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The grazing fingerprint: Modelling species responses and trait patterns along grazing gradients in semi-arid Namibian rangelands

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ABSTRACT

Persistence or disappearance of plants under grazing pressure has led to their categorisation as grazing increasers or decreasers. We aimed to extend this classical indicator concept in rangeland ecology by interpreting the shape of species responses and trait patterns modelled along continuous grazing gradients at different spatial scales.

Taking transects of two different lengths, we recorded the cover of vascular plant species along grazing gradients in central Namibian rangelands. We used a hierarchical set of ecologically meaningful models with increasing complexity – the HOF (Huisman–Olff–Fresco) approach – to investigate species' grazing responses, diversity parameters and pooled cover values for two traits: growth form and life cycle.

Based on our modelling results, we classified species responses into eight types: no response, monotonic increasers/decreasers, threshold increasers/decreasers, symmetric unimodal responses, left skewed and right skewed unimodal responses.

The most common category was that of no response (42% of the short and 79% of the long transect responses). At both scales, decreaser responses with higher grazing pressure were more frequent than increaser responses. Monotonic and threshold responses were more frequent along the short transects.

Diversity parameters showed a slight but continuous decline towards higher grazing intensities. Responses of growth form and life cycle categories were mostly consistent at both scales. Trees, shrubs, dwarf shrubs, and perennials declined continuously. Woody forbs tended to show a symmetric unimodal distribution along the gradients, while herbaceous forbs and annuals showed skewed unimodal responses towards lower grazing intensities.

The different grazing response types proposed in this study allow for a differentiated picture of niche patterns along grazing gradients and provide a basis to use species as indicators for a continuum of vegetation states altered by livestock impact. The general decline of plant diversity with increasing grazing intensities highlights the importance of reserves that are less impacted by grazing to support the resilience of the studied system.

1. Introduction

Gradients of grazing pressure in arid and semi-arid rangelands have often been used as a model system for studying the ecological consequences of large herbivore impact (Fernandez-Gimenez and Allen-Diaz, 2001; Landsberg et al., 2003; Perkins and Thomas, 1993; Todd, 2006). These studies have aimed on understanding the complexity of ecosystem responses to grazing and to inform sustainable rangeland management. In this context, it has been crucial to differentiate between regular and reversible vegetation changes according to equilibrium models (Dyksterhuis, 1949) on the one hand, and non-linear and discontinuous behaviour consistent with non-equilibrium models (Ellis and Swift, 1988; Westoby et al., 1989) on the other. Over the last decade, it has been increasingly recognised that natural dynamics in dry ecosystems accommodate elements of both equilibrium and non-equilibrium paradigms (Briske et al., 2003; Gillson and Hoffman, 2007; Miehe et al., 2010). Therefore, a classification of grazing responses of species and vegetation parameters should cover the range of possible response types along the equilibrium–non-equilibrium continuum.

With regard to indicator species for grazing impact, rangeland ecologists have, until now, mostly made the simple distinction between "grazing increasers" and "decreasers" (Dyksterhuis, 1949;

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Noy-Meir et al., 1989; Todd and Hoffman, 1999; Vesk and Westoby, 2001). Trollope (1990) suggested a greater range of response categories for southern African grass species that included several levels of increaser response types. In order to derive refined response types (Landsberg et al., 2003; Todd, 2006; van Rooyen et al., 1991) or indicate proximity to ecological thresholds (Sasaki et al., 2011), different kinds of regression analyses have been applied on grazing gradients, using distance from watering points as a proxy for grazing intensity. However, a coherent concept which encompasses ecologically meaningful grazing response types, addressing issues related to equilibrium and non-equilibrium dynamics, and offering a sound analytical framework, has not yet been established.

An effective approach for studying the shape of species responses along environmental gradients is that of Huisman et al. (1993), also named 'HOF' (after the authors Huisman, Olff and Fresco). It is based on a hierarchical set of species response curves of increasing complexity that are tested for adequacy based on an information theoretic approach. The HOF approach covers five plausible types of response curves: none, monotonic, monotonic with threshold, symmetric and skewed. It thus represents a framework for gradient analyses that offers both a manageable number of ecologically well-founded response types and a sound basis for inference. The method has been used to analyse plant species responses to elevation (Suchrow and Jensen, 2010), soil related (Peppler-Lisbach, 2008) or climatic gradients (Uğurlu and Oldeland, 2012). It has also been applied recently to test for discontinuities in species composition along grazing gradients (Peper et al., 2011). However, data used for the HOF approach have mostly been based on species presence/absence, which does not allow inferences to be drawn on changes in species dominance patterns.

In the present study we applied the HOF approach to the analysis of grazing responses using species cover values recorded in semi-arid savannas of central Namibia. We sampled along transects in piospheres (from Greek "pios" = to drink, Lange, 1969), i.e. zones of livestock impact around watering points (Andrew, 1988). Such piospheres, if selected carefully, offer the opportunity to analyse vegetation responses to grazing independent of confounding environmental variation (Todd, 2006). Simple geometry means that grazing intensity at piospheres decreases in a non-linear fashion with distance from the watering point (Manthey and Peper, 2010). Species turnover in the highly disturbed area at the centre of each piosphere, also referred to as "sacrifice zone" (Andrew, 1988), is expected to be much higher than at greater distances. Species may thus show scale-dependent responses, being dependent on the length of the gradient. Whilst issues related to the spatial scale have rarely been addressed in the modelling of grazing responses (but see Landsberg et al., 2002), they are critical to the identification of discontinuities, thresholds or state transitions (Bestelmeyer et al., 2011). In our modelling of species grazing responses, we took this into account by using two different transect lengths.

Community parameters, such as cover of major plant functional types and species diversity patterns, have been found to diverge from related species responses (Fernandez-Gimenez and Allen-Diaz, 1999). Although these parameters are important proxies for ecosystem function, few studies have analysed them along grazing gradients around piospheres (Sasaki et al., 2008; Todd, 2006). Furthermore, for our study area, which is supposed to have a long history of large ungulate grazing (cf. Owen-Smith and Danckwerts, 1997), general models of grazing–diversity relationships predict a relatively flat response curve of decreasing species diversity with increasing grazing pressure (Cingolani et al., 2005; Milchunas et al., 1988). This prediction has rarely been tested for semi-arid southern African rangelands. Additionally, the highly degraded sacrifice zone around watering points might influence diversity patterns in a fundamentally different way, and research on the particular effect of this zone on diversity patterns is still lacking.

In this study, we applied the HOF approach for classifying the responses of plant species and community parameters. Specifically, our aims were to: (i) model and compare the cover-based responses of dominant plant species along grazing gradients in Namibian semi-arid rangelands at two spatial scales; (ii) interpret these species responses in terms of a refined grazing increaser/decreaser concept that is relevant to the assessment and management of dry rangelands; and (iii) model plant species diversity measures and major plant functional traits along the gradients, comparing these responses to general predictions made for semi-arid rangelands.

2. Materials and methods

2.1. Study area

The study area is located near the district town of Rehoboth in central Namibia (from 23.1° to 23.7° S, from 16.8° to 17.3° E; Fig. 1). The area is flat to slightly undulating with altitudes ranging from 1400 m to 1650 m a.s.l. The main soil types are shallow Leptosols, Regosols, Calcisols, and deep Arenosols (Jürgens et al., 2010). The climate is semi-arid with a mean annual rainfall of 200–300 mm, mainly occurring in late summer between December and April. Precipitation is spatially and temporally highly variable, with an inter-annual coefficient of variation of 40–50% (Mendelsohn et al., 2002). The mean annual temperature is 19 °C, with an average minimum of 2 °C in the coldest month of July and an average maximum of 32 °C in the hottest month of December (Mendelsohn et al., 2002).

The study sites belong to the Nama-Karoo Biome, bordering the slightly moister Thornbush Savanna Biome of southern Africa (Jürgens et al., 2010; Rutherford and Westfall, 1994). In this northernmost part of the Nama-Karoo, the vegetation is an open shrub or dwarf shrub savanna with a matrix of usually perennial grasses covering 30–60% of the soil surface, and a shrub layer with a height of up to 2 m. Trees are largely restricted to drainage lines and seasonal watercourses. Like most of the southern African biomes, the Nama-Karoo has a long history of grazing by large native ungulates (Owen-Smith and Danckwerts, 1997). Beginning ca. 2000 years ago, southern Namibia was used by nomadic pastoralists for livestock husbandry (Barnard, 1992) before permanent settlers occupied the land in the late 19th century. Nowadays, sizes of the privately owned farms range from 1000 ha to 9000 ha. The main farming activity is livestock grazing with cattle, sheep and goats. Most farms are divided by fences into paddocks, which can be used by the farmers for different types of livestock or rotational grazing.

2.2. Selection of the study sites

We chose nine paddocks, from seven different farms, with access to an artificial watering point. The average stocking rates in these paddocks were retrieved from the farmers, and varied from 8 to 20 ha per large stock unit (LSU, equivalent to one cow of ∼450 kg). The selected paddocks represented the major soil and land management regimes (livestock type and stocking rate) of the region. The paddocks were all grazed by cattle and to a lesser degree by sheep, goats and native antelopes. In a previous study we found that stocking rates had much less influence on species and trait composition than distance from the watering points, despite varying widely (Wesuls et al., 2012). Furthermore, we expected that differences in stocking rate, management and environmental differences between sites will have lesser impact on the results when using a large data set, and will only weaken but not completely change the response signal of many species. Within the paddocks, we sampled along transects. To avoid interference with

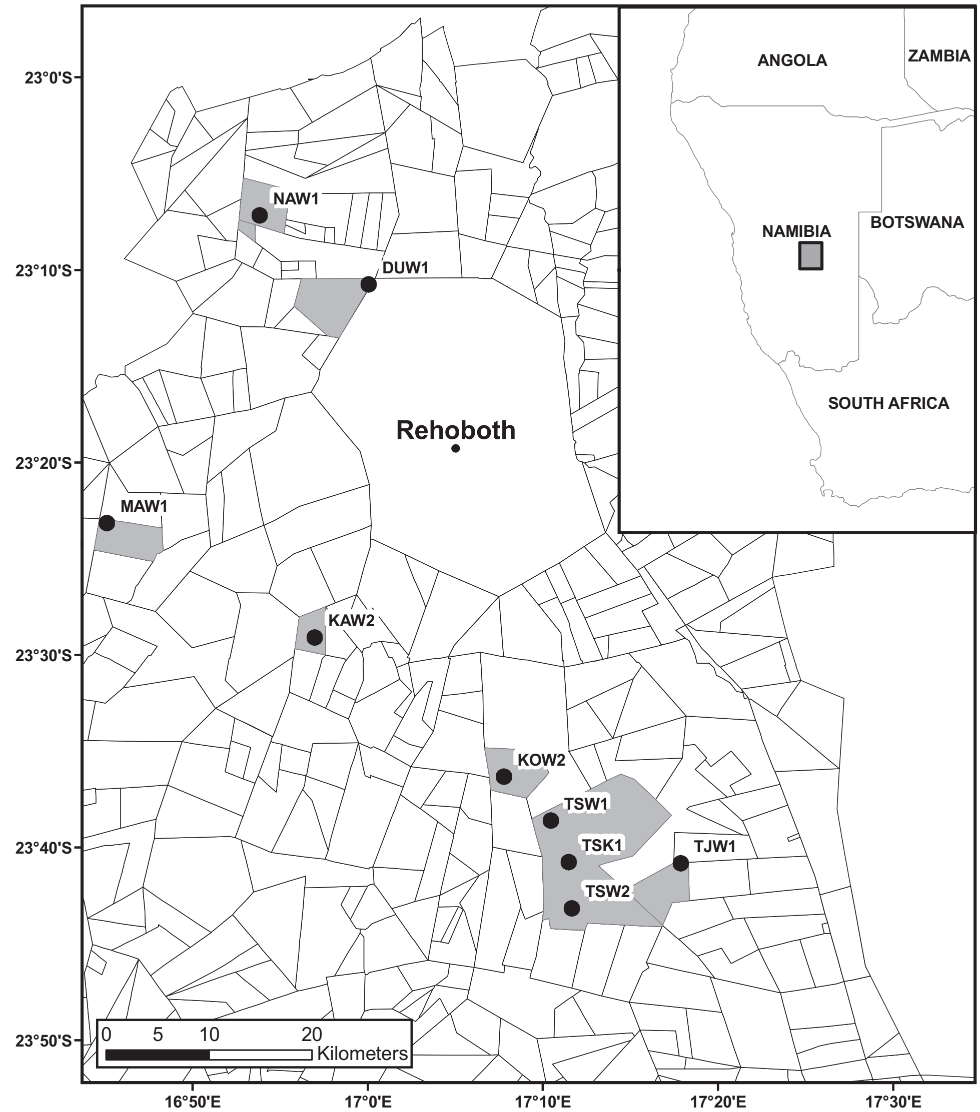


Fig. 1. Study area in central Namibia (grey rectangle in the insert) including investigated transects and farms Narais (NAW1); Duruchaus (DUW1); Marienhof (MAW1); Kamasis (KAW2); Kojeka (KOW2); Tsumis Agricultural College (TSW1, TSW2, TSK1); Tsumis Ged. 5 (TJW1). Lines indicate farm borders. Black circles represent watering points.

other environmental gradients, these were selected such that they were: (i) not dissected by fences or streams; (ii) situated in similar landscape positions within each paddock; (iii) not showing wide within-transect variations in slope angle; and (iv) located within the range of only one watering point. In order to take into account differences of grazing responses with regard to spatial scale, in each piosphere, we sampled one long transect (LT) and several short transects (STs). The LT represented the larger and coarser scale while the STs were established to capture changes at a smaller scale and finer grain size close to the highly disturbed sacrifice zone.

2.3. Transect data

We sampled short transects (STs; 150 m; $n = 41$) during the rainy season between February and May 2008. Starting from each watering point, we set up three to five STs, depending on accessibility. Along each transect, we placed plots of size 1 m × 1 m every 5 m along the first 100 m, and every 10 m thereafter, totalling 25 plots per ST. In each of these 1025 plots, the percentage cover of vascular plant species was estimated visually (cover >1% recorded as integer values; cover <1% assigned to the categories 0.5% or 0.1%).

Data from the long transects (LTs; 1500 m; $n = 9$) were collected between February and May in the rainy seasons of 2007 and 2008. We divided each of the piospheres into six concentric circular zones with distance from the centre 0–20, 20–80, 80–200, 200–400, 400–800 and 800–1500 m, assuming a homogenous distribution of grazing pressure within each. The maximum distance was limited by the paddock sizes. Thus, we assumed the grazing impact at a distance of 1500 m to be minimal (although not completely absent). In each zone, we randomly placed five plots of 10 m × 10 m, except in the first zone (0–20 m) where one to three were placed due to space constraints. Hence, in contrast to the STs, the LT plots were not arranged in lines but in spheres with replicated samples in each of the spheres. For each plot, the distance to the watering point was determined with a hand-held GPS. The vegetation in 244 LT plots from nine piospheres was sampled in total, following the same methodology as for the STs.

2.4. Species diversity and plant functional traits

On each plot, we recorded all vascular plant species that had a vertical projection on a plot. Plant nomenclature follows

Germishuizen and Meyer (2003). For each plot, we calculated species richness and Simpson diversity index (Magurran, 2004). The latter reflects the equitability in species cover and therefore covers another aspect of species diversity. For each species, we recorded two traits: life cycle (annual, weak perennial – i.e., survival depending on environmental conditions – or perennial) and growth form (grass/sedge, herbaceous forb, woody forb – i.e. perennial or weak perennial forbs with woody stem base, dwarf shrub, or shrub/tree). See Appendix C for species occurrences and traits.

2.5. Modelling of grazing responses

As a proxy parameter for grazing intensity and predictor variable for the modelling of grazing responses, we used the inverse distance (in m^{-1}) from the watering point. In comparison with normal distance, which is usually used for the modelling of piospheres, inverse distance better represents the non-linear distribution of grazing pressure around circular grazing gradients (Manthey and Peper, 2010). Furthermore, the interpretation is straightforward in the sense that high values of inverse distance imply high levels of grazing intensity. The use of this metric is based on the fact that a circular area impacted by livestock becomes larger with increasing distance. Under the simplifying assumption that livestock presence is evenly distributed in relation to distance from the watering point, this means that animal density decreases in a non-linear fashion. By using inverse distance, the study of grazing responses is less confounded by spatial piosphere patterns, e.g. non-linearity or thresholds emerging close to the sacrifice zone.

The grazing responses of single species, as well as diversity measures and selected plant functional traits, were modelled using the HOF approach (Huisman et al., 1993). This method selects the minimum adequate model out of a set of five increasingly complex models that correspond to typical responses of species to environmental gradients (Appendix A, see also Appendix D). Model I indicates no change along a gradient, whereas models II–V correspond to the following responses: (II) monotone sigmoid; (III) monotone sigmoid with plateau (i.e. threshold); (IV) symmetric unimodal; and (V) skewed unimodal. We based the selection of the best model on the Akaike information criterion, corrected for small n (AICc; Burnham and Anderson, 2002). For model comparison, we determined Akaike weights (w_i), representing "normalised relative likelihoods" that sum up to 1, giving the probability that model i is the best among the set of alternatives considered (Burnham and Anderson, 2002).

For the unimodal responses (models IV and V), we calculated each species' optimum, i.e. the distance from the watering point with the highest predicted cover. We restricted the HOF modelling to species with at least 40 occurrences (3.9% frequency) in the 1025 ST plots and a minimum of ten occurrences (4.1% frequency) in the 244 LT plots. If two or more models for one species were ascribed the same value of w_i, we chose the one with the fewest parameters as the best possible. For model evaluation, we considered both the respective best model, and all models with $w_i \geq 0.01$. For modelling a life cycle or growth form category, we summed up the cover values of the respective species. The modelling and calculation of species optima were performed using the *vegdata.dev* package (Jansen, 2008; version 0.2.1, http://geobot.botanik.uni-greifswald.de/download) in the R environment (R Development Core Team, 2011).

3. Results

Some 162 species occurred in the 1025 ST plots, with a mean density of 8 species per 1 m^2 (range: 1–18). The annual grass *Eragrostis porosa* was most frequent (72%). In the 244 LT plots, 208 species occurred, with a mean density of 18 species per 100 m^2 (range: 3–32). Here, the perennial grass *Stipagrostis uniplumis* was most frequent (82%). Combining both transect types, we found 225 species, with 145 being common (see also Appendix C).

3.1. Species response curves

Among the 48 modelled species from the STs, no response (model I) was ranked top most often, followed by monotonic increases or decreases (model II; Tables 1 and 2). Threshold increases (model III); symmetric (model IV) and skewed unimodal responses (model V) were chosen with almost equal frequency. Akaike weights averaged over all species modelled along the STs were highest for model I. Decreases (13 species), either monotonic (model II) or with threshold (model III), were more frequent than increases (six species, see Table 2). Optima of unimodal responses (models IV and V) ranged from 8 m to 55 m (Fig. 2A, for parameters and curves of best models see Appendix E and Appendix B).

Among the 94 modelled species from the LTs, model I was also most frequently rated as the best. The responses of the other species were mainly monotonic decreases (model II) or symmetric unimodal (model IV), and less often skewed unimodal (model V) or threshold decreases (model III; Table 1). Mean Akaike weights for all modelled species from the LTs were highest for model I, while averaged Akaike weights of all cases where the respective model type performed best revealed the highest w_i for models V and III (Table 1). Along the LTs, there were decreases but no increases (Table 2). Optima of unimodal responses ranged from 13 to 111 m (Fig. 2B).

For 20 out of the 41 species modelled at both gradient lengths, the best fitting model (including direction of responses and skewness) was the same (Table 2 and Fig. 3). Most frequently, model I (no response) was consistent for both transects (13 species). Four species consistently decreased, either monotonically or with threshold (models II and III), and three species showed a consistent symmetric or skewed unimodal response (model IV and V) for both transect types (see Appendix D and Appendix B). None of the species showed an increasing trend towards high grazing intensity at both sampling scales.

3.2. HOF-modelling of diversity measures and plant functional traits

Along the STs, species richness and the Simpson diversity index decreased monotonically with increasing grazing intensity (Fig. 4). Predicted species richness decreased slightly from 8.5 to 6.0 species per square metre between the lowest and highest grazing intensities (i.e. inverse distance).

For the LTs, species richness also showed a slightly decreasing trend with grazing intensity (Fig. 4), while the Simpson index showed no response. Modelled species richness per 100 m^2 was about 18 at the lowest grazing intensity and 13 at the highest.

In terms of growth form, trees and shrubs (13 species) as well as dwarf shrubs (14 species) decreased monotonically with increasing grazing intensity along the STs (Fig. 5). Woody forbs (22 species) showed a symmetric unimodal response and herbaceous forbs (74 species) a left skewed unimodal response. Only grasses and sedges (39 species) increased with higher grazing intensity along STs.

For trees and shrubs (19 species), dwarf shrubs (20 species), woody forbs (28 species) and herbaceous forbs (98 species), model shape and direction was the same along the LTs and STs. In contrast to the STs, grasses (43 species) decreased monotonically along the LTs towards higher grazing intensities (Fig. 5).

Perennials (53 species) decreased monotonically in cover with increasing grazing intensity along the STs (Fig. 6). Weak perennial

Table 1
Frequency of occurrence (total numbers and percentages) of best HOF model types for the short transects (48 species modelled) and long transects (94 species modelled). Presented here are the mean percentage Akaike weights (w_i AICc) ascribed to each model type for all modelled species (sum per transect-length is not exactly 100% because averages were rounded to one decimal place), and mean percentage Akaike weights of all cases where the respective model type performed best.

Model	Short transects			Long transects		
	Predicted as best model	Mean Akaike weights (w_i) all models	Mean Akaike weights (w_i) best models	Predicted as best model	Mean Akaike weights (w_i) all models	Mean Akaike weights (w_i) best models
I	20 (41.7%)	24.9%	55.6%	74 (78.7%)	49.9%	61.5%
II	11 (22.9%)	21.6%	49.5%	8 (8.5%)	20.5%	54.4%
III	8 (16.7%)	23.0%	85.6%	2 (2.1%)	9.3%	70.3%
IV	5 (10.4%)	17.2%	61.2%	7 (7.4%)	11.9%	56.7%
V	4 (8.3%)	13.9%	77.3%	3 (3.2%)	8.3%	100.0%

Table 2
Number of species per response type resulting from HOF modelling along the short and long transects, including those that responded consistently (same response type along both gradient lengths). In brackets are given the percentage of species per model type relative to the total number of modelled species.

Response type and HOF model	Short transects (48 species)	Long transects (94 species)	Consistent on both transects (41 species)
Neutral (I)	20 (41.7%)	74 (78.7%)	13
Monotonic decrease (II)	10 (20.8%)	8 (8.5%)	3
Monotonic increase (II)	1 (2.1%)	–	–
Threshold decrease (III)	3 (6.3%)	2 (2.1%)	1
Threshold increase (III)	5 (10.4%)	–	–
Symmetric unimodal (IV)	5 (10.4%)	7 (7.4%)	1
Asymmetric unimodal, right skewed (V)	3 (6.3%)	2 (2.1%)	1
Asymmetric unimodal, left skewed (V)	1 (2.1%)	1 (1.1%)	1

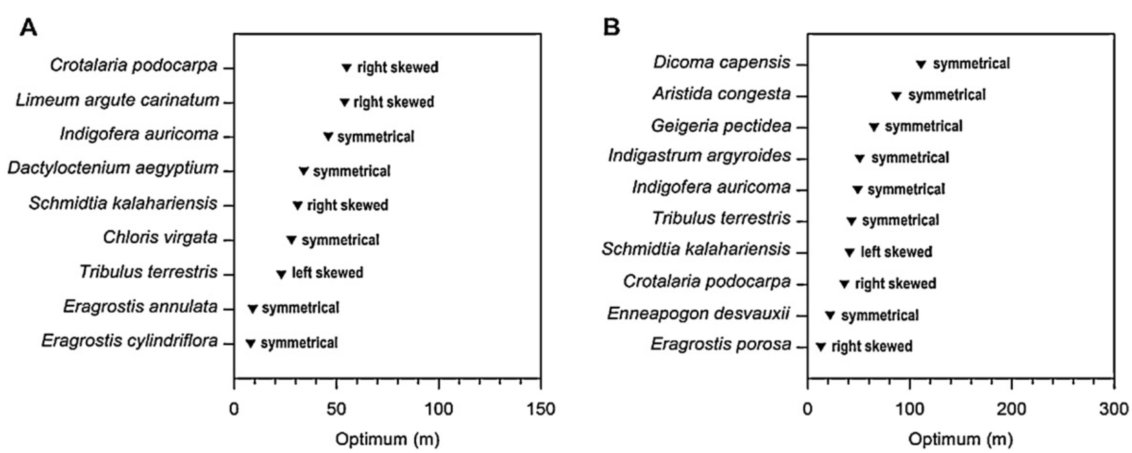


Fig. 2. Optima derived from HOF models for species with unimodal response types on short transects (A) and long transects (B). Model types are indicated as symmetric (model IV) or skewed (model V), either left skewed (abrupt changes towards lower grazing intensities) or right skewed (abrupt changes towards higher grazing intensities). The x-axis denotes distance from piosphere centre in metres (while the modelling was done for inverse distance).

species (28 species) showed a left skewed unimodal response. The response of annual plants (81 species) was similar, although the decline towards lower grazing intensity was less steep.

Along the LTs, perennials (88 species) and annuals (85 species) responded in the same way as along the STs (Fig. 6). In contrast to the ST response, the weak perennial plants (35 species) showed a threshold increase with increasing grazing intensity at the LT scale.

4. Discussion

4.1. Classification of grazing responses

Based on the results of our HOF modelling of Namibian savanna plant species, we propose a classification of their grazing responses into eight types: neutral species, monotonic increasers, monotonic decreasers, threshold increasers, threshold decreasers, symmetric unimodal species, left skewed unimodal species and right skewed unimodal species (Fig. 3).

Neutral species are those that show no grazing response, and this was the model most frequently rated best along both gradient lengths. Similarly, Landsberg et al. (2003) noticed that nearly half of the ground layer species from grazing gradients in semi-arid Australian rangelands showed no discernable pattern. In our study area, it is likely that the long grazing history and aridity together have selected for a high number of opportunistic species, since adaptations to aridity, such as low shoot:root ratios and high lignin or cellulose contents, also promote grazing resistance (Quiroga et al., 2010). The larger proportion of neutral species along the LTs compared to the STs is possibly due to their coarser scale, at which changes of grazing-related environmental variables do not have significant effects on the species turnover. However, we cannot rule out the possibility that the lower number of samples within the inner sacrifice zone, together with a relatively low minimum requirement of ten occurrences for modelling responses along the LTs, may have resulted in flattened response curves (Coudun and Gegout, 2006). Further, abiotic differences between sites and

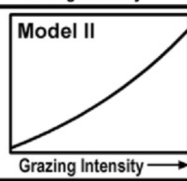
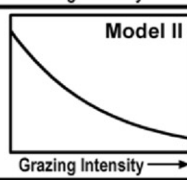
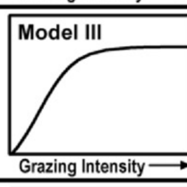
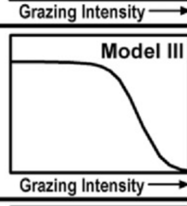
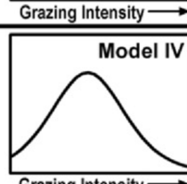
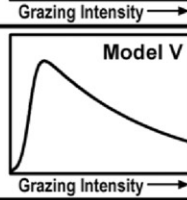
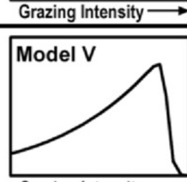
Response	Best-fitting model	Transect type	Growth form: Tree /Shrub	Growth form: Dwarf shrub	Growth form: Woody forb	Growth form: Herbaceous forb	Growth form: Grass / sedge	Life cycle: Perennial	Life cycle: Weak perennial	Life cycle: Annual	Total (*n*)
No response		Short	1		2	14	3	3	2	15	**20**
		Long	6	10	6	37	15	27	11	36	**74**
Monotonic increaser		Short					1			1	**1**
		Long									
Monotonic decreaser		Short	1	1		3	5	4	3	3	**10**
		Long	2	1			5	7		1	**8**
Threshold increaser		Short				2	3		2	3	**5**
		Long									
Threshold decreaser		Short					3	2	1		**3**
		Long	1				1	2			**2**
Symmetric unimodal		Short				1	4			5	**5**
		Long			1	4	2		4	3	**7**
Left skewed unimodal		Short				1				1	**1**
		Long					1			1	**1**
Right skewed unimodal		Short				2	1			3	**3**
		Long				1	1			2	**2**
No. of species		Short	2	1	2	23	20	9	8	31	**48**
No. of species		Long	9	11	7	42	25	36	15	43	**94**

Fig. 3. Grazing responses according to the HOF modelling of the most frequent species (48 from short transects and 94 from long transects), counted on the basis of growth form and life cycle category. The *x*-axes denote inverse distance (assumed to be proportional to grazing intensity) with the watering point at the right-hand end of the axes.

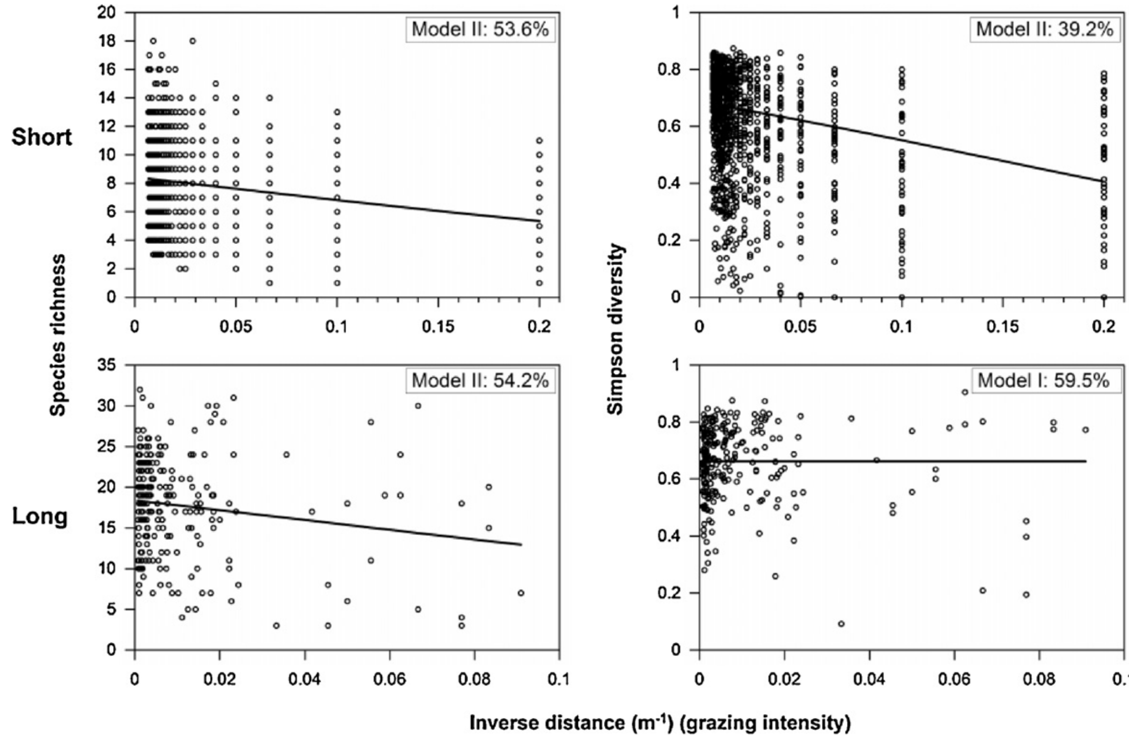


Fig. 4. HOF models for species richness and Simpson diversity index of all short transect plots (short, 1 m^2) and long transect plots (long, 100 m^2). Model type and Akaike weight (AICc) of the best-fitting model are given. The *x*-axis (inverse distance) is supposed to be proportional to grazing intensity, i.e. the watering point is at the right-hand end of the axis. Note the different scaling of the *x*-axes in the upper and lower panels.

different stocking rates were expected to bias the response patterns of some species with weak response signals leading to neutral responses because of the strict model selection framework.

Monotonic increasers refer to species that increase continuously with increasing grazing pressure, while *monotonic decreasers* react the opposite way, but with the same shape of the response curve. Monotonic responses along our gradients included almost linear, as well as, more typically, exponential curves. Decreasers outnumbered increasers, which is consistent with findings from the rangelands of the southern Nama-Karoo (Todd, 2006) and semi-arid Australia (Landsberg et al., 2003). As expected, many species showed monotonic responses (decreases) along the short gradients. Since the low-grazing end of the STs still represents a relatively high grazing pressure, it is quite probable that the monotonic shape of response curves at this scale corresponds only to one part of the total grazing response. Accordingly, some species that responded with a monotonic decrease at the ST scale showed unimodal responses at the LT scale, supporting the notion of Peppler-Lisbach and Kleyer (2009) that a high proportion of monotonic compared to unimodal responses may occur when the gradient is too short, being truncated at one end.

Threshold increasers and *threshold decreasers* exhibit strong non-linear behaviour with a plateau area of the curve, where no changes along the gradient occur, up to a breakpoint beyond which there is a more or less steep decrease. We detected more threshold responses at the ST scale due to the steep environmental gradients

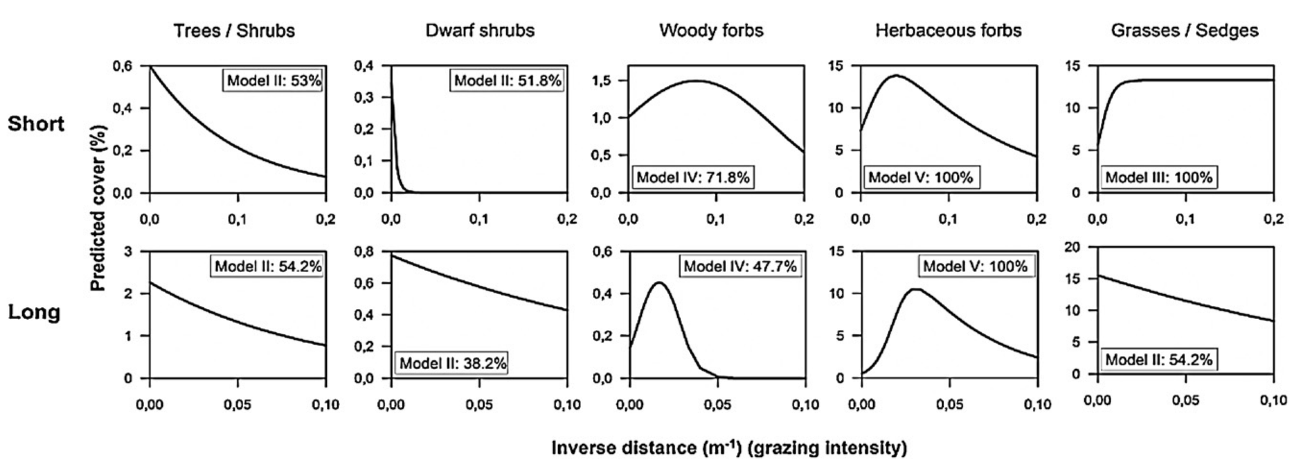


Fig. 5. HOF models for sum of cover of all plant species according to growth form categories along short and long transects. Model type and Akaike weight (AICc) of the best-fitting model are given. The *x*-axis (inverse distance) is assumed to be proportional to grazing intensity, i.e. the watering point is at the right-hand end of the axis. Note the different scaling of the *x*-axes in the upper and lower panels.

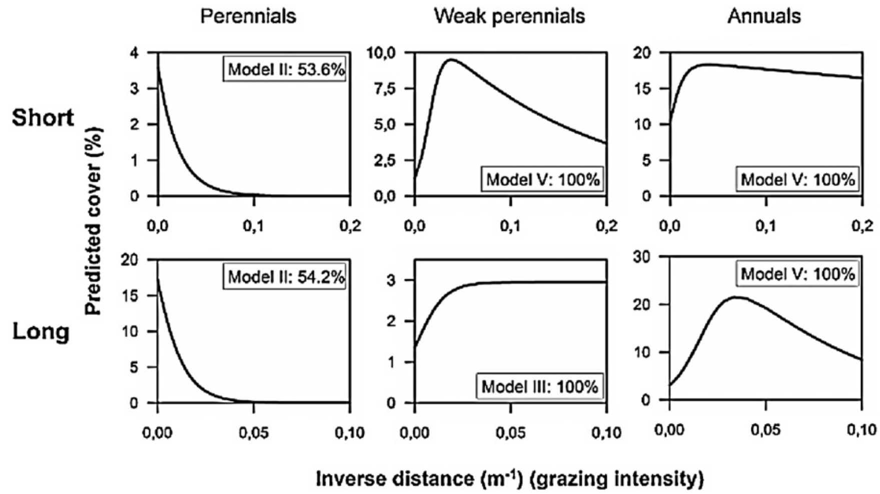


Fig. 6. HOF models for sum of cover of all plant species according to life cycle categories along short and long transects. Model type and Akaike weight (AICc) of the best-fitting model are given. The *x*-axis (inverse distance) is assumed to be proportional to grazing intensity, i.e. the watering point is at the right-hand end of the axis. Note the different scaling of the *x*-axes in the upper and lower panels.

resulting from the formation of the sacrifice zone. Sacrifice zones represent areas of extreme degradation that in normal rangelands are relatively unlikely to occur away from animal concentration points. Nevertheless, they retain distinct vegetation patterns up to decades after the abandonment of watering points, indicating the existence of different stable vegetation states. Transitions between these states appear to be revealed by a high number of threshold species in the overall species pool, although the testing for grazing-induced discontinuities might require an examination of the ratio of all niche model types present (Peper et al., 2011). However, if dominant species show thresholds, the presence of transitions between different vegetation states seems quite likely.

The differences in threshold responses between STs and LTs in our study points to the importance of detecting the relevant spatial scale at which thresholds occur (Bestelmeyer, 2006). Land managers should be aware of species that potentially indicate thresholds, such as the perennial grass *Stipagrostis uniplumis* (threshold decreaser at the ST scale). If not attributable to changes in landscape or soil conditions, the absence of this species, which is otherwise the most common (Appendix C), seems to be a certain indicator of an impoverished vegetation state (Klintenberg and Verlinden, 2008; van Rooyen et al., 1991).

Species with *unimodal response types* (HOF models IV and V) prefer neither of the extremes of the gradient. They can be subdivided into *symmetric*, *left skewed* and *right skewed unimodal species*. Three aspects of the response curve are relevant to the interpretation of their grazing response. Firstly, the position of the optimum identifies the section of the gradient at which a species finds its most suitable growing conditions with respect to competitive interactions, disturbance and resource availability. Secondly, the shape of the curve (flat vs. sharply peaking) characterises the breadth of the niche and the level of tolerance of gradient extremes. Thirdly, the direction and degree of skewness of the curve indicates a relative tolerance towards one direction of the gradient, while altered levels of disturbance (grazing intensity) or competitive interaction (Oksanen and Minchin, 2002) in the opposite direction cause more or less abrupt cover changes. Hence, as with threshold increasers/decreasers, species with skewed unimodal responses show threshold behaviour towards high or low grazing pressure, but they differ in not retaining a constant cover after passing the threshold level. Many of the unimodal species in our study were annual forb and grass species (Fig. 3, Appendix B) that are commonly known as grazing increasers in southern Africa (van Oudtshoorn, 2004; van Rooyen et al., 1991). The decline of these species towards the centre of the sacrifice zone is a sign of limited ability to tolerate extreme grazing pressure, trampling and high nutrient concentrations. Since their optima were mostly at relatively high levels of grazing intensity close to the watering point (Fig. 2), they are nevertheless useful indicators of overgrazing, representing the transitional zone between the extremely degraded and the less impacted rangeland.

4.2. Grazing responses at the community level

At both the scales considered in this study, plant diversity showed a slightly decreasing trend with increasing grazing intensity. We could not detect any intermediate level of disturbance at which diversity should peak according to the intermediate disturbance hypothesis (IDH, Grime, 1973). Instead, our results confirm the predictions of Milchunas et al. (1988) and Cingolani et al. (2005) for less productive systems with a long history of grazing, that diversity will show a constant, moderately decreasing trend. This is explained by aridity and grazing history selecting for a large number of tolerant species (Milchunas et al., 1988). Our findings concur with those of Sasaki et al. (2009) who could not corroborate the IDH under harsh environmental conditions in Mongolian rangelands, proposing that grazing was of less importance compared to other environmental factors in creating diversity.

The relatively weak diversity response along our gradients can be partly explained by the replacement patterns of growth forms and plants with different life history traits. While perennials (mostly trees, shrubs, dwarf shrubs and perennial grasses – often the most palatable species) decrease, ephemeral species such as short-lived herbs and grasses increase up to a certain grazing intensity. They only decrease in cover in the highly degraded zone. Similar patterns have been found in many other studies of semi-arid rangelands (Klintenberg and Verlinden, 2008; Landsberg et al., 2003; Perkins and Thomas, 1993; Sasaki et al., 2008; Todd, 2006). Our discovery of left-skewed unimodal responses of herbaceous forbs and annuals (Figs. 5 and 6) corresponds to the responses of some species with optima at relatively high grazing levels and thresholds towards lower levels of grazing intensity (Appendix B). They include two well-known grazing increasers: the prostrate forb *Tribulus terrestris*, and the annual grass *Schmidtia kalahariensis* (Thrash and Derry, 1999; van Rooyen et al., 1991). The decrease of these functional groups in the highly degraded zone is related to a general decline in vegetation cover (results not shown). Therefore, we interpret the unimodal response curves of individual ephemerals, and the ephemeral group as a whole (see previous section), as a grazing increaser response with "sacrifice-zone effect", i.e. a decline towards extreme animal impact.

4.3. Advances in the modelling of piospheres

The approach presented here offers at least three methodological advances in the assessment of plant responses along grazing gradients. Firstly, the hierarchical HOF modelling, and the use of species cover values instead of presence/absence data, better characterised the spectrum of different species grazing responses in semi-arid Namibian rangelands. Both continuous and discontinuous changes were identified. Furthermore, the model selection approach based on Akaike weights allows for a careful examination of best models and possible alternatives. Secondly, the modelling of species and community responses at two gradient lengths provides a detailed insight into scale-related differences in grazing responses. In our study, one of the demonstrations of this was the effect of the sacrifice zone, with a higher number of both increases/decreases and threshold responses at the ST scale. Thirdly, the use of inverse distance from the watering point as a proxy for grazing intensity compensated for the high degree of non-linearity associated with spatial gradients around piospheres (Manthey and Peper, 2010). Our modelling results are thus less biased with regard to non-linear patterns that might otherwise be misinterpreted as thresholds.

5. Conclusions

The different types of species responses to grazing exemplified here represent clear patterns of species dominance/occurrence along complex grazing gradients. The fact that some species show continuous changes along the gradients, while others exhibit thresholds, points to the complexity of semi-arid rangeland ecosystems. The scale-specific responses of some species further add to this complexity. The degree to which the specific responses found in this study occur beyond the studied region needs to be confirmed by other studies, and is likely to be influenced by local climatic and other abiotic conditions. However, the proposed set of response types generally allows for a more differentiated picture of niche patterns along grazing gradients and offers the opportunity to use species as indicators for a continuum of vegetation states. In particular, species showing peaking abundances or thresholds at certain gradient zones could be useful indicators of grazing impact levels, which in turn may determine the extent and appropriateness of management actions.

From a conservation and land management perspective, our discovery that plant diversity decreased slightly but constantly towards watering points provides an argument for the creation of high diversity grazing refuges in order to guarantee a rich local species pool. Such reserves of high species richness could be of great importance for the resilience of Namibian Nama-Karoo ecosystems, facilitating self-regeneration after droughts or periods of heavy grazing.

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Author contributions: D.W. conceived the idea for the study, which then was carried out by M.P. as a final thesis under the supervision of D.W. and J.D. Field sampling and data analysis was done by D.W. and M.P. They were assisted in modelling by F.J., S.S. and J.O. The article was written by D.W., M.P. and J.D., and all authors contributed to its revision.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2012.11.008.

References

Andrew, M.H., 1988. Grazing impact in relation to livestock watering points. Trends Ecol. Evol. 3, 336–339.

Barnard, A., 1992. Hunters and Herders of Southern Africa — A Comparative Ethnography of the Khoisan Peoples. Cambridge University Press, Cambridge.

Bestelmeyer, B.T., 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. Restor. Ecol. 14, 325–329.

Bestelmeyer, B.T., Goolsby, D.P., Archer, S.R., 2011. Spatial perspectives in state-and-transition models: a missing link to land management? J. Appl. Ecol. 48, 746–757.

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. J. Appl. Ecol. 40, 601–614.

Burnham, K., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer, New York.

Cingolani, A.M., Noy-Meir, I., Diaz, S., 2005. Grazing effects on rangeland diversity: A synthesis of contemporary models. Ecol. Appl. 15, 757–773.

Coudun, C., Gegout, J., 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. Ecol. Model. 199, 164–175.

Dyksterhuis, E.J., 1949. Condition and management of range land based on quantitative ecology. J. Range Manage. 2, 104–115.

Ellis, J.E., Swift, D.M., 1988. Stability of African pastoral ecosystems – alternate paradigms and implications for development. J. Range Manage. 41, 450–459.

Fernandez-Gimenez, M.E., Allen-Diaz, B., 1999. Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. J. Appl. Ecol. 36, 871–885.

Fernandez-Gimenez, M., Allen-Diaz, B., 2001. Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. Plant Ecol. 157, 101–118.

Germishuizen, G., Meyer, N. (Eds.), 2003. Plants of Southern Africa: An Annotated Checklist. National Botanical Institute, Pretoria.

Gillson, L., Hoffman, M.T., 2007. Rangeland ecology in a changing world. Science 315, 53–54.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.

Huisman, J., Olff, H., Fresco, L.F.M., 1993. A hierarchical set of models for species response analysis. J. Veg. Sci. 4, 37–46.

Jansen, F., 2008. Shape of species resonses: Huisman–Olff–Fresco models revisited. In: Mucina, L., Kalwij, J.M., Smith, V.R. (Eds.), Frontiers of Vegetation Science – An Evolutionary Angle. Keith Phillips Images, Somerset West, South Africa, pp. 80–81.

Jürgens, N., Haarmeyer, D.H., Luther-Mosebach, J., Dengler, J., Finckh, M., Schmiedel, U. (Eds.), 2010. Biodiversity in Southern Africa. Volume 1: Patterns at Local Scale – The BIOTA Observatories. Klaus Hess Publishers, Göttingen, Windhoek.

Klintenberg, P., Verlinden, A., 2008. Water points and their influence on grazing resources in central northern Namibia. Land Degrad. Dev. 19, 1–20.

Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J., Tynan, R., 2002. Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. J. Appl. Ecol. 39, 427–444.

Landsberg, J., James, C.D., Morton, S.R., Müller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. J. Appl. Ecol. 40, 1008–1024.

Lange, R.T., 1969. The piosphere: sheep track and dung patterns. J. Range Manage. 22, 396–400.

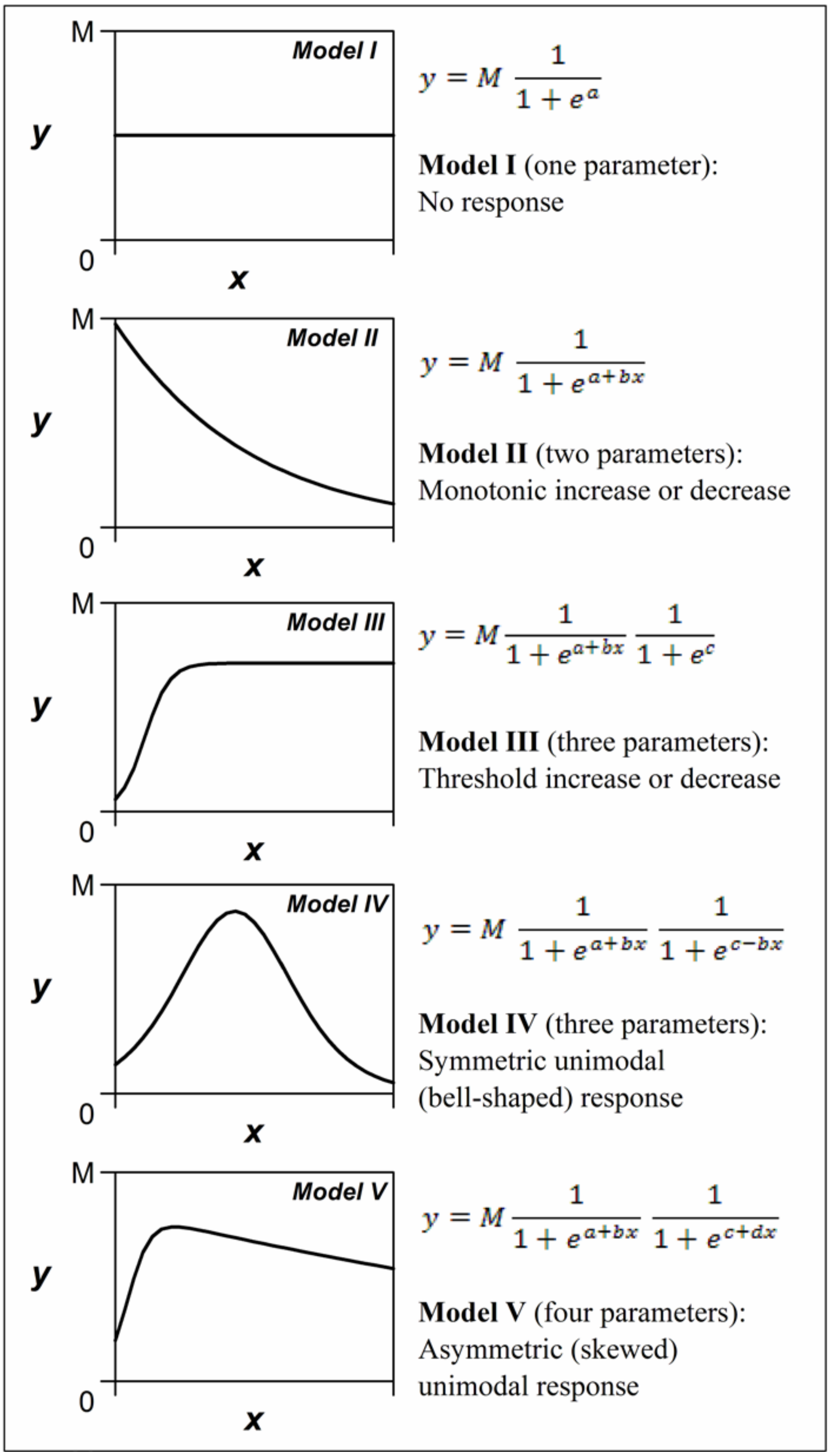
Magurran, A., 2004. Measuring Biological Diversity. Blackwell, Malden, MA.

Manthey, M., Peper, J., 2010. Estimation of grazing intensity along grazing gradients – the bias of nonlinearity. J. Arid Environ. 74, 1351–1354.

Mendelsohn, J., Jarvis, A., Roberts, C., Robertson, T., 2002. Atlas of Namibia. David Philip Publishers, Cape Town.

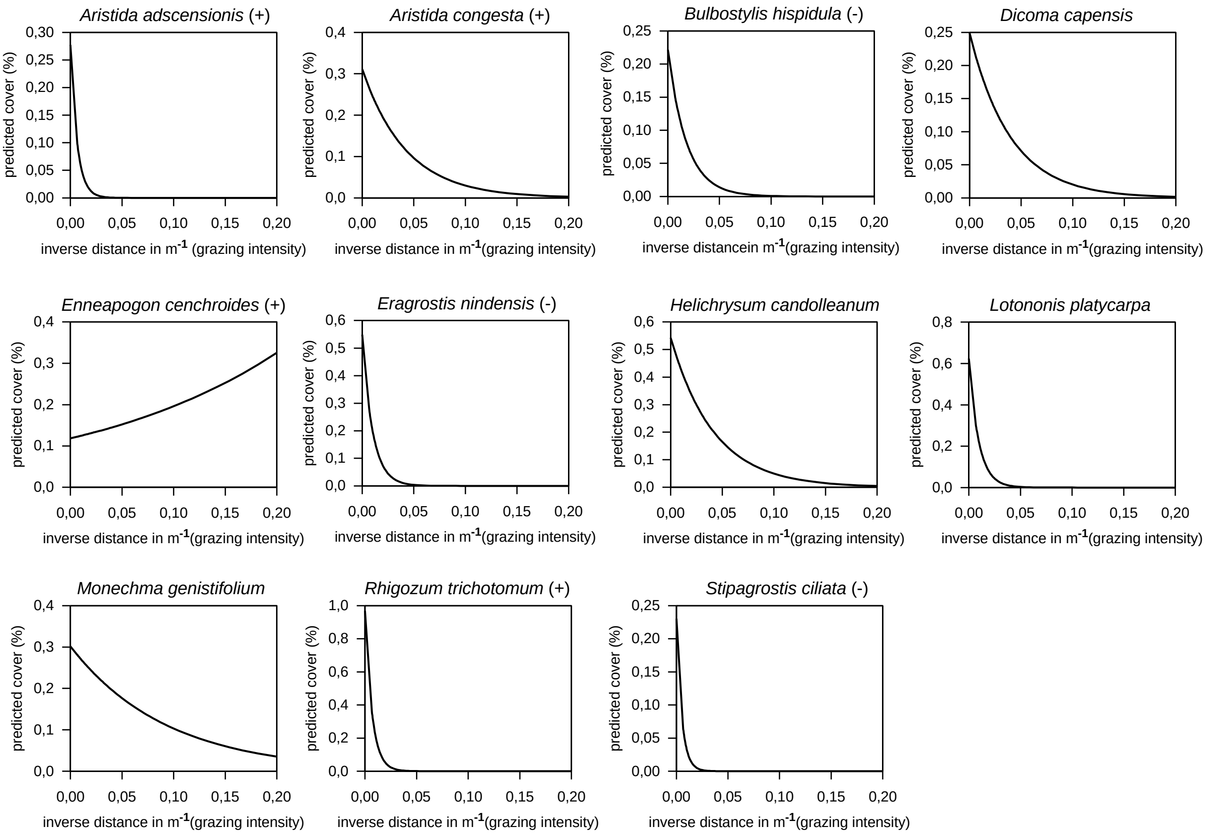
Miehe, S., Kluge, J., Von Wehrden, H., Retzer, V., 2010. Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. J. Appl. Ecol. 47, 692–700.
Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. Am. Nat. 132, 87–106.
Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. J. Ecol. 77, 290–310.
Oksanen, J., Minchin, P.R., 2002. Continuum theory revisited: what shape are species responses along ecological gradients? Ecol. Model. 157, 119–129.
Owen-Smith, N., Danckwerts, J.E., 1997. Herbivory. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, pp. 397–420.
Peper, J., Jansen, F., Pietzsch, D., Manthey, M., 2011. Patterns of plant species turnover along grazing gradients. J. Veg. Sci. 22, 457–466.
Peppler-Lisbach, C., 2008. Using species-environmental amplitudes to predict pH values from vegetation. J. Veg. Sci. 19, 437–444.
Peppler-Lisbach, C., Kleyer, M., 2009. Patterns of species richness and turnover along the pH gradient in deciduous forests: testing the continuum hypothesis. J. Veg. Sci. 20, 984–995.
Perkins, J.S., Thomas, D.S.G., 1993. Environmental responses and sensitivity to permanent cattle ranching semi-arid western Central Botswana. In: Thomas, D.S.G., Allison, R.J. (Eds.), Landscape Sensitivity. Wiley, Chichester, pp. 273–286.
Quiroga, R.E., Golluscio, R.A., Blanco, L.J., Fernandez, R.J., 2010. Aridity and grazing as convergent selective forces: an experiment with an Arid Chaco bunchgrass. Ecol. Appl. 20, 1876–1889.
R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rutherford, M., Westfall, R.H., 1994. Biomes of Southern Africa: An Objective Categorization. National Botanical Institute, Pretoria.
Sasaki, T., Okayasu, T., Jamsran, U., Takeuchi, K., 2008. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. J. Ecol. 96, 145–154.
Sasaki, T., Okubo, S., Okayasu, T., Jamsran, U., Ohkuro, T., Takeuchi, K., 2009. Management applicability of the intermediate disturbance hypothesis across Mongolian rangeland ecosystems. Ecol. Appl. 19, 423–432.
Sasaki, T., Okubo, S., Okayasu, T., Jamsran, U., Ohkuro, T., Takeuchi, K., 2011. Indicator species and functional groups as predictors of proximity to ecological thresholds in Mongolian rangelands. Plant Ecol. 212, 327–342.
Suchrow, S., Jensen, K., 2010. Plant species responses to an elevational gradient in German North Sea salt marshes. Wetlands 30, 735–746.
Thrash, I., Derry, J.F., 1999. The nature and modelling of piospheres: a review. Koedoe 42, 73–94.
Todd, S.W., 2006. Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. J. Appl. Ecol. 43, 293–304.
Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecol. 142, 169–178.
Trollope, W.S.W., 1990. Development of a technique for assessing veld condition in the Kruger National Park using key grass species. Journal of the Grassland Society of Southern Africa 7, 46–51.
Uğurlu, E., Oldeland, J., 2012. Species response curves of oak species along climatic gradients in Turkey. Int. J. Biometeorol. 56, 85–93.
van Oudtshoorn, F., 2004. Guide to Grasses of Southern Africa. Briza Publications, Pretoria South Africa.
van Rooyen, N., Bredenkamp, G.J., Theron, G.K., 1991. Kalahari vegetation: veld condition trends and ecological status of species. Koedoe 34, 61–72.
Vesk, P.A., Westoby, M., 2001. Predicting plant species' responses to grazing. J. Appl. Ecol. 38, 897–909.
Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42, 266–274.
Wesuls, D., Oldeland, J., Dray, S., 2012. Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. J. Veg. Sci. 23, 98–113.

Appendix A: HOF-models according to Huisman *et al.* (1993). The predicted cover of a species (y) is modelled along an environmental gradient (x) taking the maximum cover (M) and parameters (a, b, c, d) according to each HOF-model type.

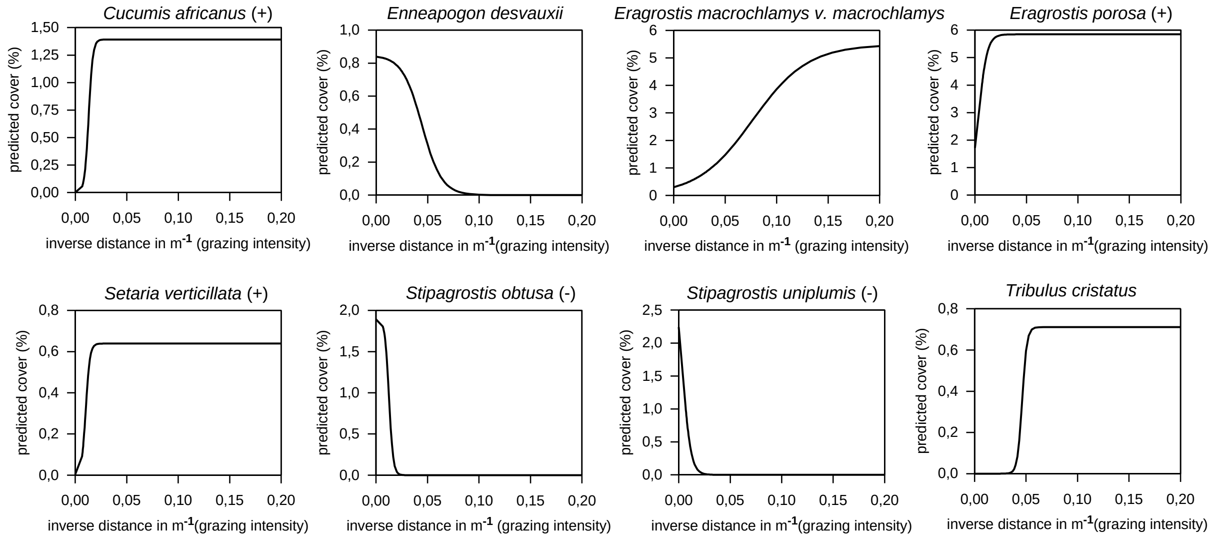


Appendix B: Figures of best HOF models according to Akaike weights for species with non-neutral grazing responses (HOF models II-V) recorded along short and long transects along watering points gradients in central Namibian rangelands. The x-axes display inverse distance (in m^{-1}), i.e. the watering point is at the right-hand end of the axes. The y-axes show percentage cover predicted by the respective model. If literature data for species' grazing responses were available, (-) indicates if the species is known as a grazing decreaser or the species indicates rangeland in good condition, and (+) if a decreasing grazing response or occurrence of that species under poor rangeland conditions was reported (Trollope 1989, Van Rooyen et al. 1991, 1994, Strohbach 2000, Van Oudtshoorn 2004, Getzin 2005, Müller 2007, Zimmermann 2009). If no data were available or information from literature was inconsistent for the respective species, a sign behind species name is missing.

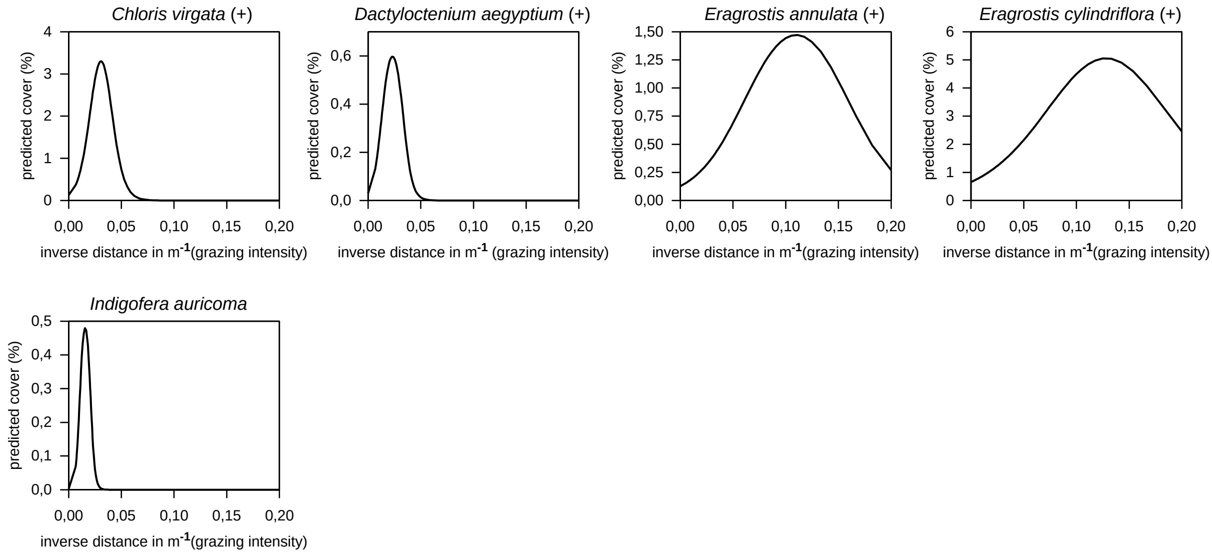
Short transects Model II



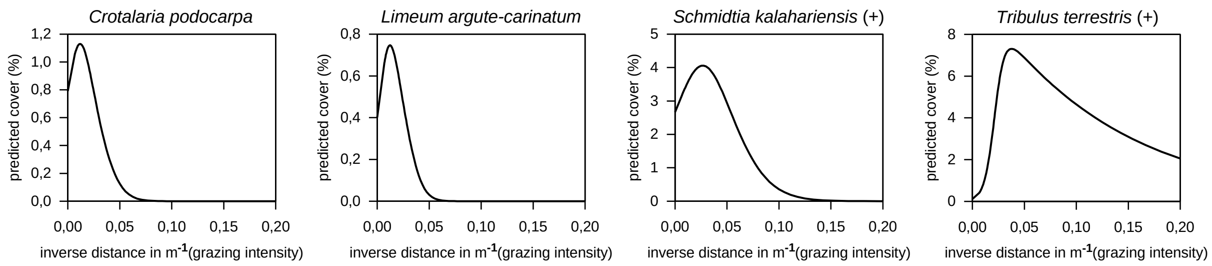
Short transects Model III



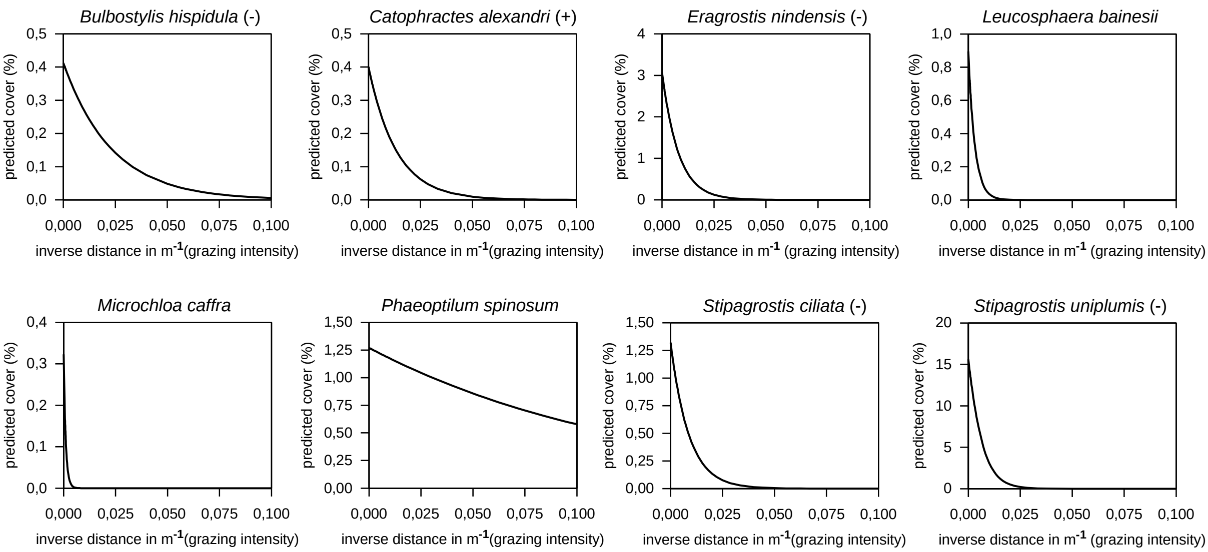
Short transects Model IV



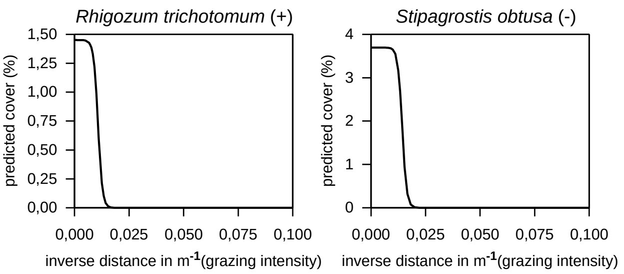
Short transects Model V



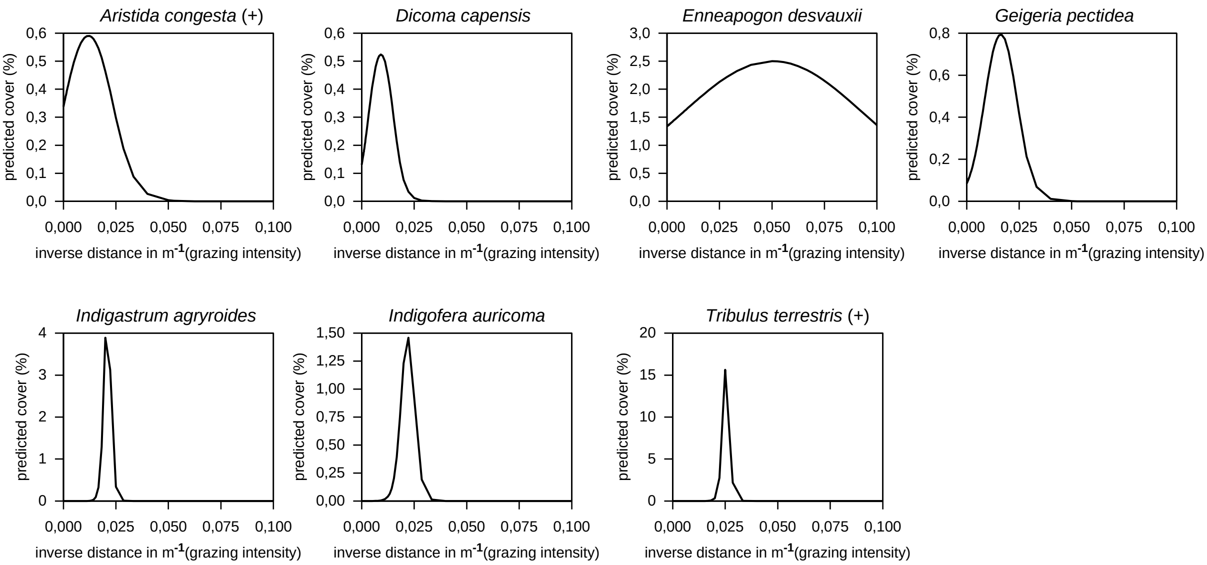
Long transects Model II



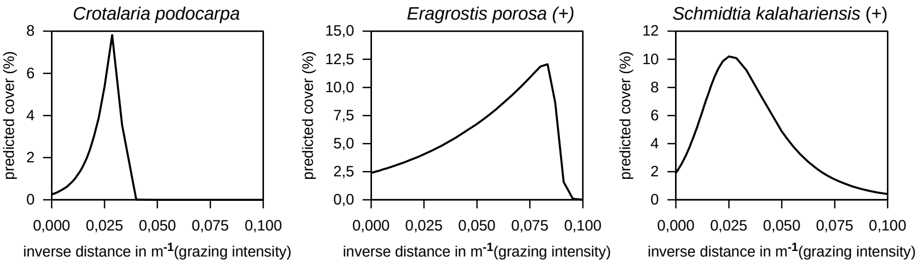
Long transects Model III



Long transects Model IV



Long transects Model V



References for species grazing responses

Getzin, S. 2005. The suitability of the degradation gradient method in arid Namibia. African Journal of Ecology 43:340–351.

Müller, M. A. N. 2007. Grasses of Namibia, revised edition. Ministry of Agriculture, Water and Forestry, Windhoek, Namibia.

Van Oudtshoorn, F. 2004. Guide to Grasses of Southern Africa, 2nd edition. Briza Publications, Pretoria, South Africa.

Van Rooyen, N., G. J. Bredenkamp, and G. K. Theron. 1991. Kalahari vegetation: veld condition trends and ecological status of species. Koedoe 34:61–72.

Van Rooyen, N., G. J. Bredenkamp, G. K. Theron, J. D. Bothma, and E. A. N. Leriche. 1994. Vegetational Gradients Around Artificial Watering Points in the Kalahari-Gemsbok-National-Park. Journal of Arid Environments 26:349–361.

Strohbach, B. J. 2000. Vegetation degradation trends in the northern Oshikoto Region: IV. The Broad-leafed savannas with associated pans. Dinteria 26:93–112.

Trollope, W. S. W. 1989. Assessing veld condition in the Kruger National Park using key grass species. Koedoe 32:67–93.

Zimmermann, I. 2009. Causes and consequences of fenceline contrasts in Namibian rangeland. PhD thesis, University of the Free State, Bloemfontein, South Africa.

Appendix C: List of recorded species along short and long piosphere transects in central Namibian rangelands. Growth form (GF) and life cycle (LC) are listed for all species. Growth forms: grass/sedge (grass), herbaceous forb (forb), woody forb (wforb), dwarf shrub (dwarf), tree (tree), shrub (shrub). Life cycles: annual (ann), perennial (per) and weak perennial (wper). Number of occurrences (No.Occ.), percentage of occurrences (%Occ.) Maximum cover (Max.Cov) in % and Mean cover (MeanCov.) in % of 1025 short transect plots and 244 long transect plots are listed.

Species	Traits		Short transects				Long transects			
	GF	LC	No.Occ.	%Occ.	Max.Cov.	MeanCov.	No.Occ.	%Occ.	Max.Cov.	MeanCov.
Acacia erioloba	tree	per	38	3.7	4	0.4	33	13.5	4	0.7
Acacia fleckii	shrub	per	1	0.1	0.1	0.1	1	0.4	0.1	0.1
Acacia hebeclada	shrub	per	16	1.6	35	5.4	20	8.2	8	1.7
Acacia mellifera	shrub	per	13	1.3	30	8.0	40	16.4	10	1.9
Acanthosicyos naudinianus	forb	per					1	0.4	0.1	0.1
Achyranthes aspera var. *sicula*	forb	ann	3	0.3	15	5.2				
Acrotome fleckii	forb	ann	12	1.2	0.5	0.1	7	2.9	0.1	0.1
Acrotome inflata	forb	ann	88	8.6	10	1.0	3	1.2	1	0.4
Aizoon asbestinum	dwarf	per	5	0.5	1	0.5	10	4.1	0.1	0.1
Aizoon schellenbergii	dwarf	per	14	1.4	4	2.1	24	9.8	2	0.5
Alternanthera pungens	forb	ann	20	2.0	5	0.9	7	2.9	5	1.1
Amaranthus praetermissus	forb	ann	28	2.7	2	0.3	19	7.8	0.5	0.1
Anthephora schinzii	grass	ann	1	0.1	0.5	0.5				
Aptosimum albomarginatum	dwarf	per	13	1.3	4	1.5	49	20.1	3	0.6
Aptosimum arenarium	wforb	per					4	1.6	0.1	0.1
Aptosimum lineare	wforb	per	41	4.0	2	0.4	8	3.3	0.1	0.1
Aptosimum sp.	wforb	per	31	3.0	1	0.2	22	9.0	0.5	0.1
Aptosimum spinescens	dwarf	per	19	1.9	9	1.5	77	31.6	4	0.5
Argemone ochroleuca	forb	ann	1	0.1	0.1	0.1				
Aristida adscensionis	grass	ann	101	9.9	7	1.0	60	24.6	7	1.0
Aristida congesta	grass	wper	169	16.5	5	1.3	93	38.1	6	1.1
Aristida meridionalis	grass	per	11	1.1	1	0.5	15	6.1	4	0.6
Asparagus sp.	shrub	per					3	1.2	0.1	0.1
Barleria rigida	dwarf	per	1	0.1	0.5	0.5	16	6.6	0.5	0.1
Bidens pilosa	forb	ann	1	0.1	0.5	0.5				
Blepharis leenderitziae	wforb	per	1	0.1	1	1.0				
Blepharis mitrata	wforb	per	16	1.6	0.1	0.1	28	11.5	0.5	0.2
Boscia albitrunca	tree	per					13	5.3	2	0.3
Boscia foetida	shrub	per	3	0.3	7	3.0	8	3.3	1	0.8
Bulbostylis densa	grass	ann	1	0.1	0.1	0.1				
Bulbostylis hispidula	grass	ann	220	21.5	4	0.6	57	23.4	5	1.3
Cadaba aphylla	shrub	per					2	0.8	0.5	0.3
Catophractes alexandri	shrub	per	6	0.6	6	1.8	49	20.1	4	1.3
Cenchrus ciliaris	grass	per	15	1.5	8	2.3	19	7.8	1	0.2
Chascanum pinnatifidum	forb	per	3	0.3	0.1	0.1	28	11.5	2	0.3
Chenopodium amboanum	forb	ann	2	0.2	0.1	0.1	1	0.4	0.1	0.1

Species	Traits		Short transects				Long transects			
	GF	LC	No.Occ.	%Occ.	Max.Cov.	MeanCov.	No.Occ.	%Occ.	Max.Cov.	MeanCov.
Chenopodium pumilio	forb	ann	18	1.8	7	0.8	1	0.4	0.1	0.1
Chloris virgata	grass	ann	151	14.7	50	5.3	21	8.6	1	0.2
Citrullus lanatus	forb	ann	39	3.8	30	5.0	19	7.8	20	2.3
Cleome angustifolia	forb	ann	1	0.1	0.1	0.1	10	4.1	2	0.5
Cleome elegantissima	forb	ann					1	0.4	0.1	0.1
Cleome gynandra	forb	ann	31	3.0	30	2.1	16	6.6	1	0.2
Cleome rubella	forb	ann	12	1.2	3	0.4	30	12.3	0.1	0.1
Cleome suffruticosa	forb	ann					1	0.4	0.1	0.1
Coccinia rehmannii	forb	per					2	0.8	0.1	0.1
Commicarpus pentandrus	forb	wper	14	1.4	1	0.5	7	2.9	0.1	0.1
Convolvulus argillicola	forb	wper					1	0.4	0.1	0.1
Corallocarpus welwitschii	forb	wper					1	0.4	0.1	0.1
Corchorus asplenifolius	forb	ann	5	0.5	0.1	0.1	4	1.6	0.1	0.1
Crinum sp.	forb	per					1	0.4	0.1	0.1
Crotalaria argyraea	wforb	per	2	0.2	0.1	0.1	3	1.2	0.5	0.2
Crotalaria dinteri	forb	per					1	0.4	0.1	0.1
Crotalaria heidmannii	forb	ann	3	0.3	0.1	0.1	4	1.6	0.1	0.1
Crotalaria podocarpa	forb	ann	148	14.4	25	5.7	46	18.9	20	4.2
Cucumis africanus	forb	wper	109	10.6	40	3.8	63	25.8	6	0.5
Cucumis anguria	forb	ann	2	0.2	0.1	0.1	2	0.8	0.1	0.1
Cullen obtusifolia	forb	ann	4	0.4	1	0.4				
Dactyliandra welwitschii	forb	ann	1	0.1	3	3.0	11	4.5	1	0.3
Dactyloctenium aegyptium	grass	ann	69	6.7	25	1.8	4	1.6	1	0.3
Datura sp.	dwarf	ann					1	0.4	0.1	0.1
Dicoma capensis	forb	wper	180	17.6	10	1.0	156	63.9	5	0.4
Dicoma schinzii	wforb	wper					2	0.8	0.1	0.1
Ehretia rigida	shrub	per					1	0.4	0.1	0.1
Enneapogon cenchroides	grass	ann	173	16.9	8	0.8	63	25.8	4	0.5
Enneapogon desvauxii	grass	wper	277	27.0	20	2.6	77	31.6	20	5.0
Entoplocamia aristulata	grass	wper	35	3.4	1	0.2	43	17.6	1	0.2
Eragrostis annulata	grass	ann	216	21.1	20	1.4	47	19.3	20	2.0
Eragrostis biflora	grass	ann					2	0.8	0.1	0.1
Eragrostis cylindriflora	grass	ann	137	13.4	60	8.8	9	3.7	40	7.7
Eragrostis echinochloidea	grass	wper	61	6.0	5	0.5	30	12.3	10	1.2
Eragrostis macrochlamys var. *macrochlamys*	grass	ann	123	12.0	30	4.6	3	1.2	6	2.7
Eragrostis nindensis	grass	per	143	14.0	10	1.6	102	41.8	15	4.1
Eragrostis pilgeriana	grass	ann	1	0.1	0.1	0.1				
Eragrostis porosa	grass	ann	738	72.0	80	6.0	141	57.8	60	5.4
Eragrostis rotifer	grass	per	19	1.9	3	0.6	1	0.4	0.1	0.1
Eragrostis sp.	grass	per	9	0.9	2	0.5	6	2.5	0.5	0.2
Eragrostis trichophora	grass	wper	1	0.1	0.5	0.5	16	6.6	3	0.4
Eragrostis viscosa	grass	ann					2	0.8	0.1	0.1

Species	Traits		Short transects				Long transects			
	GF	**LC**	**No.Occ.**	**%Occ.**	**Max.Cov.**	**MeanCov.**	**No.Occ.**	**%Occ.**	**Max.Cov.**	**MeanCov.**
Eriocephalus luederitzianus	dwarf	per					21	8.6	2	0.5
Eriospermum abyssinicum	forb	per	2	0.2	0.1	0.1	4	1.6	0.1	0.1
Erucastrum arabicum	forb	ann	20	2.0	8	2.3				
Euphorbia glanduligera	forb	ann	2	0.2	0.1	0.1	9	3.7	0.1	0.1
Euphorbia inaequilatera	forb	ann	32	3.1	1	0.1	18	7.4	0.1	0.1
Evolvulus alsinoides	forb	ann					1	0.4	0.1	0.1
Felicia clavipilosa	wforb	per	1	0.1	0.1	0.1	8	3.3	0.1	0.1
Felicia smaragdina	forb	ann	112	10.9	2	0.2	40	16.4	1	0.2
Fingerhuthia africana	grass	per					2	0.8	0.1	0.1
Galenia africana	shrub	per	5	0.5	1	0.3	7	2.9	2	0.9
Geigeria acaulis	forb	ann	18	1.8	1	0.2	23	9.4	1	0.2
Geigeria ornativa	forb	ann	35	3.4	2	0.3	25	10.2	0.5	0.1
Geigeria pectidea	wforb	wper	117	11.4	2	0.3	74	30.3	9	1.0
Gisekia africana	forb	ann	133	13.0	5	0.4	48	19.7	2	0.2
Grewia flava	shrub	per					8	3.3	2	1.2
Harpagophytum procumbens	wforb	per					6	2.5	1	0.4
Helichrysum candolleanum	forb	wper	382	37.3	15	1.0	111	45.5	10	0.6
Heliotropium ciliatum	forb	per					3	1.2	0.1	0.1
Heliotropium steudneri	wforb	per					1	0.4	0.1	0.1
Hermannia affinis	dwarf	per	5	0.5	2	0.8	24	9.8	1	0.2
Hermannia argillicola	forb	ann					6	2.5	0.1	0.1
Hermannia modesta	forb	ann	97	9.5	3	0.2	43	17.6	0.1	0.1
Hermannia rautanenii	wforb	per					1	0.4	0.1	0.1
Hermannia tomentosa	forb	per					8	3.3	0.1	0.1
Hermbstaedtia linearis	forb	ann	3	0.3	0.5	0.2	1	0.4	0.1	0.1
Hermbstaedtia odorata	forb	per					1	0.4	0.1	0.1
Hibiscus fleckii	forb	per					1	0.4	0.1	0.1
Hirpicium gazanioides	forb	ann	55	5.4	1	0.3	47	19.3	2	0.2
Hypertelis bowkeriana	forb	ann	4	0.4	0.1	0.1	2	0.8	0.1	0.1
Indigastrum argyroides	forb	ann	108	10.5	6	0.9	22	9.0	30	2.8
Indigastrum parviflorum	forb	ann	78	7.6	5	0.6	31	12.7	1	0.2
Indigofera alternans	forb	per	4	0.4	1	0.5	14	5.7	10	1.0
Indigofera auricoma	forb	ann	165	16.1	15	0.9	57	23.4	10	0.8
Indigofera charlieriana	forb	ann					2	0.8	0.1	0.1
Indigofera holubii	forb	ann	57	5.6	15	1.4	10	4.1	0.5	0.3
Indigofera vicioides	forb	per	59	5.8	2	0.3	60	24.6	0.5	0.1
Ipomoea bolusiana	forb	per					2	0.8	0.1	0.1
Ipomoea sinensis	forb	ann	24	2.3	4	0.5	3	1.2	0.5	0.2
Jamesbrittenia canescens var. *seineri*	dwarf	per					1	0.4	0.1	0.1
Kleinia longiflora	dwarf	per					2	0.8	0.1	0.1
Kohautia caespitosa	forb	ann	25	2.4	1	0.2	37	15.2	0.1	0.1
Kohautia cf. *azurea*	forb	ann					3	1.2	0.5	0.2

Species	**Traits**		**Short transects**				**Long transects**			
	GF	**LC**	**No.Occ.**	**%Occ.**	**Max.Cov.**	**MeanCov.**	**No.Occ.**	**%Occ.**	**Max.Cov.**	**MeanCov.**
Kyllinga alba	grass	per	12	1.2	2	0.9	48	19.7	0.5	0.2
Kyphocarpa angustifolia	forb	ann					1	0.4	0.1	0.1
Laggera decurrens	wforb	wper	5	0.5	5	1.2	15	6.1	0.5	0.2
Ledebouria sp.	forb	per					3	1.2	0.1	0.1
Leucas pechuelii	forb	ann					3	1.2	0.5	0.2
Leucosphaera bainesii	dwarf	per	10	1.0	20	4.5	36	14.8	11	2.3
Limeum aethiopicum	wforb	wper	2	0.2	0.5	0.3	9	3.7	0.1	0.1
Limeum argute-carinatum	forb	ann	322	31.4	15	1.6	62	25.4	4	0.4
Limeum fenestratum	forb	ann	15	1.5	0.5	0.2	6	2.5	0.1	0.1
Limeum myosotis	forb	ann	75	7.3	6	1.0	32	13.1	4	0.6
Limeum pterocarpum	forb	ann	9	0.9	0.5	0.2	9	3.7	0.1	0.1
Limeum sulcatum	forb	ann					2	0.8	0.1	0.1
Lophiocarpus tenuissimus	wforb	wper					1	0.4	0.1	0.1
Lotononis platycarpa	forb	ann	194	18.9	25	1.3	66	27.0	4	0.5
Lycium eenii	shrub	per	5	0.5	4	1.6	36	14.8	2	0.8
Lycium hirsutum	shrub	per	1	0.1	3	3.0				
Lycium oxycarpum	shrub	per	7	0.7	25	8.3	25	10.2	8	1.7
Melhania virescens	wforb	wper	12	1.2	0.5	0.1	4	1.6	0.1	0.1
Melinis repens	grass	ann	13	1.3	5	0.8	15	6.1	0.1	0.1
Melolobium adenodes	dwarf	wper					6	2.5	0.1	0.1
Melolobium microphyllum	dwarf	wper	15	1.5	2	0.4	3	1.2	0.1	0.1
Microchloa caffra	grass	per	14	1.4	1	0.3	28	11.5	8	0.5
Mollugo cerviana	forb	ann	41	4.0	0.1	0.1	9	3.7	0.1	0.1
Monechma divaricatum	wforb	wper	3	0.3	0.5	0.2	7	2.9	0.1	0.1
Monechma genistifolium	dwarf	per	59	5.8	25	4.3	46	18.9	10	2.3
Monechma spartioides	wforb	wper	3	0.3	0.1	0.1	1	0.4	0.1	0.1
Monelytrum luederitzianum	grass	per					1	0.4	0.1	0.1
Monsonia angustifolia	forb	ann					1	0.4	1	1.0
Monsonia senegalensis	forb	ann	1	0.1	3	3.0	10	4.1	0.5	0.1
Monsonia umbellata	forb	ann	29	2.8	3	0.6	30	12.3	3	0.6
Nelsia quadrangula	forb	ann	9	0.9	2	0.4	10	4.1	0.1	0.1
Nidorella resedifolia	forb	ann	8	0.8	2	0.4	37	15.2	0.5	0.1
Nymania capensis	shrub	per	1	0.1	0.1	0.1	1	0.4	0.1	0.1
Ocimum americanum var. *americanum*	dwarf	wper	7	0.7	0.5	0.3	25	10.2	3	0.5
Ondetia linearis	forb	ann	7	0.7	0.5	0.2	16	6.6	2	0.4
Oropetium capense	grass	per	6	0.6	0.1	0.1	8	3.3	0.5	0.2
Osteospermum muricatum subsp. *muricatum*	forb	ann	7	0.7	3	0.5	1	0.4	0.1	0.1
Otoptera burchellii	wforb	per					2	0.8	0.1	0.1
Oxygonum alatum	forb	ann	1	0.1	0.1	0.1				
Panicum arbusculum	grass	per	1	0.1	3	3.0	1	0.4	0.1	0.1
Panicum lanipes	grass	per					1	0.4	0.1	0.1
Parkinsonia africana	shrub	per					2	0.8	0.1	0.1

Species	Traits		Short transects				Long transects			
	GF	LC	No.Occ.	%Occ.	Max.Cov.	MeanCov.	No.Occ.	%Occ.	Max.Cov.	MeanCov.
Pavonia burchellii	wforb	wper	1	0.1	0.1	0.1	5	2.0	0.5	0.2
Pegolettia pinnatilobata	wforb	wper	2	0.2	0.5	0.3				
Pegolettia senegalensis	forb	ann	41	4.0	1	0.2	2	0.8	0.1	0.1
Pelargonium leucophyllum	forb	wper					1	0.4	0.1	0.1
Peliostomum leucorrhizum	wforb	wper	5	0.5	0.1	0.1	14	5.7	0.1	0.1
Pentarrhinum insipidum	forb	per					2	0.8	0.1	0.1
Pentzia calva	dwarf	per	6	0.6	6	2.1	10	4.1	0.5	0.2
Pergularia daemia	forb	per					1	0.4	0.1	0.1
Phaeoptilum spinosum	shrub	per	41	4.0	40	8.1	122	50.0	10	2.4
Phyllanthus maderaspatensis	wforb	wper	1	0.1	0.1	0.1	1	0.4	0.1	0.1
Phyllanthus pentandrus	wforb	per	1	0.1	0.1	0.1				
Platycarpha carlinoides	forb	per	12	1.2	3	0.8	20	8.2	0.5	0.1
Pogonarthria fleckii	grass	ann	113	11.0	10	0.7	30	12.3	1	0.3
Pollichia campestris	dwarf	per					6	2.5	0.5	0.2
Polygala leptophylla	wforb	wper	5	0.5	0.1	0.1	5	2.0	0.1	0.1
Pseudogaltonia clavata	forb	per	7	0.7	2	1.2	25	10.2	1	0.5
Pteronia mucronata	dwarf	per	1	0.1	4	4.0				
Ptycholobium biflorum	wforb	wper	7	0.7	1	0.4	8	3.3	0.1	0.1
Pupalia lappacea	forb	ann					1	0.4	0.5	0.5
Requienia sphaerosperma	forb	per					3	1.2	0.5	0.2
Rhigozum trichotomum	shrub	per	69	6.7	30	5.2	100	41.0	10	2.7
Schkuhria pinnata	forb	ann	15	1.5	15	1.9				
Schmidtia kalahariensis	grass	ann	627	61.2	40	5.0	170	69.7	40	5.4
Schmidtia pappophoroides	grass	per					8	3.3	1	0.2
Seddera suffruticosa	forb	per					2	0.8	0.1	0.1
Selago dinteri	forb	per					1	0.4	0.1	0.1
Senecio consanguineus	forb	ann	60	5.9	7	0.7	26	10.7	1	0.2
Senna italica	wforb	per					2	0.8	0.1	0.1
Sericorema sericea	forb	ann	18	1.8	2	0.6	12	4.9	0.5	0.1
Sesamum triphyllum	forb	ann	87	8.5	2	0.3	60	24.6	0.5	0.1
Setaria verticillata	grass	ann	70	6.8	55	4.4	16	6.6	5	0.9
Sida ovata	wforb	wper	6	0.6	0.5	0.2	13	5.3	0.5	0.2
Solanum capense	dwarf	per	4	0.4	4	2.1	5	2.0	1	0.4
Solanum delagoense	wforb	per					2	0.8	0.1	0.1
Sporobolus nervosus	grass	per					4	1.6	0.1	0.1
Stipagrostis anomala	grass	wper					1	0.4	0.1	0.1
Stipagrostis ciliata	grass	per	40	3.9	8	1.9	63	25.8	20	2.9
Stipagrostis hirtigluma	grass	wper	1	0.1	0.1	0.1	5	2.0	0.1	0.1
Stipagrostis hochstetteriana	grass	per	10	1.0	4	1.4	21	8.6	8	1.1
Stipagrostis obtusa	grass	per	154	15.0	60	4.9	57	23.4	30	12.6
Stipagrostis uniplumis	grass	per	308	30.0	50	2.8	199	81.6	50	10.1
Tagetes minuta	forb	ann	9	0.9	5	0.7	1	0.4	0.1	0.1
Talinum arnotii	forb	per	1	0.1	0.1	0.1	32	13.1	0.1	0.1

Species	**Traits**		**Short transects**				**Long transects**			
	GF	**LC**	**No.Occ.**	**%Occ.**	**Max.Cov.**	**MeanCov.**	**No.Occ.**	**%Occ.**	**Max.Cov.**	**MeanCov.**
Tapinanthus oleifolius	dwarf	per					6	2.5	0.1	0.1
Tephrosia burchellii	forb	ann	3	0.3	0.5	0.2	11	4.5	0.1	0.1
Tephrosia dregeana	wforb	wper	12	1.2	0.5	0.2	20	8.2	0.1	0.1
Tetragonia calycina	wforb	per	2	0.2	0.5	0.3	1	0.4	0.1	0.1
Tragus berteronianus	grass	ann	161	15.7	5	0.6	51	20.9	10	0.6
Trianthema parvifolia	forb	ann	5	0.5	0.5	0.2	8	3.3	0.1	0.1
Tribulus cristatus	forb	wper	44	4.3	20	2.9	10	4.1	7	1.1
Tribulus pterophorus	forb	wper					9	3.7	0.1	0.1
Tribulus terrestris	forb	ann	201	19.6	90	10.2	56	23.0	60	5.3
Tribulus zeyheri	forb	wper	4	0.4	0.1	0.1	3	1.2	0.1	0.1
Trichogyne cf. *paronychioides*	forb	ann	3	0.3	0.1	0.1	5	2.0	0.1	0.1
Triraphis purpurea	grass	ann	12	1.2	1	0.4				
Urochloa brachyura	grass	ann	17	1.7	20	2.4	1	0.4	0.1	0.1
Urochloa panicoides	grass	ann	1	0.1	0.5	0.5	1	0.4	0.1	0.1
Ursinia nana	forb	ann	7	0.7	1	0.2	4	1.6	0.1	0.1
Xerophyta humilis	forb	per	1	0.1	3	3.0	4	1.6	0.1	0.1
Zehneria marlothii	forb	ann					1	0.4	0.1	0.1
Ziziphus mucronata	tree	per					1	0.4	0.1	0.1
Zygophyllum suffruticosum	dwarf	per					3	1.2	0.5	0.4
Zygophyllum tenue	dwarf	per	1	0.1	2	2.0				

Appendix D: Results of HOF modelling for all species with at least 40 occurrences on 1025 short transect plots and at least 10 occurrences on 244 long transect plots sampled around watering points in central Namibian rangelands. For each species the Akaike weights calculated from AICc values of all possible HOF models (I-V) are listed. The best model according to AICc is indicated.

species	Short transects: HOF model Akaike weights						Long transects: HOF model Akaike weights					
	I	II	III	IV	V	Best model	I	II	III	IV	V	Best model
Acacia erioloba							74.6%	9.9%	3.6%	8.6%	3.3%	**I**
Acacia hebeclada							91.8%	3.1%	1.1%	2.9%	1.2%	**I**
Acacia mellifera							37.8%	13.8%	5.0%	29.5%	13.9%	**I**
Acrotome inflata	54.1%	24.6%	9.0%	9.0%	3.3%	**I**						
Aizoon asbestinum							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Aizoon schellenbergii							56.6%	23.4%	8.7%	8.4%	3.0%	**I**
Amaranthus praetermissus							60.3%	21.5%	7.7%	7.7%	2.8%	**I**
Aptosimum albomarginatum							58.6%	27.6%	11.7%	1.5%	0.5%	**I**
Aptosimum lineare	60.0%	22.2%	8.1%	7.0%	2.6%	**I**						
Aptosimum sp							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Aptosimum spinescens							42.3%	29.0%	12.0%	10.4%	6.4%	**I**
Aristida adscensionis	8.9%	48.9%	17.9%	17.9%	6.5%	**II**	45.6%	29.5%	10.6%	10.6%	3.8%	**I**
Aristida congesta	1.8%	43.1%	21.3%	22.8%	11.1%	**II**	26.9%	17.9%	14.9%	28.5%	11.8%	**IV**
Aristida meridionalis							47.5%	28.5%	10.2%	10.2%	3.6%	**I**
Barleria rigida							60.0%	21.8%	7.8%	7.7%	2.7%	**I**
Blepharis mitrata							59.7%	22.1%	7.9%	7.5%	2.8%	**I**
Boscia albitrunca							59.4%	22.4%	8.0%	7.5%	2.7%	**I**
Bulbostylis hispidula	8.9%	47.1%	18.5%	18.5%	6.9%	**II**	19.7%	44.3%	36.0%	0.0%	0.0%	**II**
Catophractes alexandri							19.6%	45.4%	16.3%	13.1%	5.6%	**II**
Cenchrus ciliaris							60.1%	21.8%	7.8%	7.5%	2.8%	**I**
Chascanum pinnatifidum							59.4%	22.7%	8.1%	6.9%	2.9%	**I**
Chloris virgata	0.0%	0.0%	0.0%	51.7%	48.3%	**IV**	60.8%	21.2%	7.6%	7.6%	2.7%	**I**
Citrullus lanatus							98.5%	0.8%	0.3%	0.3%	0.1%	**I**
Cleome angustifolia							60.7%	23.3%	8.4%	7.6%	0.0%	**I**
Cleome gynandra							60.3%	21.5%	7.7%	7.7%	2.7%	**I**
Cleome rubella							60.0%	21.8%	7.8%	7.6%	2.7%	**I**
Crotalaria podocarpa	0.0%	0.0%	0.1%	32.8%	67.1%	**V**	0.0%	0.0%	0.0%	0.0%	100%	**V**
Cucumis africanus	0.0%	0.0%	98.2%	0.9%	0.9%	**III**	48.2%	20.3%	12.8%	11.0%	7.6%	**I**
Dactyliandra welwitschii							60.0%	21.8%	7.8%	7.7%	2.7%	**I**
Dactyloctenium aegyptium	0.7%	0.0%	0.0%	91.2%	8.1%	**IV**						
Dicoma capensis	9.2%	48.6%	17.8%	17.8%	6.6%	**II**	24.6%	11.4%	6.9%	40.2%	17.0%	**IV**
Enneapogon cenchroides	38.4%	38.7%	22.8%	0.0%	0.0%	**II**	89.4%	5.0%	1.8%	2.8%	1.0%	**I**
Enneapogon desvauxii	0.0%	2.4%	96.4%	0.9%	0.3%	**III**	0.0%	0.0%	0.0%	64.6%	35.4%	**IV**
Entoplocamia aristulata							62.1%	22.5%	8.1%	7.3%	0.0%	**I**
Eragrostis annulata	0.0%	0.0%	0.0%	50.7%	49.3%	**IV**	78.0%	0.0%	0.0%	16.0%	6.0%	**I**
Eragrostis cylindriflora	0.0%	0.0%	0.0%	62.4%	37.6%	**IV**						
Eragrostis echinochloidea	67.9%	15.4%	5.6%	5.6%	5.4%	**I**	89.4%	2.4%	0.9%	5.4%	2.0%	**I**

species	Short transects: HOF model Akaike weights						Long transects: HOF model Akaike weights					
	I	II	III	IV	V	Best model	I	II	III	IV	V	Best model
Eragrostis macrochlamys var. macrochlamys	0.0%	0.0%	63.0%	34.2%	2.7%	**III**						
Eragrostis nindensis	0.0%	61.6%	38.4%	0.0%	0.0%	**II**	0.0%	88.4%	0.8%	1.6%	9.2%	**II**
Eragrostis porosa	0.0%	0.0%	100%	0.0%	0.0%	**III**	0.0%	0.0%	0.0%	0.0%	100%	**V**
Eragrostis trichophora							57.3%	21.2%	8.6%	9.5%	3.4%	**I**
Eriocephalus luederitzianus							56.9%	24.7%	9.1%	6.1%	3.2%	**I**
Euphorbia inaequilatera							60.0%	21.7%	7.8%	7.7%	2.8%	**I**
Felicia smaragdina	58.3%	22.3%	8.2%	8.2%	3.0%	**I**	60.3%	21.8%	7.8%	7.2%	2.9%	**I**
Geigeria acaulis							59.9%	22.1%	7.9%	7.4%	2.6%	**I**
Geigeria ornativa							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Geigeria pectidea	61.1%	22.7%	8.3%	3.9%	3.9%	**I**	2.3%	0.9%	0.3%	61.7%	34.8%	**IV**
Gisekia africana	58.8%	22.0%	8.1%	8.1%	3.1%	**I**	60.4%	22.2%	9.1%	6.2%	2.2%	**I**
Helichrysum candolleanum	0.0%	53.6%	19.6%	19.6%	7.2%	**II**	94.0%	0.0%	0.3%	4.8%	1.0%	**I**
Hermannia affinis							61.6%	22.6%	8.1%	7.7%	0.0%	**I**
Hermannia modesta	60.1%	22.6%	8.3%	6.6%	2.4%	**I**	60.2%	21.8%	7.8%	7.5%	2.7%	**I**
Hirpicium gazanioides	59.5%	22.2%	8.1%	7.2%	3.0%	**I**	60.4%	22.2%	8.0%	7.0%	2.5%	**I**
Indigastrum argyroides	51.4%	48.6%	12.8%	12.9%	4.7%	**I**	0.0%	0.0%	0.0%	73.8%	26.2%	**IV**
Indigastrum parviflorum	51.7%	28.9%	11.9%	2.6%	5.0%	**I**	60.3%	21.8%	7.8%	7.2%	2.8%	**I**
Indigofera alternans							54.1%	28.9%	10.4%	4.9%	1.7%	**I**
Indigofera auricoma	1.0%	0.4%	0.2%	50.0%	48.4%	**IV**	0.1%	0.1%	23.2%	54.8%	21.8%	**IV**
Indigofera holubii	55.5%	27.4%	10.0%	0.3%	6.8%	**I**	60.1%	21.7%	7.8%	7.7%	2.7%	**I**
Indigofera vicioides	59.6%	22.6%	8.3%	7.0%	2.6%	**I**	60.3%	22.4%	8.0%	6.9%	2.4%	**I**
Kohautia caespitosa							60.0%	21.8%	7.8%	7.6%	2.8%	**I**
Kyllinga alba							59.3%	22.9%	8.2%	6.7%	2.9%	**I**
Laggera decurrens							61.5%	22.5%	8.1%	7.9%	0.0%	**I**
Leucosphaera bainesii							0.0%	56.8%	9.6%	33.6%	0.0%	**II**
Limeum argute carinatum	0.0%	0.2%	0.5%	32.7%	66.6%	**V**	81.3%	10.1%	3.6%	3.6%	1.3%	**I**
Limeum myosotis	63.5%	23.5%	8.6%	0.6%	3.8%	**I**	56.5%	10.6%	3.8%	21.5%	7.6%	**I**
Lotononis platycarpa	0.0%	53.6%	19.6%	19.6%	7.2%	**II**	57.2%	22.4%	8.0%	9.0%	3.3%	**I**
Lycium eenii							59.9%	21.7%	7.8%	7.8%	2.8%	**I**
Lycium oxycarpum							52.5%	19.0%	6.8%	15.2%	6.4%	**I**
Melinis repens							59.9%	21.7%	7.8%	7.8%	2.8%	**I**
Microchloa caffra							31.3%	37.2%	13.4%	13.4%	4.8%	**II**
Mollugo cerviana	59.4%	21.8%	8.0%	8.0%	2.9%	**I**						
Monechma genistifolium	0.3%	49.5%	0.3%	49.5%	0.3%	**II**	40.4%	13.0%	17.2%	16.7%	12.8%	**I**
Monsonia senegalensis							59.9%	21.7%	7.8%	7.8%	2.8%	**I**
Monsonia umbellata							60.4%	24.3%	9.7%	4.1%	1.4%	**I**
Nelsia quadrangula							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Nidorella resedifolia							61.9%	22.4%	8.0%	7.6%	0.0%	**I**
Ocimum americanum var. *americanum*							60.4%	23.3%	8.3%	5.9%	2.1%	**I**

species	Short transects: HOF model Akaike weights						Long transects: HOF model Akaike weights					
	I	II	III	IV	V	Best model	I	II	III	IV	V	Best model
Ondetia linearis							60.1%	22.3%	8.0%	7.1%	2.5%	**I**
Pegolettia senegalensis	59.4%	21.8%	8.0%	8.0%	2.9%	**I**						
Peliostomum leucorrhizum							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Pentzia calva							60.0%	21.7%	7.8%	7.7%	2.7%	**I**
Phaeoptilum spinosum	35.2%	16.4%	6.0%	27.8%	14.6%	**I**	18.3%	44.3%	15.9%	15.9%	5.7%	**II**
Platycarpha carlinoides							60.0%	21.7%	7.8%	7.7%	2.7%	**I**
Pogonarthria fleckii	34.9%	30.2%	11.0%	17.2%	6.7%	**I**	59.6%	21.9%	7.8%	7.9%	2.8%	**I**
Pseudogaltonia clavata							59.4%	21.9%	7.9%	8.0%	2.8%	**I**
Rhigozum trichotomum	0.0%	53.6%	19.6%	19.6%	7.1%	**II**	0.0%	0.0%	44.5%	25.7%	29.8%	**III**
Schmidtia kalahariensis	0.0%	0.0%	0.0%	24.3%	75.7%	**V**	0.0%	0.0%	0.0%	0.0%	100%	**V**
Senecio consanguineus	60.3%	25.5%	9.3%	3.6%	1.3%	**I**	60.0%	22.0%	7.9%	7.4%	2.6%	**I**
Sericorema sericea							59.9%	21.8%	7.8%	7.7%	2.8%	**I**
Sesamum triphyllum	59.0%	22.0%	8.0%	8.0%	2.9%	**I**	60.5%	21.9%	7.9%	7.0%	2.8%	**I**
Setaria verticillata	0.0%	0.0%	100%	0.0%	0.0%	**III**	68.1%	15.6%	5.6%	7.8%	2.8%	**I**
Sida ovata							61.7%	22.4%	8.0%	7.9%	0.0%	**I**
Stipagrostis ciliata	14.7%	45.7%	16.7%	16.7%	6.1%	**II**	0.0%	53.6%	46.4%	0.0%	0.0%	**II**
Stipagrostis hochstetteriana							50.5%	22.8%	8.2%	12.7%	5.7%	**I**
Stipagrostis obtusa	0.0%	0.0%	41.8%	37.8%	20.4%	**III**	0.0%	0.0%	96.2%	2.8%	1.0%	**III**
Stipagrostis uniplumis	0.0%	10.0%	85.1%	3.6%	1.3%	**III**	0.0%	65.0%	3.3%	3.3%	28.5%	**II**
Talinum arnotii							60.0%	21.8%	7.8%	7.6%	2.7%	**I**
Tephrosia burchellii							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Tephrosia dregeana							60.0%	21.7%	7.8%	7.8%	2.8%	**I**
Tragus berteronianus	41.8%	18.9%	39.2%	0.1%	0.0%	**I**	65.5%	4.2%	1.5%	21.2%	7.6%	**I**
Tribulus cristatus	0.0%	0.0%	100%	0.0%	0.0%	**III**	65.8%	18.4%	6.6%	6.7%	2.4%	**I**
Tribulus terrestris	0.0%	0.0%	0.0%	0.0%	100%	**V**	0.0%	0.0%	0.0%	73.7%	26.3%	**IV**

Appendix E: Parameters of the best HOF models for all species models (except for model type I) and parameters of best HOF models for diversity measures and functional traits for short and long transects recorded around watering points in central Namibian rangelands.

Species, diversity parameters, functional traits	Best HOF model	Parameters of the best HOF model a	b	c	d
SHORT TRANSECTS					
Species					
Aristida adscensionis	II	5.77881531	31.3297618		
Aristida congesta	II	5.66367871	4.69285374		
Bulbostylis hispidula	II	6.00436974	11.0641693		
Dicoma capensis	II	5.88702236	5.03428845		
Enneapogon cenchroides	II	6.63350329	-1.01535693		
Eragrostis nindensis	II	5.09349792	20.0872819		
Helichrysum candolleanum	II	5.10451058	4.78724816		
Lotononis platycarpa	II	4.96490915	21.4516423		
Monechma genistifolium	II	5.69461225	2.14878072		
Rhigozum trichotomum	II	4.52098041	29.8327924		
Stipagrostis ciliata	II	5.965463	38.820426		
Cucumis africanus	III	6.474698	-100	4.153337	
Enneapogon desvauxii	III	-4.636899	20.838118	4.655517	
Eragrostis macrochlamys var. *macrochlamys*	III	2.861899	-7.45734	2.735001	
Eragrostis porosa	III	0.88090937	-48.9112396	2.66678113	
Setaria verticillata	III	5.11772567	-100	4.9405911	
Stipagrostis uniplumis	III	-0.99383415	50.5356283	3.34289325	
Tribulus cristatus	III	20.3303961	-87.8689543	4.83242718	
Stipagrostis obtusa	III	-6.300553	100	3.839171	
Chloris virgata	IV	-3.641838	33.108667	6.522159	
Dactyloctenium aegyptium	IV	-3.103525	47.668249	7.949526	
Eragrostis annulata	IV	-2.65429418	8.31104823	6.49403546	
Eragrostis cylindriflora	IV	-2.49597302	5.71246394	4.83332977	
Indigofera auricoma	IV	-5.3129973	100	10.3949757	
Crotalaria podocarpa	V	-1.2287169	28.5746397	4.46560127	18.1099143
Limeum.argute carinatum	V	-1.46855623	36.9192469	5.19982911	26.1406009
Schmidtia kalahariensis	V	-1.57154635	13.493306	3.29312337	8.35680367
Diversity					
Species richness	II	0.1247207	0.7355585		
Simpson diversity	II	-0.8757142	1.2053007		
Functional traits					
Tree / shrub	II	5.004013	2.081488		
Dwarf shrub	II	5.559032	45.854257		
Grass	III	0.3068038	-27.6971076	1.7560216	
Woody forb	IV	0.09371698	4.70648479	3.72814437	
Herbaceous forb	V	1.2056761	1.8032857	0.6066668	13.3527441
Annual	V	1.3236041	0.1746091	-0.2034319	24.7311136
Perennial	II	3.184723	9.610143		
Weak perennial	V	1.837002	1.326776	2.183407	27.882645

Species, diversity parameters, functional traits	Best HOF model	Parameters of the best HOF model a	b	c	d
LONG TRANSECTS					
Species					
Bulbostylis hispidula	II	4.97364798	4.28769526		
Catophractes alexandri	II	5.00232231	7.48014213		
Microchloa caffra	II	5.21808351	100		
Phaeoptilum spinosum	II	3.83392625	0.79884843		
Stipagrostis ciliata	II	3.793848	11.51067		
Leucosphaera bainesii	II	4.18991114	32.0614427		
Eragrostis nindensis	II	2.92150003	13.0527565		
Stipagrostis uniplumis	II	1.04430881	18.5469702		
Rhigozum trichotomum	III	-10.7513716	100	3.69744597	
Stipagrostis obtusa	III	-14.30264	100	2.72352	
Aristida congesta	IV	-0.1265087	19.5641739	4.53855192	
Dicoma capensis	IV	-1.35702518	39.4621949	5.90162892	
Enneapogon desvauxii	IV	3.33946174	-3.92925403	-0.61904082	
Geigeria pectidea	IV	-2.39087627	27.2508284	6.47208182	
Indigastrum .argyroides	IV	-19.8766406	100	21.830274	
Indigofera auricoma	IV	-11.3600983	59.523146	14.7324238	
Tribulus terrestris	IV	-25.3244823	100	25.2062618	
Crotalaria podocarpa	V	-32.351602	100	5.452479	12.528559
Eragrostis porosa	V	3.181037	-2.232431	-59.353057	-67.587124
Schmidtia kalahariensis	V	-0.1485588	5.1210848	2.7595771	14.3731254
Bulbostylis hispidula	II	4.97364798	4.28769526		
Catophractes alexandri	II	5.00232231	7.48014213		
Diversity					
Species richness	II	-0.2993253	0.7551722		
Simpson diversity	I	-0.9779995			
Functional traits					
Tree / shrub	II	3.239268	1.102897		
Dwarf shrub	II	4.3386109	0.5967508		
Grass	II	1.0528267	0.7732461		
Woody forb	IV	-1.018796	20.119067	5.72553	
Herbaceous forb	V	0.6158192	2.5627471	3.6347099	18.7583087
Annual	V	-0.3546541	2.1678316	2.3519609	12.9851882
Perennial	II	0.9117727	10.647555		
Weak perennial	III	0.1598957	-13.8921272	2.9626467	