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Influence of differently managed bush-encroached sites on the large herbivore distribution in the Namibian Savannah

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Abstract

Bush encroachment is reported from savannah regions worldwide. Different management strategies are used to rehabilitate these areas. In this context, the mutual interaction between vegetation and large herbivore's distribution is evident. We studied effects of land management on vegetation structure in regard to encroaching species and the subsequent habitat use of two grazing (oryx, *Oryx gazella* L.; common warthog, *Phacochoerus africanus* GMELIN) and one browsing (greater kudu, *Tragelaphus strepsiceros* PALLAS) herbivore species. We assumed that (i) cleared areas will be favoured by grazers and (ii) noncleared areas will be favoured by browsers. Specifically, we asked: Which factors determine the habitat use of these different feeding guilds? Consistently with our expectations, we found that warthog favoured sites with high grass cover. For oryx, surprisingly shrubs with a height of 80–150 cm influenced their distribution positively, whereas for kudu, only the interaction of site and grass cover was significant in our models. However, this was related to the occurrence of shrubs of 80–150 cm height. We conclude that the management of encroachers, resulting in differences in vegetation, did not influence herbivore distribution as expected. Other factors like human impact and vegetation cover among others are discussed as additional drivers of habitat use.

Résumé

Nous rapportons l'envahissement des broussailles dans des régions de savane de par le monde. Différentes stratégies sont utilisées pour réhabiliter ces zones. Dans ce contexte, l'interaction entre la végétation et les grands herbivores est évidente. Nous avons étudié les effets de l'aménagement des terres sur la structure de la végétation, au point de vue des espèces envahissantes, et la fréquentation des habitats qui en découle par deux espèces qui mangent de l'herbe (l'oryx *Oryx gazella* L. et le phacochère *Phacochoerus africanus* GMELIN) et par une espèce qui broute en hauteur (le grand koudou *Tragelaphus strepsiceros* PALLAS). Nous supposions que (i) les zones dégagées seraient privilégiées par les premiers et que (ii) les zones non dégagées seraient choisies par le second. Nous nous sommes demandé : quels facteurs déterminent la fréquentation de l'habitat de ces différentes guildes alimentaires? Conformément à nos attentes, nous avons constaté que les phacochères privilégiaient les endroits où il y a une couverture de hautes herbes. Pour les oryx, étonnamment, les buissons d'une hauteur de 80–150 cm de haut influençaient positivement leur distribution, alors que pour les koudous, seule l'interaction du site avec la couverture herbeuse était significative dans nos modèles. Toutefois, ceci était lié à a présence de buissons de 80–150 cm de haut. Nous concluons que la gestion des broussailles envahissantes, qui aboutit à des différences de végétation, n'a pas influencé la distribution des herbivores comme nous l'attendions. D'autres éléments comme l'impact humain et la couverture végétale, entre autres, sont discutés comme facteurs supplémentaires de la fréquentation des habitats.

KEYWORDS
bush encroachment, distribution, grass cover, shrub cover, ungulates

1 | INTRODUCTION

A phenomenon that is reported from savannah regions worldwide is bush encroachment, that is the increase in biomass and abundance of woody plant species, accompanied by the suppression of perennial grasses and herbs (O'Connor, Puttick, & Hoffman, 2014; Ward, 2005). Bush encroachment is mainly ascribed to poor management of farmland (e.g., due to overgrazing, the suppression of fires and the absence of browsers; Lange, Barnes, & Motinga, 1997; De Klerk, 2004; Staver, Bond, Stock, Van Rensburg, & Waldram, 2009).

Different management strategies have been developed to deal with bush-encroached areas. They include, for example, the reduction in grazing intensity; and not shifting focus points of bush encroachment (e.g., boreholes, wells, kraals; Moleele, Ringrose, Matheson, & Vanderpost, 2002). Joubert et al. (2014) developed an expert system for arid rangeland management that includes several procedures to prevent bush encroachment, for example the monitoring of seed production. Also herbicides and fires are used for management (but see Haussmann, Kalwij, & Bezuidenhout, 2016; Angassa & Oba, 2009; Joubert, Smit, & Hoffman, 2012; Lohmann, Tietjen, Blaum, Joubert, & Jeltsch, 2014; Mudongo, Fynn, & Bonyongo, 2016). However, for practical and economic reasons the mechanical removal of woody plants is often used as management strategy for promoting natural grass growth or restoring bush-encroached savannahs by reseeding with perennial grasses (Smit, 2004). At the same time, the impact of removing vast numbers of shrubs and trees on the savannah ecosystem is not well understood and does influence different ecosystem components from soils (Buyer & Maul, 2016) to large herbivore communities.

In this context, the mutual interaction between vegetation and large herbivore's distribution is evident. For most herbivore species across different taxons (e.g., bovides, cervides), habitat selection is connected with habitat structure, forage availability and quality (Bobrowski, Gillich, & Stolter, 2015; Dörgeloh, 2001), but also disturbance and predation risk (Frid & Dill, 2002; Pays et al., 2012; Rettie & Messier, 2000). Habitat selection is evidently connected to food choice which is influenced by the seasonal and spatial availability as well as the nutritional composition of forage plants (Searle, Thompson Hobbs, & Shipley, 2005; Shipley, Blomquist, & Danell, 1998; Stolter, Ball, & Julkunen-Tiitto, 2013; Stolter, Ball, Julkunen-Tiitto, Lieberei, & Ganzhorn, 2005; Wallgren, Bergström, Bergqvist, & Olsson, 2013). Particularly for grazers available forage, biomass is inversely related to the corresponding nutritional quality (Hobbs & Swift, 1988; Wilmshurst, Fryxell, & Bergman, 2000). This might result in a search for optimal grazing patches. In particular, in the growing season, grazers might thus favour areas with lower biomass (e.g., regrowth of grasses) but higher quality over habitats with high food availability but less quality (e.g., tall grasses). However, open small grass areas might enhance predation risk (but see Valeix et al., 2011; Pays et al., 2012). Furthermore, food quality for a given herbivorous animal depends largely on its nutritional requirements that vary between species, but also between sexes and life stages. One driver of interspecific differences in food selection is body size (Bell, 1971; Jarman, 1974; Wilmshurst et al., 2000 but see Arsenault & Owen-Smith, 2008), which may also account for intraspecific differences of species with distinctive sexual dimorphism (e.g., sexual segregation, Perez-Barberia, Pérez-Fernández, Robertson, & Alvarez-Enriquez, 2008). Moreover, reproductive requirements in females result in different nutritional demands (Robbins, 1993). Therefore, an herbivore has to make decisions on different hierarchies to select the optimal habitat (Rettie & Messier, 2000).

In addition, the plant response to feeding damage is species specific. While some plant species react with defence mechanisms (Zinn, Ward, & Kirkman, 2007), others facilitate a higher quality for subsequent consumers resulting in a positive feedback loop (Stolter, 2008). In particular in grazing systems, the removal in biomass leads to enhanced plant quality for subsequent herbivores as grasses regrow but also due to the facilitation of available suitable plant heights (Arsenault & Owen-Smith, 2002).

Apart from that, feeding habits and habitat use often differ between seasons and specific regions and thus cannot be generalized. Insight about plant-herbivore interactions, feeding preferences and habitat use of herbivores are thus crucial to develop sustainable land management systems.

This study aimed to explore the indirect effect of different land management strategies on the habitat use of two grazing (oryx, *Oryx gazella*; common warthog, *Phacochoerus africanus*) and one browsing (greater kudu, *Tragelaphus strepsiceros*) herbivore species in a bush-encroached environment in the dry season. Four sites with different management regimes were identified on a cattle farm in the central Namibian thornbush savannah. First, we investigated differences in grass and bush encroacher species cover between different managed sites and the distribution of large herbivores using faecal pellet counts. Specifically, it was hypothesized that grazing species favour

TABLE 1 Overview of management intervention at study sites

	Site			
	a	b	c	d
Intervention type	None	Bulldozer cleared in 2010	Stump-burned in 2010	None
Regeneration management		Buffalo grass (*Cenchrus ciliaris*) seeded	Dead wood not removed, grass mixture was seeded	
Other		Continuously grazed by cattle in 2013		
Size [ha]	100	33	44	106
No of transects and relevés	20	12	12	12
Mean thornbush cover [%]	15.52	5.83	4.33	13.15
Mean thornbush height [cm][a]	24.32	86.44	35.30	65.84
Mean thornbush number per relevé	26	9	9	10
Mean annual grass cover [%]	2.00	0.00	0.83	0.00
Mean perennial grass cover [%]	17.78	33.75	23.96	21.83
Mean total grass cover [%]	19.78	33.75	24.79	21.83

[a] Mean height values per relevés were used to calculate mean cover per site.

open, grassy habitats while browsing kudu prefer areas with denser vegetation (Bothma, Van Rooyen, & Du Toit, 2010; Dekker, Van Rooyen, & Bothma, 1996; Hofmann, 1973; Knight, 1991; Rodgers, 1984; Valeix et al., 2011). In a second step, we investigated whether factors like thornbush cover, tree number, tree height and grass cover determine the habitat use of the different herbivores to understand the interaction between bush clearing management and herbivore distribution.

2 | MATERIALS AND METHODS

2.1 | Study area

Data were collected on the private cattle farm Erichsfelde, Namibia (21°38′S, 16°52′E) during the dry season 2013. Rainfall in that area is highly variable with a mean annual precipitation of approximately 350 mm. Both open grassland and patches with dense, thorny shrub cover occur. The farm is separated in several paddocks but not high fenced; thus, game is allowed to move freely between the paddocks and beyond the borders of the farm. We chose four study sites (paddocks) within the farm. The selection of these sites was based on the application of different bush clearing measures on the respective paddocks (bulldozer cleared, stem burning, none). The size of the chosen study sites ranged between 33 and 106 hectares (Table 1). All sites were located on plain land; water sources were near to all of our study cites (e.g., drinking troughs for cattle). A detailed environmental description of climate, vegetation communities, soils and various faunistic groups has been published by Jürgens et al. (2010), for further details see also www.SASSCAL.org (ObservationNet: Otjiamongombe, S05).

2.2 | Vegetation assessment

A total of 56 vegetation relevés were carried out (Table 1). All relevés had a size of 100 m^2 (10 m × 10 m). Plant cover per species was estimated in per cent. Grasses were pooled for cover estimation, because identification to species level was difficult during the dry season. Several thornbush species (*Acacia tortilis* Hayne, *Senegalia mellifera* (Benth.) Seigler & Ebinger, *Vachellia hebeclada* (DC) Kyal. & Boatwr., *V. luederitzii* (Engl.) Kyal. & Boatwr., *V. reficiens* (Wawra & Peyr) Kyal. & Boatwr., and *Dichrostachys cinerea* (L.) Wight & Arn.) were counted to determine their abundance and grouped into three different height classes (HC 1: <51 cm, HC 2: 51–180 cm, HC 3: >180 cm). These species were chosen for the study, as "*Acacia*" species (comprising of the genera *Acacia*, *Senegalia* and *Vachellia*) and *D. cinerea* are reported to be the most important encroachers in the area (Bester, 1999; Jürgens et al., 2010).

2.3 | Habitat use of herbivores

The habitat use of greater kudu, oryx and warthog was estimated using faecal pellet counts. This method is widely accepted for assessing habitat utilization and even for estimations of population numbers (Archibald, Bond, Stock, & Fairbanks, 2005; Hema, Barnes, & Guenda, 2013; Isaacs, Somers, & Dalerum, 2013; Månsson, Andrén, & Sand, 2011). In particular, in habitats with dense vegetation, like two of our study sites, it is very useful. In elephants, for example, it has been shown to be more accurate than even aerial surveys and direct counts (Barnes, 2002; Hema et al., 2013). Note, we did not use the method to determine absolute individual numbers, which also requires accurate defecation rates per species. Instead, we used pellet group counts to determine sites that were favoured as habitat by single species over other sites, for example for feeding and resting. Also, we did not use it for comparisons between species.

For the counting of pellet groups, one cross-shaped transect of 2 × 100 m was laid out at each relevé (vegetation assessment). Dung counts were conducted at the same time as the vegetation assessment, and each transect was investigated only once during the study period. Along these transects, all "fresh" pellet groups (consisting of at least 10 droppings for oryx and greater kudu) within 1 m to the left and the right were determined and counted. Pellets still dark in colour and without signs of decomposition (e.g., by termites or dung beetles) were defined as “fresh.” We did not include “older” pellets because those were undeterminable due to decomposition.

2.4 | Data analysis

Differences in pellet number and vegetation composition between different sites were analysed by one-way ANOVA. Either Dunnets-T3 test or Tukey-B test was used as post hoc tests, depending on the homogeneity of the variances (tested via Levene’s test). Generalized linear models (GzLM, using Poisson distribution) were carried out to test the impact of grass cover, thornbush cover [%], thornbush number, heights of thornbushes (explanatory variables) and sites (fixed factor) on the distribution of different herbivore species (dependent variable). To rank competing models (i.e., model selection) and to weigh the relative support, we used the Akaike information criterion (AIC). To reduce the number of variables for our models (to avoid overfitting), we used a standard procedure for the selection of variables (Burnham & Anderson, 2010; Zuur, Ieno, & Elphick, 2010), which consisted of a standard initial screening using scatter plots and a correlation matrix to detect relationships between potential explanatory variables. In case of collinearity, we calculated separate models for each explanatory variable (see also Stolter et al., 2013). Statistics were performed with PASW Statistics version 18 (PASW 2010).

3 | RESULTS

3.1 | Differences in vegetation composition and the distribution of large herbivores over sites

Highest grass cover was found at site b (33.8% ± 8.3), which was cleared and reseeded with buffalo grass. This site was significantly different to site a, which had the lowest grass cover (20.0% ± 11.8). Sites c and d were not different to the other sites (ANOVA grass cover: $F = 2.896$, $p = .044$, $N = 56$; Figure 1). Even though the result for thornbush cover gained by ANOVA was significant ($F = 2.895$, $p = .044$, $N = 56$), the post hoc test (Tukey B) showed no significant differences between all sites. However, the box plots (Figure 1) showed a high variance of the different transects, with site a having the highest thornbush cover (15.5% ± 11.6), similar to d (13.2% ± 15.6). There was no difference between the sites for thornbush number ($F = 1.843$, $p = .151$, $N = 56$) and HC1 ($F = 1.117$, $p = .351$, $N = 56$); however, for both we found a high variance of site a (total number of thornbushes 26.3 ± 41.9; number of HC1 21.6 ± 42.4) due to an extraordinary high number of small thornbush seedlings on one transect ($N = 192$, outliner in Figure 2a). Site a had the highest values for HC1. Differences between sites were found for HC2 ($F = 12.746$, $p \leq .001$) and HC3 ($F = 6.410$, $p = .001$, $N = 56$, Figure 2). Highest count of HC2 was found at site a (2.7 ± 1.9) and site d (2.1 ± 1.9), while at sites b and c almost no thorn shrubs of that size were found (site b: 0.0; site c: 0.1 ± 0.3). HC3 was most abundant at site a (2.1 ± 2.1), but quite rare at the other sites (site b: 0.2 ± 0.4; site c: 0.2 ± 0.4; site d: 0.8 ± 1.2).

For oryx, faecal pellet counts were highest on sites a and c (a: 5.5 ± 3.2; c: 3.3 ± 2.7) and lowest on b and d (ANOVA: $F = 15.889$, $p \leq .001$; Figure 3), where almost no oryx pellets were found (b: 0.4 ± 0.9; d: 0.8 ± 1.0).There was a significant difference between sites for kudu (ANOVA: $F = 4.773$, $p = .005$, $N = 56$). Kudu pellet counts were found highest on site d (1.8 ± 1.1). Almost no kudu pellets were found on site a (0.4 ± 0.9, Figure 3). Sites b and c were intermediate. Faecal pellet counts of warthog were significantly different between sites ($F = 13.858$, $p \leq .001$, $N = 56$, Figure 3). Warthog faeces were found more frequently than those of the other species. Most warthog faeces were found on the open site b (13.7 ± 7.2).

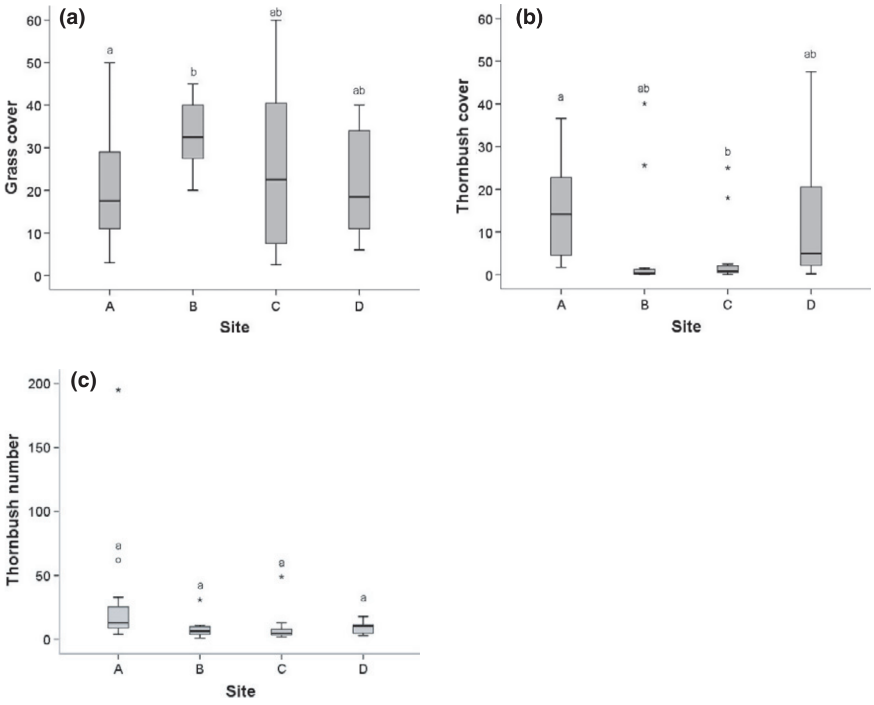

FIGURE 1 Differences in grass cover (a), thornbush cover (b) and thornbush number (c) between the four sites in 2013. Sample size of each site see Table 1. Significant results gained by a post hoc test are indicated by different small letters ($p \leq .05$). Stars and circles indicate outliners

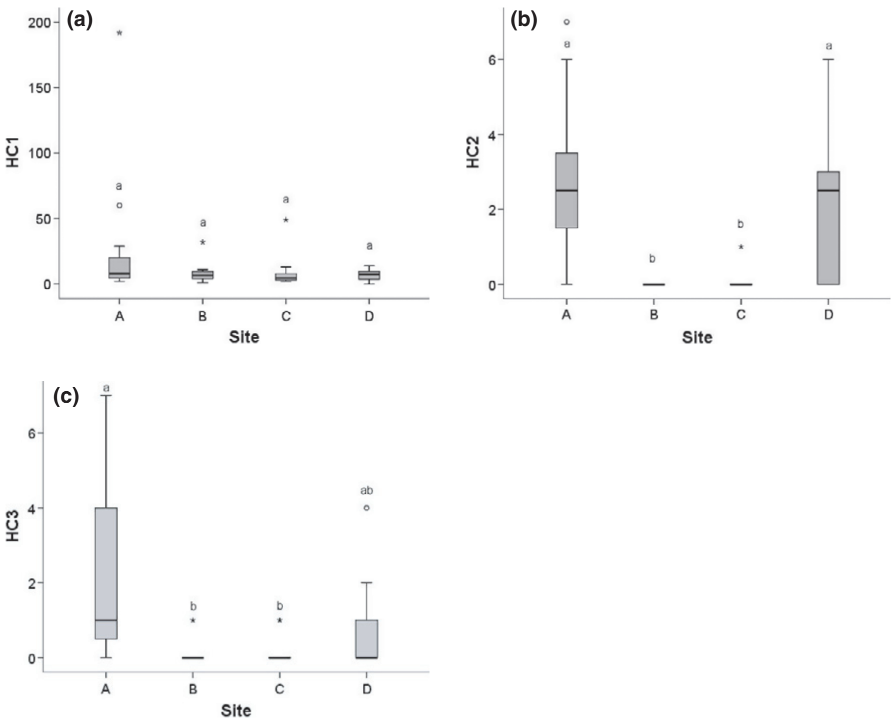

FIGURE 2 Thornbush individual numbers per height class and site. HC1: 0–0.5 m, HC2: 0.5–1.8 m, HC3: >1.8 m. Sample size of each site see Table 1. Significant results gained by a post hoc test are indicated by different small letters ($p \leq .05$). Stars and circles indicate outliners

3.2 | Influence of vegetation structure on large herbivore distribution

The results of the five best GzLM revealed the constant high influence of the sites and height categories. All height categories appear in the best five models, with the highest impact of HC2 on the distribution of oryx (Table 2). Concerning the distribution of kudu and warthog, the results of the models were more inhomogeneous. Factors such as grass cover, thornbush cover and number, as well as HC1, HC2 and HC3, were present in the best five models. However,

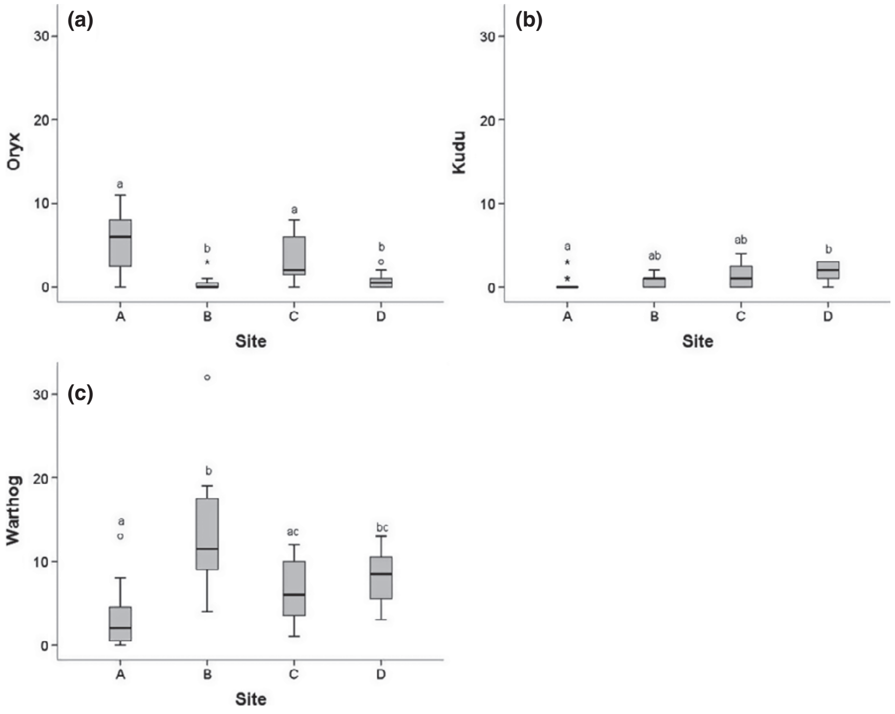

FIGURE 3 Differences in utilization of three large herbivores between the four sites in 2013. Sample size of each site see Table 1. Significant results gained by a post hoc test are indicated by different small letters ($p \leq .05$). Stars and circles indicate outliners

TABLE 2 The five best models (GzLM) for distribution of oryx, kudu, and warthog pellets

Oryx	AIC Δ AIC	Omnibus	Model effects	Kudu	AIC Δ AIC	Omnibus	Model effects
Dependent Variable "Oryx"		Likelihood-X^2	Wald-statistic	Dependent Variable "Kudu"		Likelihood-X^2	Wald-statistic
Model 1	217.956	125.876***		Model 1	139.367	33.903***	
Constant term			6.071*	Constant term			4.789*
Site			57.714***	Site			19.138***
HC 1			3.281	Grasscover			2.905
HC 2			8.177**	Site × grasscover			13.303**
HC 3			0.832	Thornbushcover			3.446
Site × HC 3			7.693				
Model 2	219.505 1.549	124.327***		Model 2	141.946 2.579	31.323***	
Constant term			10.882***	Constant term			3.861*
Site			42.354***	Site			18.829***
HC 1			0.529	HC 3			0.717
HC 2			8.362**	Grasscover			2.335
HC 3			3.457	Site × grasscover			11.104*
Site × HC 1			7.619				
Model 3	220.011 2.055	117.821***		Model 3	142.556 3.189	30.714***	
Constant term			19.019***	Constant term			3.528
Site			74.446***	Site			18.338***
HC 1			3.115	Grasscover			3.021
HC 2			8.138**	HC 1			13.181**
HC 3			3.439	Site × grasscover			0.062
Model 4	220.125 2.169	119.707***		Model 4	142.615 3.248	30.655***	
Constant term			12.993***	Constant term			3.582
Site			71.945***	Site			18.293***
HC 1			0.067	Grasscover			3.034
HC 2			1.921	Thornbush no			13.098**
HC 3			3.223	Site × grasscover			0.008
HC 1 × HC 2			1.933				
Model 5	221.142 3.186	120.690***		Model 5	143.915 4.548	31.354***	
Constant term			8.464**	Constant term			3.669
Site			38.399***	Site			18.722***
HC 1			0.536	Grasscover			2.331
HC 2			5.497*	HC 1			11.137**
Site × HC 1			7.582	HC 3			0.864
				Site × grasscover			0.411

"Warthog"	AIC Δ AIC	Omnibus	Model effects
Dependent Variable "Warthog"		Likelihood-X^2	Wald-statistic
Model 1	318.240	146.468***	
Constant term			422.985***

(Continues)

TABLE 2 (Continued)

"Warthog"	AIC Δ AIC	Omnibus	Model effects
Dependent Variable "Warthog"		**Likelihood-X^2**	**Wald-statistic**
Site			46.251***
HC 1			4.682*
HC 2			0.972
HC 3			6.835**
HC 2 × HC 3			14.454***
Model 2	318.282 0.042	148.427***	
Constant term			86.672***
Site			67.164***
HC 1			0.498
Grasscover			16.957***
Site × HC 1			17.133***
Model 3	320.226 1.986	148.483***	
Constant term			85.127***
Site			58.079***
HC 1			0.483
Grasscover			16.108***
HC 3			17.024***
Site × HC 1			0.056
Model 4	320.484 2.244	146.225***	
Constant term			69.136***
Site			57.247***
Grasscover			17.057***
Thornbush no			0.167
Site × thornbush no			14.725**
Model 5	322.815 4.575	139.894***	
Constant term			469.10***
Site			53.349***
HC 2			0.602
HC 3			7.954*
HC 2 × HC 3			14.490***

HC, Height class; HC 1, 0–50 cm; HC 2, 50–180 cm; HC 3, >180 cm.
Significance: *$p \leq .05$, **$p \leq .01$, ***$p \leq .001$.

for kudu none of these factors was significant except for the interaction of site and grass cover, which appeared to be constantly significant in all five best models (Table 2). Similarly, grass cover appeared to be important for the distribution of warthog (Table 2), with a significant result in three of the best five models. However, the best-fitting model included all the height classes with significant results for HC1, HC3 and the interaction between HC2 and HC3. Note that HC2 was negatively correlated with grass cover ($r_s = -.391$, $p = .003$, $N = 56$); therefore, models had to be calculated separately. Furthermore, we found a significant negative correlation of faecal pellet counts between oryx and warthog ($r_s = -.331$, $p = .013$, $N = 56$) but not between other animal species.

4 | DISCUSSION

Bush encroachment is known to convert valuable grassland into land not suitable for cattle and livestock keeping. To counteract the development of vast bush-encroached areas, different management strategies have been developed. Already bush-encroached areas are often mechanically cleared. However, every manipulation of ecosystems results in changes of the habitat with subsequent impacts on vegetation and faunal composition (Cogger & Cogger, 2003; Haussmann et al., 2016), including changes in habitat use or in animal movements (Archibald et al., 2005). In this matter, knowledge about the influence of bush clearing on large herbivores is of interest, as the changes in natural herbivore assemblage are described as one driver of bush encroachment (Staver et al., 2009). However, the effects of bush clearing on habitat utilization are not fully understood. Effects might differ between species due to their differences in food selection (Long, Rachlow, & Kie, 2008) as vegetation composition changes, but also due to differences in predator avoidance strategies (Pays et al., 2012; Valeix et al., 2011) as morphological characteristics of the vegetation (e.g., plant heights) change.

Different management strategies on our study areas resulted in different vegetation patterns. Site b, where encroacher species were removed and the site was reseeded with perennial grass, showed the highest grass cover, even though it was dry season and cattle was abundant throughout the study period. In contrast, shrub cover was highest at sites a and d. Contrary to our expectation, the number of new seedlings up to 50 cm (HC1) did not differ significantly between the sites as compared to older shrubs and trees. However, we found transects with high numbers of seedlings at site a, which has not been cleared for many years, leading to a high variation in the results.

It was assumed that grazers would prefer open, grassy habitats while browsers should favour areas with higher shrub and tree cover. Such habitat preferences are already well described for the study species (Bothma et al., 2010; Hofmann, 1973). Accordingly, warthog and oryx should have favoured open grassy areas, and kudu should have been associated with denser savannah vegetation (Ben-Shahar, 1992). Results of the GzLM showed that the actual site was the most important factor for herbivore distribution. This was valid for all animal species; however, the influence of the vegetation parameters differed between species and did not always match our expectations. We found a relatively clear pattern for warthog in our study. The high abundance on site b with the highest grass cover and the low abundance on site a with the highest occurrence of bush encroacher species is mirrored by the results of the GzLM and matches our expectations that warthog should favour grassy sites. Furthermore, site b was continuously used by cattle. Therefore, cattle might provide warthog with grasses of its preferred height, but warthog might also benefit from continuously utilized grasses, here mainly *Cenchrus ciliaris* L., which might be of better quality as a plant response to earlier grazing and/or fertilization (Arsenault & Owen-Smith, 2002; Treydte, Bernasconi, Kreuzer, & Edwards, 2006). However, our study took place in the dry season and we did not measure differences in grass quality between utilized and unutilized specimens.

The model for greater kudu showed a quite strong impact of the interaction site × grass cover. This contradicts our expectation as does the low abundance of kudu at site a, the site with the highest abundance of thornbushes. However, kudu showed the highest abundance on site d. This site had an intermediate grass cover but the highest number of trees with a size of 50–180 cm (HC2). The significant interaction with grass cover might therefore be related to the significant negative correlation between grass cover and HC2. This height class might mainly serve as forage for kudu.

Considering that kudu did mainly use areas with abundance of HC2, we conclude that HC2 might be in the optimal feeding heights for Kudu, which ranges between 0 and 2.0 m (Dutoit,1990) with a preference of larger bushes (De Garine-Wichatitsky, Fritz, Gordon, & Illius, 2004) and therefore preferred as food over other height classes (e.g., HC1). This might allow these plants to grow to considerable size. At the same time, HC2 plants might be kept from growing to proper tree size by rebrowsing, a behaviour that is already known from other browsers (Stolter, 2008). This might to some minor extent favour the growth of bushes and broad thickets. In this context, age of individual plants might be of interest for further studies as well as plant response, that is compensation growth and changes in plant chemical composition. Furthermore, other bush/tree species (e.g., *Boscia albitrunca* GILG & GILG-BEN., *Catophractes alexandri* D.DON, *Lycium bosciifolium* SCHINZ) were also present at this site, which typically serve as food for Kudu in the dry season (Owen-Smith, 1994). Herbaceous plant species, which are also used by kudu, presumably due to their high plant quality (Owen-Smith, 1994), were not considerably abundant in the whole area as our study took place in the dry season.

For oryx, even more surprisingly, the models demonstrate the high importance of HC2, which was totally unexpected as oryx is regarded as a typical grazer (Bothma et al., 2010; Hofmann, 1989). We therefore assumed that we would find a higher utilization on cleared sites, as e.g., Isaacs et al. (2013) reported that bush clearing can have a positive effect on grazers. In contrast to that, we found the highest abundance of oryx on sites a and c. While site a is high in HC2 and HC3, site c is low in numbers of encroacher species. Lowest dung counts of oryx were found at site d, which had the highest number of HC2 shrubs, and b, which had the highest grass cover. However, animal behaviour is not only influenced by vegetation and forage availability. Habitat preferences also strongly depend on structural diversity and spatial scales (Skarpe, 1991). Greenacre and Vrba (1984) pointed out that the “large-scale physiognomy” of a landscape is much more important for habitat frequentation than particular, small-scale patches of vegetation. There are several assumptions that can be discussed in respect to the utilization by oryx: human disturbance might be one reason for the low utilization of site b, as this area is closest to the farm house, frequently visited by humans to care for cattle and there is almost no cover. In particular for oryx, which are regularly hunted on Erichsfelde and preferred the rather shrubby site a, risk avoidance and hunting pressure could be factors in habitat selection and drive them to prefer thickets to open areas. This behaviour was already described for various ungulates (Anderson et al., 2016; Benhaiem et al., 2008; Ndaimani, Murwira, & Kativu, 2014; Root, Fritzell, & Giessman, 1988).

In addition, the grass species reseeded on site b after tree removal (*Cenchrus ciliaris*) might not be preferred by oryx, so the animals might favour site c instead, where regrowth of indigenous grasses and herbs is present. Another possibility is that cattle as well as warthog might outcompete oryx on certain sites. To some extent, a competition between oryx and warthog seems to be reasonable, as warthog is not using site c (high grass cover) but oryx is prominent and vice versa on site b.

This underpins to some extent the fact that oryx, mainly referred to as bulk and roughage grazer (Hofmann, 1989; Bothma et al., 2010; are often seen in competition with other grazers such as cattle. They are however frequently reported to feed also on dicotyledonous plants and plant parts, especially during the dry season (Hofmann, 1973 and citations therein, Bothma et al., 2010). Owen-Smith (1999) indicated a diet composition of 78% monocot and 22% dicot material during the dry season, and similar numbers are described in the review of Gagnon and Chew (2000). In our study area, Schwarz (2015) found reasonable amounts of the dwarf shrub *Leucosphaera bainesii* GILG. in oryx faeces and rumen content. Furthermore, we found a high abundance of oryx at site a, which is relatively densely covered with thorn shrubs. This strong utilization of site a by oryx might possibly explain the low utilization by kudu. This assumption has to be tested in further studies. From personal observations, we know that groups of oryx calves are mainly found in the area around site a, and therefore, a denser plant cover might be preferred. Furthermore, the occurrence of tree species is often related to an elevated grass biomass under the trees depending on the grass species (Weltzin & Coughenour, 1990), which might be beneficial for oryx as well. However, the question why site d with its high thornbush cover (mainly HC2) is not used by orxy calves remains unsolved here. In this study, we did not measure signs of predators. Further research is thus necessary to answer the questions raised by our study, as observations on small scales cannot reveal general statements.

We found that the impact of bush encroachment management clearly mirrored differences in vegetation, which consequently influenced the distribution of the studied herbivores. However, the animals did not use these sites as expected. In particular for kudu and oryx, we found deviating results, which might be better explained by differences in live stages, competition, and avoidance of disturbance, hunting or predator pressure in combination with vegetation composition. Burkepile et al. (2013), for example, found shifting habitat utilization of different ruminants between day and night in relation to vegetation composition and predator pressure. However, using dung counts we aimed to determine the overall habitat utilization and did not account for diurnal patterns. However, next to our dung count the additional use of camera traps would have been beneficial, for example, to recognize sexual differences in habitat use (Perez-Barberia et al., 2008). The interaction between herbivores and plants (e.g., feeding behaviour of greater kudu and subsequent plant response of encroacher species) is thus an important matter for future research to understand and manage bush-encroached sites. Thereby, the impact of small-scale habitat diversity should not be neglected. The high utilization of noncleared sites, even by grazer species like oryx, might indicate the importance of these sites as refugium for wild-ranging animals and as valuable sites for the conservation of diversity, especially in human-utilized, small-scale fragmented landscapes. Hence, heterogeneity in a fragmented landscape is an important attribute as highlighted by Hobbs et al. (2008). Wild and domestic herbivores have to share terrestrial ecosystems. Therefore, it is important to understand their niche differentiation, overlaps and interactions in terms of habitat and food utilization to maintain future co-existence. Knowledge about functional heterogeneity of a given habitat, for example differences in chemical and physical characteristics of food plants, will enable us to manage livestock and improve biodiversity conservation (Fynn, Augustine, Peel, & de Garine-Wichatitsky, 2016).

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