) over the longer term, protection from browsers in short-grass areas caused major increases in the size of woody plants. Thus, browsers matter when keeping grazing lawns open. This works in synergy with lawn selection by grazers, providing protection from predators and ease of grazing for larger herbivore species.

4.1 Browser attraction to grazing lawns

In addition to being favoured grazing habitats (Donaldson et al., 2017), our results show that short-grass environments in wildlife areas attract browsers. Preference for short-grass habitat scaled negatively with browser body mass (Fig. 2), despite less browse availability, suggesting instead that anti-predator benefits make grazing lawns highly attractive to mesoherbivores because of their higher susceptibility to predation (Underwood, 1982; Sinclair et al., 2003; Augustine, 2004; Sensenig et al., 2010; Burkepile et al., 2013).

A good example of where browsing mesoherbivores might maintain grazing lawn openness, is in the tree-less glades of East Africa. Glades are grazing lawns which form as a result of concentrated herbivory by wildlife following cattle kraal abandonment (Young, Patridge, & Macrae, 1995; Augustine, 2003; Veblen, 2012). Frequent grazing keeps grass short and highly sought after. Our findings might help explain why heavy grazing in glades, and on grazing lawns in general, results in woody suppression, and why open glade-type habitats persist for so long in the landscape, characteristically more than four decades (Augustine, 2003). We suggest that lawns are not only patches of concentrated grazer activity but also of browsers that select these short-grass ecosystems, in part, as an anti-predator response.

4.2 Grazing lawns and the role of mesoherbivores

The role of mesoherbivores, including small mammals, in limiting woody recruitment is relatively under-appreciated compared to that of larger browsers such as elephant and giraffe, whose negative impacts on large trees are more conspicuous (Ben Shahr, 1993; Birkett, 2002). Nonetheless, mesoherbivores, such as the ubiquitous impala, impact woody plants from young demographic stages making them essential for halting woody encroachment and maintaining open habitat (Prins & Vanderjeugd, 1993; Moe, Rutina, Hytteborn, & du Toit, 2009; O'Kane et al., 2012; Staver & Bond, 2014). This might have implications for global rewilding, which is mostly concerned with ecological impacts of large herbivores (Svenning et al., 2016; Bakker & Svenning, 2018), and gives little recognition to mesoherbivore species, such as browsers which inhibit woody recruitment (Bond, 2019).

While our results suggest that browsing mesoherbivores, including mixed feeders, are major agents of woody plant suppression on grazing lawns; large browser species may still contribute to grazing lawn open physiognomy by impacting on larger trees (Bond & Loffell, 2001; Guldemon & van Aarde 2008; Asner et al., 2009). If fewer seedlings are surviving on grazing lawns, as our results show, then the presence of kudu and giraffe, even at similar densities on and off grazing lawns, combined with occasional offtake by elephant, would be expected to drive an overall greater impact on trees that do get through the seedling and sapling phase in short- compared to tall-grass ecosystems. However, this remains to be tested.

4.3 Interactions between short-grass habitat and browsing on seedling and sapling performance

Seedling survival was lowest when grass was short and herbivores present (Fig. 3). This finding supports our hypothesis that browsers suppress seedlings on grazing lawns, despite the fact that high soil nutrient availability, a common feature of grazing lawns, confers grasses with a competitive advantage over seedlings (van der Waal et al., 2011; Porensky & Veblen, 2012). While improved predator detection appears to be responsible for encouraging

mesoherbivores onto grazing lawns, the shorter grass found in these areas might enhance seedling apparency to browsers, which could further contribute to overall seedling suppression. Furthermore, mixed feeders, such as impala in our study system and Grant's gazelle in East African glade habitats (Veblen, 2012), would very likely consume seedlings when feeding on the nutrient-rich, grass layer. Alternative explanations for low woody cover in short-grass habitats include soils that inhibit woody plant growth (Fensham, Butler, & Foley, 2015; Staver, Botha, & Hedin, 2017), poor seed dispersal into these areas (Goheen, Palmer, Keesing, Riginos, & Young, 2010) and/or alteration of the environment for germination and survival, for example, through herbivore trampling (Cumming & Cumming, 2003).

In Satara, we found no effect of browser removal on sapling growth, which contradicts our long-term HiP experiment results. We suggest that there was no enclosure effect on saplings because they were fenced for only one growing season, and that tree height is not a very good measure of tree biomass gain over such a short timescale. Furthermore, the two drought years which preceded the Satara study might have altered the grass-sapling interaction from competition to facilitation, with taller grass ameliorating saplings from harsh drought conditions. Thus, because the experimental duration was only one growing season, our study did not see the system fully return to pre-drought conditions.

Strongest support for the hypothesis that browsers drive grazing lawn openness came from our long-term (10-year) woody demographic study in HiP. Browser removal in tall-grass habitat had little impact on woody growth, which we attribute to low browsing pressure in tall-grass areas. However, as short grass area increased, differences in woody plant growth between the enclosure treatments increased considerably, suggesting that browsers limit the recruitment of saplings to the adult stage on grazing lawns but not in tall grass.

Grazing lawns rarely burn (Archibald et al., 2005). Similarly, heavily grazed short-grass sites in HiP did not burn during the study period because of insufficient grass fuel for fire. However, the matching short-grass sites that had herbivore exclusion did burn since the grass grew enough to create a fuel bed. Therefore, if fire confounded any aspect of our experiment, it was only to suppress woody plant growth in the enclosure treatments matched to short-grass

sites, thus making it more convincing that we found slower growth rates in response to browsing on short grass which did not burn.

We do acknowledge some fundamental differences between the two study areas. In HiP, exclosures were set up on existing grazing lawns (i.e. places where herbivores already concentrated), whereas the Satara exclosures were set up on fire-induced but herbivore-driven short-grass patches. Thus, it might be that short grass in HiP is not the cause of the higher browser pressure, but that they are both a consequence of some other factor that causes herbivores to concentrate, such as high soil nutrient availability (Augustine et al., 2003). That would explain the contradictory result, except that we do show that there was still a higher browser presence on the Satara grazing lawns, which is why we tend towards the explanation that grass height is indeed a key determinant of browsing pressure.

Thus, in HiP and other areas where there is chronic browsing and a dense woody layer (Riginos & Young, 2007; Staver et al., 2009; Seymour et al., 2016), grazing lawns serve as important habitats for browsers, with subsequent suppression of seedlings and saplings. However, this result is context-dependent. In a study by Morrison et al. (2018) in the Serengeti, where browsing mesoherbivores are less abundant, grass competition was overwhelmingly more important than reductions in browsing, and seedling recruitment was higher in short-grass areas. Porensky and Veblen (2012) report that grass competition and herbivory are similarly important in Kenyan glades.

4.4 Theoretical implications

Our results highlight some interesting gaps in the theoretical literature. For example, van Langevelde et al. (2003) did not consider interactions between grazers and browsers as a determinant of savanna woody structure and stability. We demonstrate that adding a browsing response to increased grazing can potentially alter the trajectory of woody biomass following heavy grazing (Fig. 6), overwhelming the existing positive impact of reduced grass competition on woody recruitment, with a negative response due to increased browsing pressure. This has further implications for the drought recruitment theory proposed in February et al. (2013), with

browsers potentially locating more saplings during dry periods when there is shorter grass over larger areas, and thus limiting the benefit of reduced grass competition on woody recruitment.

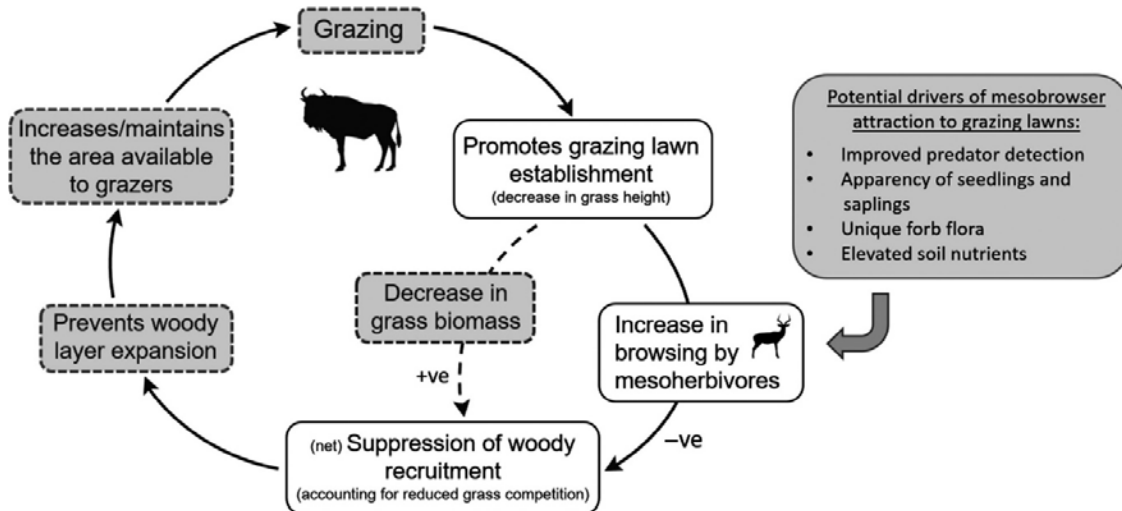


Fig. 6. A simple conceptual model demonstrating how the findings of this study feed into a broader understanding of the role browsers in maintaining grazing lawn openness. Clear boxes indicate findings from this study, while grey boxes indicate findings or suggestions from other studies. Grazing leads to the establishment of grazing lawns which attract browsing mesoherbivores that suppress woody recruitment and prevent subsequent expansion of the woody layer, thereby promoting further grazing by increasing or maintaining the area available to grazers. The alternative pathway (dashed lines) – which results in increased woody cover – would become dominant in situations without browsers.

Moreover, Archibald and Hempson (2016) highlight that feedbacks between fire and browsing are likely to depend on the preference of browsers to short- vs tall-grass areas. Large fires that disperse grazers reduce the likelihood of grazing lawn establishment (Archibald, 2008). Thus, data presented here suggest that for browsing mesoherbivores at least, large frequent fires could have a negative impact by reducing the availability of preferred short-grass habitat.

4.5 Management implications

Woody thickening is a global phenomenon in savanna grasslands, which impacts negatively on biodiversity and ecosystem service provisioning (Eldridge et al., 2011; O'Connor et al., 2014). In South Africa, Stevens et al. (2016) demonstrate that only in savannas with a full complement of wild herbivores, including elephants, has woody encroachment not taken place over a 70-year period. Our results build upon these findings by showing that for wildlife systems, where large predators create a landscape of fear, grazing lawn openness might be maintained by browsing mesoherbivores, including mixed-feeders, possibly enabling short-grass systems to maintain their highly productive grassland state by keeping trees out and enabling accessibility for grazers (Hempson et al., 2015).

The paradox of heavy grazing leading to woody thickening in cattle rangelands (Skarpe, 1990; Tobler et al., 2003; van Auken, 2009), but thinning of the woody layer on grazing lawns created by native African fauna seems to be due to the browser guild. Overgrazing leading to woody thickening is typical of cattle rangelands which lack a browser (Baumgartner, Treydte, Grant, & van Rooyen, 2015). One possibility is, that by mixing cattle with goats, which are often thought of as being functionally analogous to impala (Hoppe, Qvortrup, & Woodford, 1977), livestock farmers could suppress woody recruitment on grazing lawns created by cattle before trees escape the browse trap and become well established.

5 Conclusion

Our study provides an explanation for the apparent woody recruitment paradox between wildlife and livestock systems, by demonstrating that grass swards cropped short by herbivores in wildlife areas offer favourable habitats for some browser species. It also indicates that woody suppression is occurring at the early demographic stages and that this process is driven predominantly by mesoherbivores (Goheen, Keesing, Allan, Ogada, & Ostfeld, 2004; Riginos & Young, 2007; Maclean, Goheen, Doak, Palmer, & Young, 2011). We find that this effect on woody plants is due to higher browser presence on grazing lawns. This could be the consequence of a number of factors, including improved predator detection in short grass,

greater apparency of seedlings and saplings to browsers, the attraction of a unique forb flora and elevated soil nutrients on grazing lawns.

While our findings are consistent with predator avoidance behaviour as a key factor driving mesoherbivores to utilise grazing lawns, we recommend that future studies test this hypothesis more explicitly by acquiring a direct measure of predation risk, for example using a viewshed approach (Davies, Tambling, Kerley, & Asner, 2016), to investigate the probability of a woody plant being browsed in a short- versus tall-grass landscape. Furthermore, combined tree removal and mowing experiments would be a valuable addition to ascertain whether it is grass height alone or alternatively, habitats characterised only in part by grass height, that encourage browsing. Other elaborations on our study should include additional soil types, along a gradient of rainfall to help ascertain whether browsers and mixed-feeders remain important agents of woody suppression on grazing lawns across a range of environmental conditions.

Acknowledgements

Thank you to SANParks and Ezemvelo KZN Wildlife for their generous support throughout the study. In particular, we thank Mathew Harris (University of Pretoria), Happy Mangena (Kruger National Park), Phumlani Zwane, Sue Janse van Rensburg, An van Cauter, Julia Wakeling, Matt Waldram, Krissie Clarke, Zanele Chonco, Mendi Shelembe, Siphso Zulu, Eric Khumalo, Vincent Mkhwanazi, and Dumisani Mnomezulu (Hluhluwe-iMfolozi Park) for logistical fieldwork support. This research was funded by the USAID/NAS program “Partnerships for Enhanced Engagement in Research” (sub-grant 2000004946, Cycle 3), and the South African National Research Foundation (grant 112071). M.D.V. was funded by the South African National Research Foundation, Department of Science and Technology, Innovation and Priority Research Masters Scholarship.

Author's contributions

S.A., M.G., M.V., and A.C.S. conceived the project idea with all authors helping to design the methodology and collected the data. M.V., S.A., and M.G. analysed the data; M.V. led the

writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.76hdr7st3> (Voysey et al. 2020).

References

- Anderson, T. M., Kumordzi, B. B., Fokkema, W., Fox, H. V., & Olf, H. (2013). Distinct physiological responses underlie defoliation tolerance in African lawn and bunch grasses. *International Journal of Plant Sciences*, 174, 769-778. <https://www.jstor.org/stable/10.1086/670237>
- Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. (2005). Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96-109. <https://doi.org/10.1890/03-5210>
- Archibald, S. (2008). African grazing lawns - how fire, rainfall, and grazer numbers interact to affect grass community states. *Journal of Wildlife Management*, 72, 492-501. <https://doi.org/10.2193/2007-045>
- Archibald, S., & Hempson, G. P. (2016). Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 371, 20150309. <http://dx.doi.org/10.1098/rstb.2015.0309>
- Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., Jacobson, J., ... Martin, R. E. (2009). Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 4947-4952. <https://doi.org/10.1073/pnas.0810637106>
- Augustine, D. J. (2003). Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology*, 40, 137-149. <https://doi.org/10.1046/j.1365-2664.2003.00778.x>

- Augustine, D. J. (2004). Influence of cattle management on habitat selection by impala on central Kenyan rangeland. *Journal of Wildlife Management*, 68, 916-923.
- Augustine, D. J., McNaughton, S. J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41, 45-58.
<https://doi.org/10.1111/j.1365-2664.2004.00864.x>
- Augustine, D. J., McNaughton, S. J., & Frank, D. A. (2003). Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications*, 13, 1325-1337. <https://doi.org/10.1890/02-5283>
- Bakker, E. S., & Svenning, J-C. (2018). Trophic rewilding: impact on ecosystems under global change. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 373, 20170432. <http://dx.doi.org/10.1098/rstb.2017.0432>
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1-48.
<https://doi.org/10.18637/jss.v067.i01>
- Baumgartner, S. A., Treydte, A. C., Grant, C. C., & van Rooyen, J. (2015). Can diverse herbivore communities increase landscape heterogeneity? Comparing wild and domestic herbivore assemblages in a South African savanna. *Perspectives in Plant Ecology, Evolution and Systematics*, 17, 34-43.
<https://doi.org/10.1016/j.ppees.2014.11.002>
- Ben-Shahar, R. (1993). Patterns of elephant damage to vegetation in Northern Botswana. *Biological Conservation*, 65, 249-256. [https://doi.org/10.1016/0006-3207\(93\)90057-8](https://doi.org/10.1016/0006-3207(93)90057-8)
- Birkett, A. (2002). The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology*, 40, 276-282.
<https://doi.org/10.1046/j.1365-2028.2002.00373.x>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J-S. S. (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127-135.
<https://doi.org/10.1016/j.tree.2008.10.008>

- Bonat, W. H., Jørgensen, B., Kokonendji, C. C., Hinde, J., & Demetrio, C. G. B. (2018). Extended Poisson-Tweedie: Properties and regression models for count data. *Statistical Modelling*, 18, 24-49. <https://doi.org/10.1177/1471082X17715718>
- Bond, W. J., & Loffell, D. (2001). Introduction of Giraffe changes Acacia distribution in a South African savanna. *African Journal of Ecology*, 39, 286-294. <https://doi.org/10.1046/j.1365-2028.2001.00319.x>
- Bond, W. J., Smythe, K. A., & Balfour, D. A. (2001). Acacia species turnover in space and time in an African savanna. *Journal of Biogeography*, 28, 117-128. <https://doi.org/10.1046/j.1365-2699.2001.00506.x>
- Bond, W. J., Staver, A. C., Cramer, M. D., Wakeling, J. L., Midgley, G. F., & Balfour, D. A. (2017). Demographic Bottlenecks and Savanna Tree Abundance. In J. P. G. M. Cromsigt, S. Archibald, & N. Owen-Smith (Eds.), *Conserving Africa's Mega-diversity in the Anthropocene* (pp. 161-188). Cambridge: Cambridge University Press. <https://doi.org/10.1017/9781139382793>
- Bond, W. J. (2019). Vertebrate herbivory and open ecosystems. In W. J. Bond (Eds.), *Open ecosystems: ecology and evolution beyond the forest edge* (pp. 121-139). Oxford: Oxford University Press.
- Bransby, D. I., & Tainton, N. M. (1977). The Disc Pasture meter: possible applications in grazing management. *Proceedings of the Grassland Society of Southern Africa*, 12, 115-118. <https://doi.org/10.1080/00725560.1977.9648818>
- Burkepile, D. E., Burns, C. E., Tambling, C. J., Amendola, E., Buis, G., Govender, N., ... Smith, M. (2013). Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. *Ecosphere*, 4, 1-19. <https://doi.org/10.1890/ES13-00078.1>
- Case, M. F., Staver, A. C. (2016). Fire prevents woody encroachment only at higher-than-historical frequencies in a South African savanna. *Journal of Applied Ecology*, 1-26. <http://doi.org/10.1111/1365-2664.12805>

- Coetsee, C., Stock, W. D., & Craine, J. M. (2011). Do grazers alter nitrogen dynamics on grazing lawns in a South African savannah? *African Journal of Ecology*, 49, 62-69. <https://doi.org/10.1111/j.1365-2028.2010.01236.x>
- Cromsigt, J. P. G. M., Archibald, S., & Owen-Smith, N. (2017). *Conserving Africa's Mega-Diversity in the Anthropocene*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/9781139382793>
- Cumming, D. H. M., & Cumming, G. S. (2003). Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia*, 134, 560-568. <https://doi.org/10.1007/s00442-002-1149-4>
- Davies, A. B., Tambling, C. J., Kerley, G. I. H., & Asner, G. P. (2016). Effects of vegetation structure on the location of lion kill sites in African thicket. *PLoS ONE*, 11: e0149098. <https://doi.org/10.1371/journal.pone.0149098>
- Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., & Parr, C. L. (2017). Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*, 00:1-11. <https://doi.org/10.1111/1365-2664.12956>
- du Toit, J. T., Rogers, K. H., & Biggs, H. C. (2003). *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Washington, DC: Island Press
- Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F., & Whitford, W. G. (2011). Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecological Letters*, 14, 709-722. <https://doi.org/10.1111/j.1461-0248.2011.01630.x>
- February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94, 1155-1164. <https://doi.org/10.1890/12-0540.1>
- Fensham, R. J., Butler, D. W., & Foley, J. (2015). How does clay constrain woody biomass in drylands? *Global Ecology and Biogeography*, 24, 950-958. <https://doi.org/10.1111/geb.12319>

- Gignoux, J., Lahoreau, G., Julliard, R., & Barot, S. (2009). Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology*, 97, 484–495. <https://doi.org/10.1111/j.1365-2745.2009.01493.x>
- Goheen, J. R., Keesing, F., Allan, B. F., Ogada, D., & Ostfeld, R. S. (2004). Net effects of large mammals on Acacia seedling survival in an African savanna. *Ecology*, 85, 1555-1561. <https://doi.org/10.1890/03-3060>
- Goheen, J. R., Palmer, T. M., Keesing, F., Riginos, C., & Young, T. P. (2010). Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology*, 79, 372-382. <https://doi.org/10.1111/j.1365-2656.2009.01644.x>
- Guldmond, R., & van Aarde, R. (2008). A meta-analysis of the impact of African elephants on savanna vegetation. *Journal of Wildlife Management*, 72, 892-899. <https://doi.org/10.2193/2007-072>
- Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., ... Vickers, K. J. (2015). Ecology of grazing lawns in Africa. *Biological Reviews*, 90, 979-994. <https://doi.org/10.1111/brv.12145>
- Higgins, S. I., Bond, W. J., & Trollope, W. S. W. (2000). Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology*, 88, 213-229. <https://doi.org/10.1046/j.1365-2745.2000.00435.x>
- Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Beukes, E., ... Trollope, W. S. W. (2007). Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, 88, 1119-1125. <https://doi.org/10.1890/06-1664>
- Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications*, 19, 95-109. <https://doi.org/10.1890/07-1954.1>
- Hoppe, P. P., Qvortrup, S. A., & Woodford, M. H. (1977). Rumen fermentation and food selection in East-African sheep, goats, Thomson's gazelle, Grant's gazelle and impala.

- Journal of Agricultural Science*, 89, 129-135. <https://doi.org/10.1017/S0021859600027283>.
- Howison, R., Olf, H., Owen-Smith, N., Cromsigt, J. P. G. M., & Archibald, S. (2017). The Abiotic Template for the Hluhluwe-iMfolozi Park's Landscape Heterogeneity. In J. P. G. M. Cromsigt, S. Archibald, & N. Owen-Smith (Eds.), *Conserving Africa's Mega-Diversity in the Anthropocene* (pp. 33-55). Cambridge: Cambridge University Press. <https://doi.org/10.1017/9781139382793>
- Kraaij, T., & Ward, D. (2006). Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, 186, 235-246. <https://doi.org/10.1007/s11258-006-9125-4>
- Maclean, J. E., Goheen, J. R., Doak, D. F., Palmer, T. M., & Young, T. P. (2011). Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. *Ecology*, 92, 1626-1636. <https://doi-org.uplib.idm.oclc.org/10.1890/10-2097.1>
- Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A., & Peace, A. J. (2001). Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology*, 38, 349-363. <https://doi.org/10.1046/j.1365-2664.2001.00584.x>
- Mayengo, G., Armbruster, W., & Treydte, A. C. (2020). Quantifying nutrient re-distribution from nutrient hotspots using camera traps, indirect observation and stable isotopes in a miombo ecosystem, Tanzania. *Global Ecology and Conservation*, 23, e01073. <https://doi.org/10.1016/j.gecco.2020.e01073>
- McNaughton, S. J. (1983). Compensatory plant-growth as a response to herbivory. *Oikos*, 40, 329-336. <https://doi.org/10.2307/3544305>
- McNaughton, S. J. (1984). Grazing lawns - animals in herds, plant form, and coevolution. *American Naturalist*, 124, 863-886. <http://www.jstor.org/stable/2461305>
- Midgley, J. J., & Bond, W. J. 2001. A synthesis of the demography of African acacias. *Journal of Tropical Ecology*, 17, 871-886. <https://doi.org/10.1017/S026646740100164X>

- Moe, S. R., Rutina, L. P., Hytteborn, H., & du Toit, J. T. (2009). What controls woodland regeneration after elephants have killed the big trees? *Journal of Applied Ecology*, 46, 223-230.
- Morrison, T. A., Holdo, R. M., Rugemalila, D. M., Nzunda, M., & Anderson, M. T. (2018). Grass competition overwhelms the effects of herbivores and precipitation on early tree establishment in Serengeti. *Journal of Ecology*. 107:216–228. <https://doi.org/10.1111/1365-2745.13010>
- O'Connor, T. G., Puttick, J. R., & Hoffman, M. T. (2014). Bush encroachment in southern Africa: changes and causes. *African Journal of Range & Forage Science*, 31, 67-88. <https://doi.org/10.2989/10220119.2014.939996>
- O'Kane, C. A. J., Duffy, K. J., Page, B. R., & Macdonald, D. W. (2012). Heavy impact on seedlings by the impala suggests a central role in woodland dynamics. *Journal of Tropical Ecology*, 28, 291-297. <http://www.jstor.org/stable/41510850>
- Owen-Smith, N., & Cooper, S. M. (1989). Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. *Journal of Zoology (London)*, 219, 29-43. <https://doi.org/10.1111/j.1469-7998.1989.tb02563.x>
- Porensky, L. M., & Veblen, K. E. (2012). Grasses and large herbivores reinforce landscape heterogeneity by excluding trees from ecosystem hotspots. *Oecologia*, 168, 749-759. <https://doi.org/10.1007/s00442-011-2123-9>
- Prins, H. H. T., & Vanderjeugd, H. P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*, 81, 305-314. <https://doi.org/10.2307/2261500>
- R Core Team. (2018). R: A language and environment for statistical computing, version 3.5.0, computer program, R Foundation for Statistical Computing, Vienna, Austria.
- Riginos, C., & Young, T. P. (2007). Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia*, 153, 985-995. <https://doi.org/10.1007/s00442-007-0799-7>

- Riginos, C., & Grace, J. B. (2008). Savanna tree density, herbivores and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, 89, 2228-2238. <https://doi.org/10.1890/07-1250.1>
- Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84(1), 124–133. <https://doi.org/10.1111/1365-2656.12262>
- Roques, K. G., O'Connor, T. G., & Watkinson, T. G. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38, 268-280. <https://doi.org/10.1046/j.1365-2664.2001.00567.x>
- Sankaran, M., Augustine, D. J., & Ratnam, J. (2013). Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology*, 101, 1389-1399. <https://doi.org/10.1111/1365-2745.12147>
- Seymour, C. L., Joseph, G. S., Makumbe, M., Cumming, G. S., Mahlangu, S., & Cumming, D. H. M. (2016). Woody species composition in an African savanna: determined by centuries of termite activity but modulated by 50 years of ungulate herbivory. *Journal of Vegetation Science*, 27, 824-833. <https://doi.org/10.1111/jvs.12393>
- Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28, 517-544. <https://doi.org/10.1146/annurev.ecolsys.28.1.517>
- Sensenig, R. L., Demment, M. W., & Laca, E. A. (2010). Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology*, 91, 2898-2907. <https://doi.org/10.1890/09-1673.1>
- Sinclair, A. R. E., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature*, 425, 288-290. <https://doi.org/10.1038/nature01934>
- Skarpe, C. (1990). Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, 27, 873-885. <https://doi.org/10.2307/2404383>

- Skinner, J. D., & Smithers, R. H. N. (1990). *The Mammals of the Southern African Subregion* (2nd ed.). Pretoria: University of Pretoria.
- Smit, I. P. J., Asner, G. P., Govender, N., Kennedy-Bowdoin, T., Knapp, D. E., & Jacobson, J. (2010). Effects of fire on woody vegetation structure in African savanna. *Ecological Applications*, 20, 1865-1875. <https://doi.org/10.1890/09-0929.1>
- Staver, A. C., & Bond, W. J. (2014). Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology*, 102, 595-602. <https://doi.org/10.1111/1365-2745.12230>
- Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J., & Waldram, M. S. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19, 1909-1919. <https://doi.org/10.1890/08-1907.1>.
- Staver, A. C., Botha, J., & Hedin, L. (2017). Soils and fire jointly determine vegetation structure in an African savanna. *New Phytologist*, 216, 1151-1160. <https://doi.org/10.1111/nph.14738>
- Stevens, N., Erasmus, B. F. N., Archibald, S., & Bond, W. J. (2016). Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 371, 20150437, pii: 20150437. doi:10.1098/rstb.2015.0437
- Stock, W. D., Bond, W. J., & van de Vijver, C. A. D. M. (2010). Herbivore and nutrient control of lawn and bunch grass distributions in a southern African savanna. *Plant Ecology*, 206, 15-27. <https://doi.org/10.1007/s11258-009-9621-4>
- Svenning, J.-C., Pedersen, P. B. M., Donlan, C. J., Ejrnæs, R., Faurby, S., Galetti, M., ... Vera, F. W. M. (2016). Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 898-906. <https://doi.org/10.1073/pnas.1502556112>
- Tobler, M. W., Cochard, R., & Edwards, R. (2003). The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology*, 40, 430-444. <https://doi.org/10.1046/j.1365-2664.2003.00816.x>

- Underwood, R. (1982). Vigilance behaviour in grazing African antelopes. *Behaviour*, 79, 81-107.
- Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90, 23-30. <https://doi.org/10.1890/08-0606.1>
- van Auken, O. W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management*, 90, 2931-2942. <https://doi.org/10.1016/j.jenvman.2009.04.023>
- van der Waal, C., Kool, A., Meijer, S. S., Kohi, E., Heitkönig, I. M. A., de Boer, W. F., ... de Kroon, H. (2011). Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia*, 165, 1095-1107. <https://doi.org/10.1007/s00442-010-1899-3>
- van Langevelde, F., van de Vijver, C., Kumar, L., van de Koppel, J., de Ridder, N., van Andel, J., ... Rietkerk, M. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84, 337-350. [https://doi.org/10.1890/0012-9658\(2003\)084\[0337:EO FAHO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0337:EO FAHO]2.0.CO;2)
- Veblen, K. E. (2012). Savanna glade hotspots: plant community development and synergy with large herbivores. *Journal of Arid Environments*, 78, 119-127. <https://doi.org/10.1016/j.jaridenv.2011.10.016>
- Veldhuis, M. P., Howison, R. A., Fokkema, R. W., Tielens, E., & Olff, H. (2014). A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. *Journal of Ecology*, 102, 1506-1517. <https://doi.org/10.1111/1365-2745.12322>
- Venter, F. J., Scholes, R. J., & Eckhardt, H. C. (2003). The abiotic template and its associated vegetation pattern. In J. T. Du Toit, H. C. Biggs, & K. H. Rogers (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (pp. 83-129). Washington, DC: Island Press.

- Verweij, R. J., Verrelst, T. J., Loth, P. E., Heitkönig, I. M. A., & Brunsting, A. M. H. (2006). Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos*, 114, 108-116. <https://doi.org/10.1111/j.2006.0030-1299.14209.x>
- Voysey, M. D., Archibald, S., Bond, W., Donaldson, J. E., Staver, A. C., & Greve, M. (2020). Data from: The role of browsers in maintaining the openness of savanna grazing lawns, *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.76hdr7st3>
- Waldram, M. S., Bond, W. J., & Stock, W. D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems*, 11, 101-112. <https://doi.org/10.1007/s10021-007-9109-9>
- Walters, M., Midgley, J. J., & Somers, M. J. (2004). Effects of fire and fire intensity on the germination and establishment of *Acacia karroo*, *Acacia nilotica*, *Acacia luederitzii* and *Dichrostachys cinerea* in the field. *BMC Ecology*, 4, 3. <http://dx.doi.org/10.1186/1472-6785-4-3>
- Whateley, A., & Porter, R. N. (1983). The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex. *Bothalia*, 14, 745-758. <http://doi:10.4102/abc.v14i3/4.1236>
- Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, 37, 969-982. <https://doi.org/10.1111/ecog.00534>
- Young, T. P., Patridge, N., & Macrae, A. (1995). Long-term glades in *Acacia* bushland and their edge effects in Laikipia, Kenya. *Ecological Applications*, 5, 97-108. <https://doi.org/10.2307/1942055>