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Impact of bush encroachment management on plant response and animal distribution

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Abstract: The transformation of grassland by bush encroachment causes socioeconomic problems in arid and semi-arid regions. At the moment, de-bushing is the only way to control bush encroachment. In this context, we conducted two independent projects within SASSCAL. First, in a greenhouse experiment, we investigated the morphological plant response to damage of four different bush encroacher species in order to understand if intervention in the plants' early life stage may reasonably fight bush encroachment and if treated plants are used differently by livestock (e.g., sheep and goats). In a second project, we investigated the influence of bush clearing on the habitat utilisation of different large herbivores (e.g., greater kudu, warthog, and gemsbok). Specifically, we wanted to know if typical grazers (e.g., warthog and gemsbok) are found at open cleared sites and typical browsers (greater kudu) in encroached regions and if vegetation parameters (e.g., grass cover) drive this distribution. For our greenhouse experiment, we found that all seedlings reacted morphologically to the damage of top-shoots, but to different extents. Damaged plants show species-specific responses, like differences in branching and thorn sizes and survival rates. In contrast to sheep, goats were not absolutely deterred by mechanical defences of the offered plant species. Therefore, we assume that under controlled grazing regimes, goat feeding could be a useful tool to interfere with the establishment of large numbers of seedlings. In our second project, the animal distribution did not consistently match our expectations. While warthog and cattle shared open bush-cleared sites, we found gemsbok utilising non-cleared sites with high thornbush cover of medium height, which was similar to patterns shown by greater kudu. The results are discussed in light of competition, risk avoidance, and habitat heterogeneity.

Resumo: A transformação dos prados pela densificação de plantas lenhosas causa problemas socioeconómicos em regiões áridas e semi-áridas. De momento, a remoção de plantas lenhosas é a única maneira de controlar a sua densificação. Assim, conduzimos dois projectos independentes no contexto do SASSCAL. Numa experiência numa estufa, investigámos a resposta morfológica a danos de quatro espécies invasoras diferentes, de modo a compreender se a intervenção no estágio inicial de vida é razoável para combater a invasão das lenhosas, bem como se estas plantas tratadas são usadas de forma diferente pelo gado (ovelhas e cabras). Num segundo projecto, investigámos a influência do desmatamento na utilização do habitat por diferentes grandes herbívoros (cudu, javali-africano e órix). Especificamente, queríamos saber se típicos herbívoros de pasto (e.x.: javali-africano e órix) eram encontrados em locais abertos, e típicos *browsers* (cudu) em regiões invadidas, e se os parâmetros da vegetação (e.x.: cobertura de gramíneas) conduzem esta distribuição. Na nossa experiência na estufa, descobrimos que todas as plântulas reagiram morfológicamente, mas em extensões diferentes aos danos dos rebentos superiores. As plantas danificadas mostram respostas específicas à espécie, tais como diferenças na ramificação, tamanho dos espinhos e taxas de sobrevivência. Em contraste com as ovelhas, as cabras não foram de todo dissuadidas pelas defesas mecânicas das espécies de plantas oferecidas. Desta forma, assumimos que, sob regimes de pastagem controlados, a alimentação de cabras pode ser uma ferramenta útil para interferir no estabelecimento de grandes números de plântulas. No nosso segundo projecto, a distribuição animal não correspondeu invariavelmente às nossas expectativas. Enquanto que o javali-africano e o gado partilharam locais desmatados abertos, observámos o órix a utilizar locais não desmatados com uma elevada cobertura de plantas espinhosas de altura média, semelhante ao cudu. Os resultados são discutidos à luz da competição, prevenção de riscos e heterogeneidade do habitat.

Introduction

Savannas are important ecosystems, as they hold one-fifth of the world's human population and the most livestock and other large herbivores (Graz, 2008). Due to the enormous rangelands covered by savannas, these ecosystems are also of high economic value. Furthermore, they bear a high value of cultural services, not only for indigenous people but also for tourism. Here, people have the increasingly rare opportunity to watch the spectacular diversity of wild large herbivores. Nowadays, tourism contributes a significant share to the gross national product of southern Africa. However, at the moment, the world's savannas are undergoing rapid and radical human-induced transformation (Lehmann et al., 2009) caused by bush encroachment. Bush encroachment is described as the increase of biomass, cover, and abundance of woody plant species, accompanied by the suppression of perennial grasses and herbs (Ward, 2005; O'Connor et al., 2014). The reasons for the increasing numbers of tree species outcompeting grasses are multiple and complex, and are mainly ascribed to poor management of farmland, including overgrazing (Skarpe, 1990; Scholes & Archer, 1997; Lange et al., 1998), the suppression of fires (Scholes & Archer, 1997; Joubert et al., 2008), and the absence of browsers (e.g., Staver et al., 2009). Other drivers such as climate change and increased CO₂ levels have also been identified (e.g. Archer et al., 1995; Ward, 2005; Bond, 2008).

The consequence of this transformation is a reduced grazing capacity of herbivores including livestock, which might also lead to enhanced soil erosion and desertification (De Klerk, 2004; Stevens et al., 2017). Furthermore, due to the limitation of sight, the visibility of wild herbivores is reduced which might lead to negative consequences for tourism. Even though bush encroachment has some beneficial aspects (e.g., the accumulation of carbon in the standing biomass and the possibility of charcoal production), the transformation of grassland by bush encroachment causes socio-economic problems in arid and semi-arid regions to an extent that many previously profitable

areas are no longer economically viable (Smit, 2004).

At the moment de-bushing is the only way to control bush encroachment and to maintain the economically and ecologically valuable open savanna ecosystems. Therefore, farmers use a variety of methods to fight bush encroachment (de Wet, 2015). Because of the high costs of these interventions (for example, beef producers in Namibia spend about US \$54 million per year; De Klerk, 2004), there is a great agreement in the affected countries regarding the need to develop sustainable management options to suppress bush encroachment. In this context, we conducted two independent projects. The first project presented here deals with the impact of mechanical cutting of bush encroacher species seedlings. Reducing the density of bush encroacher species through intervention in the early life stage of the plants is a reasonable potential intervention. As cutting and/or grazing are appropriate management tools, we tested the plant response to damage of four different bush encroacher species (*Acacia mellifera*, *A.reficiens*, *A. tortilis*, and *Dichrostachys cinerea*). Specifically, we wanted to know if cutting top shoots leads to a morphological plant response and to subsequent consequences for livestock. In the second project, we investigated the impact of de-bushing activities on the distribution of large herbivores on a farm level. In this study, we wanted to explore whether the distribution of different large herbivores (browser and grazer) is related to the different management of sites (e.g., to the different degrees of bush-encroached areas). In the following, we present extended summaries of both projects.

Understanding the influence of damage on bush encroacher seedlings

Introduction

Why is it important? - Intense interventions, e.g. clearing by mechanical cutting, the use of bulldozers, and the use of herbicides are commonly employed to address the problem of bush encroachment once shrubs have reached a size large enough to use these methods. In contrast,

an intervention at an early life stage of the plants seems to be much more reasonable and cost effective. Joubert et al. (2014) developed a management expert system for arid and semi-arid savanna ecosystems in order to manage this problem. The proposed management interventions in these systems include pulling out seedlings and saplings, mowing, grazing and browsing, and the use of fire in the early stages of seedling development. In order to expand on these proposed interventions, we wanted to understand how early-stage seedlings of different bush encroacher species react to damage, e.g. by browsing or cutting.

Plants show multiple reactions to damage, and these reactions are specific to the damaged plant species. That is to say, not every plant might react with a defence strategy such as increasing thorniness (mechanical defence) or increasing plant defence (e.g. tannins; chemical strategy). There are examples where plants react with compensation to tissue loss, which leads to even higher attractiveness for herbivores (e.g. willows are known to react like this, Stolter, 2008). Regardless of the type of reaction to damage, it will have an impact on the subsequent herbivory.

In our study, we tested:

- if different bush encroacher species react differently to damage of the top shoot. Here, we focused on morphological plant response; e.g., the development of larger thorns or multiple branching;
- if different bush encroacher species show differences in mortality rate after cutting to the ground;
- if plant response results in a reduction of utilisation for subsequently feeding livestock (e.g., goats and sheep).

Methods

In a greenhouse experiment (Fig. 1), four different plant species involved in bush encroachment (*Acacia mellifera* [*Senegalia mellifera*, blackthorn, swarthaak], *A. tortilis* [*Vachellia tortilis*, umbrella thorn acacia], *A. reficiens* [*Vachellia reficiens*, red bark acacia, rooihak], and *Dichrostachys cinerea* [sicklebush]) were tested for their response to damage by cutting the upper top shoots of



Figure 1: Greenhouse experiment with different bush encroacher seedlings.

three-month-old seedlings. Three months after manipulation, we determined the morphological changes in the plants (e.g., the size of thorns). In the next step, we fed the plants, now about six months old, to female Cameroon blackbelly sheep and female boer goats in order to test for consequences on subsequent consumers. In this phase, we monitored 4-5 animals in 4-7 feeding trials (depending on availability of the plants) with red bark acacia, sicklebush, and blackthorn, using 14 plants in each trial in a random design. And in the last step, we cut all seedlings consistently to ground level immediately after the feeding trials and investigated the survival/mortality rate in the follow-

ing months. The latter was done to understand the influence of ground cutting (e.g., mowing) on seedlings.

Results

All investigated species reacted with changes in morphology to the damage of the top shoots, e.g., by building larger thorns (mean values for 40 sicklebush specimens: 9.74 mm for treated plants; 3.95 mm for control plants). We found that damage to the top shoot of acacia species led to an increase in branching and the loss of a leader shoot; this was most evident for blackthorn (mean: 4.52 side branches per treated plant vs. 2.60 side branches per control plant, Fig. 2). In particular, red bark acacia and umbrella thorn acacia more often grew a substitute top shoot and continued to grow normally (mean of 20 red bark acacia: 2.73 side branches per treated plant). Sicklebush started to build adventive (additional) ground shoots after cutting the top shoot (2 of 20 specimens), which can be seen as a sort of asexual reproduction (Fig. 3).

Additionally, we tested the survival rate after cutting. Severe cuttings, in which the seedlings (*A. mellifera*, *A. reficiens*, and *D. cinerea*) were cut down to ground level, resulted in the highest survival rates for *A. reficiens* (red bark acacia, roihak; over 90% of the seedling showed a vigorous resprout), while *A. mellifera* (blackthorn) survived with 50%

and less than 8% of the *D. cinerea* (sicklebush) seedlings survived the severe ground cutting.

From the results of the damage experiment, we expected differences in palatability between damaged plants and control plants. Interestingly, goat browsing was unaffected by either thorn size or number, nor was it affected by differences in chemical composition (for changes in plant chemistry, see Stolter et al., 2018 in this volume). Interestingly, sicklebush was favoured over the other encroacher species (mean biomass eaten: 42% of red bark acacia and 32% of blackthorn) by goats, despite its enormous (but softer) spines, and was eaten almost down to the ground (mean biomass eaten: 90%). In contrast, sheep totally refused to feed on any of the species offered, no matter if it was a treated plant or a control plant. (More detailed results will be published by Stolter & Joubert elsewhere).

Synthesis and outlook

All the tested encroacher species reacted to top shoot damage. In particular, blackthorn reacted to the loss of the top shoot with increased, enhanced branching (e.g., more side branches, no substitute leader shoot). Browsing and other damage to blackthorn seedlings would likely result in exacerbating the problem of bush encroachment by promoting an increasingly multi-stemmed individual which is more difficult to control at a



Figure 2: Plant response three months after top shoot damage: (a) blackthorn seedling showing multiple branching after cutting the top shoot; (b) totally undisturbed control plant (blackthorn) with one leader shoot (top shoot).



Figure 3: Sicklebush developed additional ground shoots after cutting the top shoot.

later stage. Bearing in mind that the survival rate of blackthorn was about 50% after ground-cutting, the results imply that any intervention would have to start at a much earlier stage after germination, e.g., when seedlings are only a few centimetres high. Browsing by many different ground-feeding herbivores (e.g. goats, oryx, and hares) might be effective to reduce plant recruitment. Hares have been shown to have a significant impact on blackthorn seedling survival (Joubert et al., 2011). Blackthorn leaves are very nutritious, with the highest protein content of all four species (Stolter et al., 2018, in this volume), and the species is thus potentially beneficial for game and livestock. However, the small but very hard and hooked thorns are an effective defence against browsing in later growing stages, which might lead to a lower acceptance of this species (e.g., by Cameroon blackbelly sheep in our experiment, Fig. 4), especially when plants are of a certain height and multi-stemmed. In contrast to blackthorn, the development of multiple branched individuals was less pronounced in red bark acacia (*A. reficiens*), but the survival rate of this species was very high. Therefore, we assume that ground cutting or grazing of this species might only be effective in combination with pulling out seedlings for control. Sicklebush showed also less branching in comparison with blackthorn, but reacted with the development of large, but softer thorns on the side branches. When only cut at the first centimetres of the top shoot, plants sometimes developed adventive shoots. This might lead to an increasing number of plants after damage occurs. In contrast to the other investigated plant species, sicklebush might only have a low survival rate when cut or fed down to the ground level.

The post-damage changes, especially in morphology, might lead to differences in attractiveness between damaged and undamaged plants for subsequent herbivores. Furthermore, different herbivores might react differently to morphological defences such as thorns, as our results from the feeding trial show. In our test, the sheep breed (Cameroon blackbelly, Fig. 4) did not feed on any of the offered plants; this might disqualify them for any manage-



Figure 4: (a) Cameroon blackbelly sheep and, (b) boer goats (in the experimental setup). Bush encroacher seedlings were offered to several animals for several days. Sheep refused to feed on the seedlings.

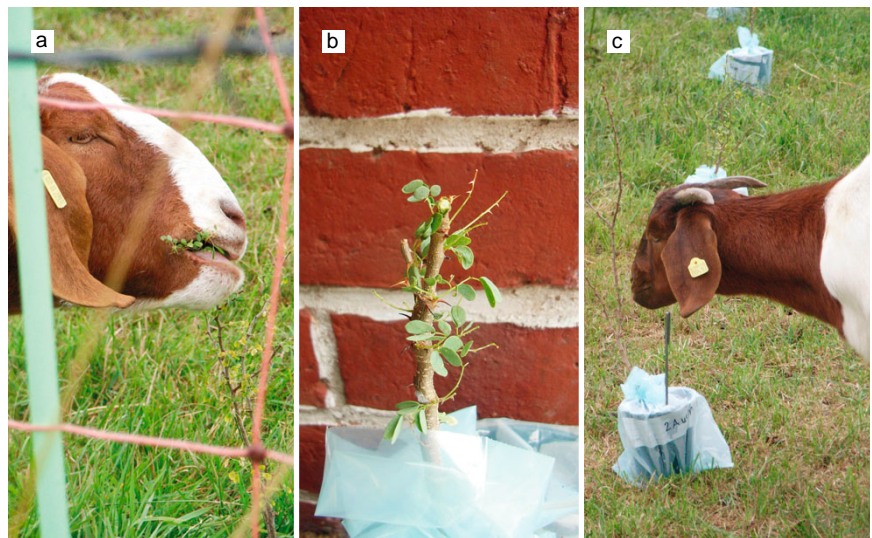


Figure 5: (a) Boer goat feeding on blackthorn, (b) stem feeding on blackthorn and, (c) leaf stripping on red bark acacia by goats.






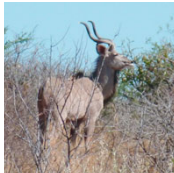

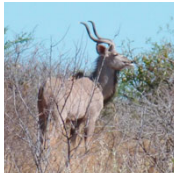
ment purposes in this respect. However, we have to admit that the diet of neither sheep nor goats was restricted; therefore, food choice in a harsh environment, with fewer feeding opportunities, might lead to the acceptance of these plants by Cameroon blackbelly. In contrast, the chosen boer goats were not concerned about lower plant nutritional quality or enhanced morphological plant defence (such as thorns) and fed on all bush encroacher seedlings (Fig. 4, 5). Interestingly, there was a strong preference for sicklebush, resulting in an almost total loss of the above-ground plant material. In combination with the low survival rate of sicklebush, goats (under controlled conditions) might be a 'natural option' to effectively decrease sicklebush seedling populations.

Impacts of bush encroachment management on large herbivore distribution

Introduction

Why is it important? - Different management strategies have been developed to deal with bush-encroached areas (e.g., Joubert et al., 2014). In particular, the removal of woody plants, so-called bush clearing, combined with reseeding with perennial grasses is a frequently used, cost-effective strategy (Smit, 2004). At the same time, the removal of large amounts of bushes and shrubs in the savanna ecosystem might influence ecosystem processes and function with impacts on factors ranging from soils to large herbivore communities (e.g., Buyer & Maul,

Table 1. Summary of the results of habitat utilization in relation to different management types on a farm in Namibia. HC = Height classes: small: <51cm (HC1), medium: 51-180cm (HC2), tall: >180cm (HC3).

	Site			
	A	B	C	D
Intervention type	None	Bulldozer cleared in 2010	Stump-burned in 2010	None
Regeneration management etc.		Buffalo grass (<i>Cenchrus ciliaris</i>) seeded, grazed by cattle in 2013	Dead wood not removed, grass mixture was seeded	
Results: vegetation characteristics	Lowest grass cover, highest thornbush cover (all height classes).	Highest grass cover, lowest occurrence of height class HC2 and 3.	Lowest thornbush cover, low occurrence of HC2	High occurrence of HC2 but low occurrence of HC3
Habitat utilisation	 	 	 	 

2016). Therefore, it is vital to understand these influences of bush clearing in order to develop sustainable management strategies likely to result in the maintenance of savannas' capacity to deliver ecosystem services and functions in the long term. In this context, the influence of bush clearing on the habitat utilisation of different large herbivores is both evident and important.

Large herbivores are of high importance not only for ecosystem processes but also for humans, e.g., as a food resource (livestock, game, and bush meat) and as flagships for tourism and nature conservation. The re-transformation of encroached sites will enhance carrying capacity for livestock and free-ranging grazers, but it will also result in a better visibility for large wild herbivores, which is important for tourism and countability for management purposes (for example, for conservation issues). On the other hand, bushes and dense vegetation offer food resources for browsers and the possibility for shelter (see also Joubert et al., 2018 in this volume)

In this regard, we wanted to know which vegetation factor (e.g., thornbush

number, thornbush cover, tree heights, grass cover) determines the habitat utilisation (measured via faecal pellet counts) of two typical grazers (warthog, gemsbok) and one browser (greater kudu). Several studies have dealt with the distribution of grazers and browsers (e.g. Rodgers, 1984; Knight, 1991; Dekker et al., 1996; Valeix et al., 2011). Due to their results, we expected that typical grazers would prefer the open bush-cleared areas, while typical browsers should prefer non-cleared sites. For example, we wanted to know, if a typical grazer is always found in an open area and if grass cover is the “driver” for this.

Methods

On a private cattle farm, we chose four sites differing in bush encroachment management (for details, see Schwarz et al., 2017). Grass cover, thornbush cover, and the abundance of different thornbush species (e.g., *Acacia mellifera* [blackthorn], *Dichrostachys cinera* [sicklebush]) was determined, and those species were additionally grouped into height classes (HC) (small: < 51 cm [HC1]; medium: 51-180 cm [HC2]; tall: > 180 cm [HC3]).

The habitat use of greater kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), and common warthog (*Phacochoerus africanus*) were determined using faecal pellet counts (see also Joubert et al., 2018 for this method). Two sites were not subjected to bush clearing (see Tab. 1, sites A, D). One site was cleared by stump burning and reseeded with a grass mixture (site C); the other site was cleared by bulldozers and reseeded with blue buffalo grass (buffel grass, *Cenchrus ciliaris*, site B). The impact of bush encroachment management was clearly mirrored by differences in vegetation structure and composition determined by a vegetation survey (Schwarz et al., 2017). Sites A and D (no intervention) had the highest thornbush cover (A: 15.5%, D: 13.5%) but differed in number of small bushes (A mean number: 26, mean height: 24.3 cm; D mean number: 10, mean height 65.8 cm). Sites B and C had similar low thornbush cover and number (mean cover B: 5.83%; C: 4.33%; mean number for both sites: 9), but differed in mean thornbush height (B: 86.44 cm, C: 35.30 cm) and grass cover was highest on site B (33.75%). The influence of different vegetation parameters

(e.g., thornbush and grass cover, height classes of bushes, thornbush number) on herbivore habitat utilisation was calculated using generalised linear models (detailed results are presented in Schwarz et al., 2017).

Results

In line with our expectations, the results of our model show a strong relationship between greater kudu and the occurrence of thorn bushes of medium size, which were mainly found at site D (highest mean faecal pellet counts for greater kudu: 1.8 at site D), but greater kudu were also found on the site with the lowest thornbush cover (see Tab. 1, sites C, D) but virtually absent at site A. We found warthog using the same site as cattle, which was an open site with only a few trees, reseeded with blue buffalo grass after bush clearing (see Tab. 1, site B, highest mean faecal pellet counts: 13.7) and our models revealed the impact of grass cover and high trees (HC 3) on warthog distribution. But against expectation, gemsbok did not share this open, bush-cleared site. Instead, gemsbok preferred a non-cleared site relatively high in thornbush cover of medium height (Tab. 1, site A). Faecal pellet counts were highest at sites A and C (mean A: 5.5; C: 3.3) and lowest at B and D (B: 0.4 ; D: 0.8). Accordingly, we gained the best models by including thornbushes of height class 2 in our models for gemsbok habitat utilisation. More detailed results are found in Schwarz et al. (2017).

Synthesis and Outlook

Every manipulation of ecosystems results in changes of the habitat with effects on vegetation composition and subsequent consequences for habitat use and movements of animals (e.g., Cogger & Cogger, 2003; Archibald et al., 2005; Haussmann et al., 2016). Changes in the natural herbivore composition are ascribed as one driver of the development of bush encroachment (e.g., Staver et al., 2009). Therefore, it is necessary to understand the habitat utilisation of wild free-ranging herbivores and the interaction between species. Our study (Schwarz et al., 2017) is a case study. Therefore, it might be interesting to investigate some

of our assumptions further in the future. The site most preferred by greater kudu was covered with bushes of medium height, which is the most favourable browsing height for this species (Dutoit, 1990; de Garine-Wichatitsky et al., 2004). If we assume a high greater kudu population density, bushes might be kept at this height, especially if plant response to browsing promotes further rebrowsing e.g., by enhanced plant quality (Stolter, 2008) or plants react to browsing by building more branches, resulting in many multiple-stemmed plants with large thorns as described in the project above, upon which only specialised herbivores will feed. Therefore, the feeding behaviour of herbivores and the responses of plants are important for future research in order to understand and manage bush-encroached sites.

We found the most warthog faecal pellets on a site reseeded with blue buffalo grass, which might not be an optimal feed for warthog, as it is a tall grass species. However, plants react to feeding damage, and some species are known to facilitate a higher quality for subsequent consumers resulting in a positive feedback loop (McNaughton et al., 1983; Stolter, 2008). We assume that due to their feeding activity, cattle might create grazing lawns, resulting in an optimal feeding height and possibly higher food quality for ground-feeding herbivores like warthog (Arsenault & Owen-Smith, 2002; Treydte et al., 2006).

In contrast, gemsbok did not utilise this reseeded bush-cleared area. We assume that either competition (e.g., between gemsbok and cattle, warthog) and/or risk avoidance (e.g., due to hunting pressure, Benhaïem et al., 2008) might lead to the utilisation of another site by gemsbok, as gemsbok are frequently hunted on the farm and the non-cleared site was mainly used by gemsbok calves (Schwarz et al., 2017). Supposing that hunting was the reason for the distribution of gemsbok, bush clearing in connection with hunting might foil the aim of gaining better visibility of the animals for tourists or management purposes (e.g., counting). Furthermore, the utilisation of the non-cleared area by gemsbok might offer different food plants without competing

with cattle or warthog. Due to adaptations to seasonal changes in vegetation, gemsbok are able to use dicotyledonous plants, e.g. *Leucosphaera bainesii*, during the dry season (e.g., Gagnon & Chew, 2000; Bothma et al., 2002; Schwarz, 2015, who determined food selection of gemsbok on this farm by investigating faecal pellets and rumen content). Therefore, the use of the non-cleared area might not only be beneficial in terms of risk avoidance but also from the nutritional perspective of the animal. We propose that habitat heterogeneity (bush-cleared sites next to sites with higher bush abundance) might be beneficial for the maintenance of a high diversity in habitat utilisation of large herbivores.

Conclusion

Our experiments on bush encroacher seedlings of the thornbush savanna demonstrate that early intervention in a seedling stage might be a useful tool to reduce bush encroachment. However, we found that different plant species reacted differently to damage of the top shoot and showed pronounced differences in survival rate. Thus, a species-specific management plan with species-specific timing of intervention is necessary to gain optimal results. This is important, as different savanna ecosystems are invaded by different bush encroacher species. Knowledge about plant species response is essential, as inappropriate procedures might exacerbate the problem of bush encroachment (e.g., creating multi-stem individuals, enhancing asexual reproduction). Ground-feeding herbivores with a wide dietary niche such as controlled goats and wild herbivores (e.g., hares, gemsbok, eland, stembok) seem to be beneficial for reducing plant recruitment in most cases. But also in this case, food choice is species-specific. Hence, we need more studies to understand plant response and diet selection of herbivores to be able to control undesirable vegetation changes in future.

We found clear effects of different bush-clearing methods on vegetation structure and composition, which was subsequently reflected in the habitat utilisation of wild herbivores. However,

some of our findings were unexpected and can only be explained by other factors (e.g., hunting or food competition). To maintain biodiversity and to ensure the coexistence of humans, cattle, and wildlife, it is essential to create a heterogeneous environment in which different requirements (e.g., for food, resting, shelter) can be satisfied. Still, we need more knowledge to understand the drivers of habitat utilisation for many wildlife species to enable optimal management in a changing world.

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