

Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern Karoo, South Africa

Admore Mureva & David Ward

To cite this article: Admore Mureva & David Ward (2016): Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern Karoo, South Africa, African Journal of Range & Forage Science, DOI: [10.2989/10220119.2016.1148775](https://doi.org/10.2989/10220119.2016.1148775)

To link to this article: <http://dx.doi.org/10.2989/10220119.2016.1148775>



Published online: 31 Mar 2016.



Submit your article to this journal [↗](#)



Article views: 12



View related articles [↗](#)



View Crossmark data [↗](#)

Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern Karoo, South Africa

Admore Mureva* and David Ward

School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

* Corresponding author, email: admury@gmail.com

Woody plant encroachment is increasing in arid and semi-arid regions of the world. We investigated the structure and fine-scale spatial pattern of encroaching species and how these patterns vary with different grazing regimes in semi-arid regions. In this study, we investigated how four encroaching shrub species (*Searsia erosa*, *S. burchellii*, *Diospyros lycioides* and *Eriocephalus ericoides*) in Middelburg (Eastern Cape, South Africa) coexist and partition space under different grazing regimes (viz. continuous rest, and continuous, summer and winter grazing). We used point-pattern analysis to assess the spatial ecology of these species. We also used an index of integration (mingling index), where low values indicate that they are surrounded by conspecifics and high values indicate that they are surrounded by heterospecifics. The three shrub species were highly mingled except in the winter-grazing plot, where *S. burchellii* and *D. lycioides* clustered. We found that the shrub species were generally aggregated in most of the grazing plots. These findings indicate that (1) at a fine spatial scale, grazing in the wet season promotes shrub encroachment, and (2) there is a tendency to aggregation among encroaching shrub species in the grazing plots.

Keywords: competition, encroaching shrubs, facilitation, grazing regimes, point-pattern analysis, spatial pattern

Introduction

Woody plant density is increasing globally in many arid and semi-arid regions (Archer et al. 1995; Springsteen et al. 2010) but our understanding of the mechanisms driving this process is limited (Archer et al. 1995; Ward 2005). However, some progress is being made in understanding the mechanisms behind bush encroachment (O'Connor et al. 2014; Ward et al. 2014). Grassland invasion by woody species has been attributed to factors such as heavy grazing, fire intensity and frequency, soil moisture, nutrients and global climate change (Ward 2005; Bond 2008; van Auken 2009). Regular fire frequency suppresses woody plant growth, destroying adult shrubs, shrub seedlings and saplings, preventing their development to fire-resistant stages. Woody plant encroachment has also been attributed to increased atmospheric carbon dioxide (Kgope et al. 2010; Ward 2010) due to the greater net photosynthetic efficiency of woody C₃ plants than competitor C₄ grasses that are often dominant in hot environments (Wolfe and Erickson 1993). Some studies (Archer et al. 1995; Sankaran et al. 2008; van Auken 2009) have identified heavy grazing by livestock as the major driver of woody species encroachment. Heavy grazing decreases the biomass and vigour of the grass, reducing the moisture absorption from the upper soil layers (Knoop and Walker 1985). Ultimately, the competitiveness of the grass against establishing tree seedlings is reduced (Riginos et al. 2009; Kgosikoma et al. 2012; Ward et al. 2013). Heavy grazing also reduces grass fuel, which diminishes the probability and intensity of fire events and increases the frequency of

juvenile trees and shrubs growing into taller, fire-resistant stages (Trollope 1980). Thus, heavy grazing may alter plant composition and structure of encroaching rangelands.

Composition of any mature vegetation stand, such as grassland, is shaped by competition (Clements et al. 1929; Wiegand et al. 2008), although there is increasing evidence of facilitation among plant species (Callaway and Walker 1997; Jeltsch et al. 2000; Bertness and Ewanchuk 2002; Bruno et al. 2003). Intense competition among woody species can result in a regular pattern of the shrubs, while weak competition from grasses may give rise to a clustered pattern of the shrubs, causing woody plant encroachment (Jeltsch et al. 2000; Wiegand et al. 2006; Meyer et al. 2008). Facilitation among woody species can also cause woody plant encroachment. Facilitation can be due to seed dispersal, nurse-plant syndrome and environmental heterogeneity. A facilitative nurse-plant syndrome often refers to seedling establishment under canopies of adult trees. In such interactions, the seedlings profit from protection against harsh temperatures, higher available soil moisture and nutrients, and reduced soil compaction and erosion (Flores and Jurado 2003). The nurse-plant syndrome has mainly been reported in arid and semi-arid regions (Tielbörger and Kadmon 2000; Chen et al. 2011; Schleicher et al. 2011).

Assessing vegetation structure and spatial patterns may reveal inter- and intra-specific interactions such as competition and facilitation (Dale 1999; Getzin et al. 2006). Spatial pattern analysis is useful in detecting competition or

facilitation by assessing the spatial distribution of trees and determining the scale at which the spatial pattern is significantly aggregated or regular (Wiegand and Moloney 2004; Getzin et al. 2006; PUNCHI-MANAGE et al. 2013). There are two major indirect means of determining spatial distribution of plants, namely point-pattern and nearest-neighbour analysis (Shackleton 2002; Wiegand and Moloney 2004). In point-pattern analyses, the position of a plant in a plot is represented by a point, and the spatial pattern analysis indicates whether the distribution of the points is random, aggregated or regular by comparing the distribution with the pattern of the plants under a specific null model (Wiegand and Moloney 2004). However, spatial pattern analyses cannot detect competitive interactions when competition does not result in differential mortality of individual plants (Getzin et al. 2006). Nearest-neighbour analysis, on the other hand, may provide a useful tool for detecting subtle interactions, where competition may result in reduced growth rather than mortality (Shackleton 2002; Getzin et al. 2006). Nearest-neighbour analysis shows that if competition is present there will be a substantial decrease in size of one or more competing neighbours (Shackleton 2002). This analysis works on the premise that there is a positive correlation between a size index (usually canopy diameter) and distance between competing neighbours (Shackleton 2002). It is therefore expected that large shrubs should have smaller neighbours. Contrastingly, facilitation among shrubs may result in increased growth, resulting in a negative correlation (Schleicher et al. 2011).

This study sought to understand the effects of grazing regime on encroachment by shrub species and their spatial patterns in the different grazing regime plots. We employed spatial indices, spatial point-pattern analyses and nearest-neighbour distances to quantify the structures and spatial patterns of encroaching semi-arid shrubs. Our predictions were (1) grazing in the wet season increases the density of encroaching species because reduction of grass allows water to percolate into the subsoil, thereby allowing woody species to proliferate (Cipriotti and Aguiar 2012; Ward et al. 2013); (2) the shrub species will be surrounded by conspecifics. Due to competition, shrub species will suppress seedlings of other species (Balanda 2013); and (3) the spatial pattern of shrub species should be regular in all grazing regimes due to competition (Shackleton 2002).

Methods

Study site

The study was conducted at the Grootfontein Research Centre, Middelburg in the Eastern Cape (28°35'0" S, 24°26'0" E), South Africa. Middelburg receives annual rainfall of 300 mm, with most rainfall occurring in autumn, with the highest rainfall (63.8 mm) in March (summer) and the lowest (10.1 mm) in June (winter) (du Toit 2010). The temperatures range from -7.2 °C (July) to 36.1 °C (January) (Mucina and Rutherford 2010). The soils are mainly aeolian sands and andesite clays. The vegetation in the vicinity of Middelburg falls under the Nama-Karoo biome (Mucina and Rutherford 2010). The principal shrubs are *Pentzia*, *Eriocephalus*, *Lycium* and *Searsia* species. The dominant

grasses include *Aristida*, *Digitaria* and *Stipagrostis* species. Grasses tend to be more common in depressions and on sandy soils.

Field study

The Bergkamp grazing trial plots were established in 1943 at Grootfontein Agricultural College in Middelburg, Eastern Cape. The purpose of these plots was to monitor the effects of sheep grazing on species composition. Grazing intensity in the trial plots was 2 sheep ha⁻¹, which is in line with the recommended stocking rates for the Nama-Karoo biome. The plots had continuous grazing (10.4 ha), summer grazing (1.7 ha), winter grazing (1.7 ha) and continuous rest (0.5 ha) treatments. There was no replication when these plots were established.

There has been a noticeable increase in shrub encroachment in the grazed plots compared with the non-grazed plot since the beginning of the study (Figures 1 and 2). The encroaching shrub species in the grazing plots are *Searsia erosa*, *S. burchellii*, *Diospyros lycioides* and *Eriocephalus ericoides*.

In this study, individual grazing plots (Figure 1) were divided into subplots. The subplots were treated as replicates. We recognise this as pseudoreplication but believe the patterns are important enough to be demonstrated. Two subplots were laid out in each of the three grazing treatments. In the continuous rest treatment, only one subplot was established because encroachment was limited to a small portion of the plot only; we wished to ascertain the interactions among the woody species. The dimensions of the subplots were determined by the density of the woody species. We aimed to have more than 30 individuals in each plot; where shrub density was very low we used bigger plots in order to have the minimum required individuals for spatial analysis. In the summer-grazing plot (Figures 1 and 2), the subplots measured 40 m by 40 m. In the winter-grazing treatment, the subplots measured 50 m by 50 m. In the continuous-grazing plot, the two subplots were 25 m by 25 m. In the continuous-rest plot, only a small portion measuring approximately 20 m by 20 m was encroached. Each subplot was laid out as a Cartesian plane with the origin (0, 0) as the reference point for the location of each shrub. The *x*- and *y*-coordinates of each encroaching shrub (*Searsia erosa*, *S. burchellii*, *Diospyros lycioides* and *Eriocephalus ericoides*) were determined using a tape measure. Data on morphological structure (specifically, shrub height and crown diameter) of each plant were also recorded. Spatial pattern analysis was done for shrub species that had at least 30 individuals in a plot (Wiegand and Moloney 2004).

Stand structure and composition analysis

Differences in stand structure (specifically, shrub height and crown diameter) among species in the different plots were analysed using analysis of variance (ANOVA). The mean nearest distance among individuals in each subplot was calculated. The Von Gadow mingling index (M_i) (Chen et al. 2011) was calculated to determine the relative spatial mix of each species. The Von Gadow mingling index is the proportion of the *n* nearest neighbours that do not belong to the same species. M_i for sample tree *i* is determined by Graz (2004) as:



Figure 1: Aerial view of the continuous grazing (1), spring grazing (2), summer grazing (3), winter grazing (4), autumn grazing (5) and continuous rest (6) plots as of 30 July 2013. The study was done in the continuous, summer and winter grazing and continuous rest plots. Black squares indicate the positions of subplots in each grazing plot. The subplots were located at mid-slope in all of the grazing plots, except in the continuous grazing plot where the subplot was situated at the foot of the plot

$$M_i = \frac{1}{n} \sum_{j=1}^n m_j \quad (1)$$

where n is the number of neighbours considered and i denotes the sample tree evaluated. The value of m_j is one if the shrub is of another species than i , otherwise it is zero. The arithmetic mean, M_{sp} of the observed values of M_i for a species sp , is such that $0 \leq M_{sp} \leq 1$. A value of M_{sp} close to zero implies that the individuals of that species occur in groups, thus indicating a low level of species mingling. High values of M_{sp} close to one, on the other hand, indicate that the individuals of the species occur in isolation from other individuals of the same species.

The M_{sp} , however, does not take into consideration the proportion of each species within the plot. Equation 2 therefore was used to evaluate the M_{sp} in relation to the proportion of the species within the grazing subplots (Graz 2004):

$$M = \frac{P_{sp}}{1 - M_{sp}} \quad (2)$$

where M is the standardised mingling index for a species in a plot, P_{sp} is the proportion of number individuals of a species in relation to the total number of individuals of all species in a plot and M_{sp} is the arithmetic mean of the observed values of M_i for a species sp .

We also used the size differentiation index (height and crown differentiation), which is the proportion of the n nearest neighbours of a given reference shrub that are bigger than the reference shrub. It is determined as indicated in Equation 3:

$$U_i = \frac{1}{n} \sum_{j=1}^n v_j \quad (3)$$

where n is the number of neighbours considered and i denotes the sample shrub evaluated. The value of v_j is one

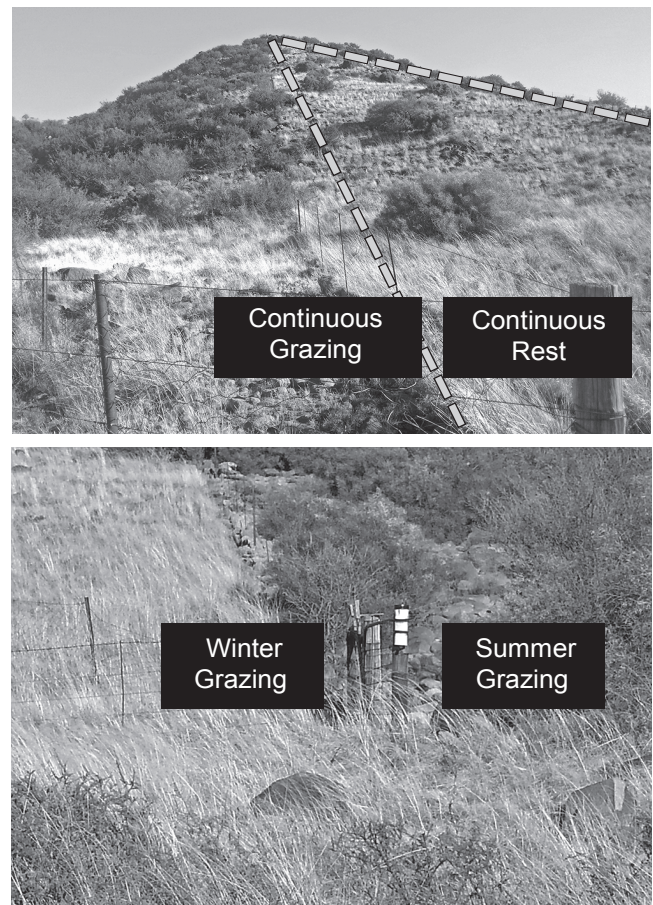


Figure 2: Grazing during the wet season (continuous and summer grazing plots) increases woody-plant density. The grazing density in these trial plots was two sheep per hectare

if the shrub is bigger than i , otherwise it is zero (Graz 2004). For the determination of both the Von Gadow mingling and size differentiation indices, we used four nearest neighbours for each individual shrub as recommended by Shackleton (2002) and Pillay and Ward (2012). The xy coordinates and height/crown diameter were used to determine the height/crown differentiation indices and for the nearest-neighbour analysis we used the xy coordinates and the crown diameters.

Spatial pattern analysis

The unbiased K -function univariate estimator for detecting intraspecific interactions is:

$$K(r) = n^{-2} |A| \sum_{i=1}^n \sum_{j \neq i} w_{ij}^{-1} I_r(u_{ij}) \quad (4)$$

where n is the number of shrubs in the study area A ; u_{ij} is the distance between the i th (focal) shrub and the j th (neighbouring) shrub, where the focal shrub is located within area A ; $I(u_{ij})$ is an indicator function, equivalent to one if $u_{ij} < r$ and is otherwise zero. The term w_{ij} corrects for the edge effect, where w_{ij} is equal to one if the entire circumference of the circle lies within A (Gray and He 2009). However, instead of using the K function, the square-root transformation of the $K(r)$ function, called the L function, is used (Wiegand and Moloney 2004). This L function is easily interpreted because it removes the scale dependence of $K(r)$ and stabilises the variance (Wiegand and Moloney 2004). The L function that was used to compare the univariate spatial pattern of dominant species in each grazing plot was determined as:

$$L(r) = \sqrt{\frac{K(r)}{\pi}} \quad (5)$$

where $L(r) = 0$ for a random pattern, $L(r) < 0$ for a regular pattern and $L(r) > 0$ for a clustered pattern. $K(r)$ is as in Equation 4 above. The bivariate K function ($K_{12}(r)$) is the expected number of points of pattern 2 within a given distance r from an arbitrary point of pattern 1 divided by the intensity of pattern 2 points (Wiegand and Moloney 2004). The second-order bivariate estimate was defined as follows:

$$K_{12}(r) = (n_1 n_2)^{-1} |A| \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_i^j I_r(u_{ij}) \quad (6)$$

where n_1 and n_2 are populations from species 1 and 2 respectively in area A . Other terms are interpreted as in Equation 4 above. The $L_{12}(r)$ function was determined as follows:

$$L_{12}(r) = \sqrt{\frac{K_{12}(r)}{\pi}} - r \quad (7)$$

If patterns 1 and 2 are randomly associated, $L_{12}(r) = 0$. When there is facilitation, $L_{12}(r) > 0$. If the shrubs are competing, $L_{12}(r) < 0$ (Gray and He 2009). $K_{12}(r)$ is calculated as in Equation 6 above.

The O -ring statistic of a univariate point pattern counts the number of points in a ring around an arbitrarily chosen point at a specific distance. This is done for all points in the pattern. The bivariate O -ring statistic can be defined as follows:

$$O_{12}(r) = \lambda_2 g_{12}(r) \quad (8)$$

where

$$g_{12}(r) = \frac{dK_{12}(r)}{dr} / 2\pi r \quad (9)$$

in which $K_{12}(r)$ is as in Equation 5 above (Wiegand and Moloney 2004).

The confidence envelopes for L and O -ring statistics were estimated from 999 Monte Carlo simulations using the complete spatial randomness null model for univariate analysis and the toroidal shift null model for the bivariate analysis (Wiegand and Moloney 2004). The confidence envelopes were estimated using the fifth lowest and the fifth highest values for each distance r . In the bivariate case, if the $L(r)$ and O -ring statistic exceeds the upper confidence limit, it indicates significant aggregation at the r spatial scales where the deviation occurs. If the function is below the lower confidence limit, it indicates significant spatial repulsion (i.e. competition). When the function lies within the confidence limits, the distribution is considered random. To avoid the problems of Type I errors associated with multiple testing (Loosmore and Ford 2006; Perry et al. 2006), we conducted a goodness-of-fit (GoF) test for each analysis. Spatial analysis and GoF test were done using Programita software (Wiegand and Moloney 2004).

Nearest-neighbour analysis

We used nearest-neighbour analysis to infer fine-scale competition. Competition does not always lead to significant mortality and may only result in growth reduction in one or more neighbouring plants (Dale 1999; Pillay and Ward 2012). We determined the correlation between the sum of canopy diameters of four nearest neighbours plus the canopy diameter of the focal shrub and the sum of the distance from the four nearest neighbours to the focal shrub (Pillay and Ward 2012). If the shrubs are directly competing, then the nearest-neighbour distance should be smaller for small shrubs than for large shrubs. A significant positive correlation between nearest-neighbour distance and shrub size indicates competition and a significant negative correlation indicates facilitation. The data points were not independent, so the nearest-neighbour correlation analyses were done using a Mantel test (Legendre and Fortin 2010).

Results

The continuous-rest plot and the winter-grazing subplots had a low shrub density of 60 stems ha^{-1} and 156 stems ha^{-1} compared with continuous-grazing subplots, which had an average of 1 708 stems ha^{-1} and summer-grazing subplots with an average of 1 524 stems ha^{-1} (Table 1, Figure 3).

Searsia erosa in the winter-grazing subplots had a larger crown diameter (3.69 ± 0.14 m, $F_{2,124} = 12.79$, $P < 0.0001$) than *S. erosa* in continuous- and summer-grazing subplots (2.02 ± 0.14 and 1.98 ± 0.87 , respectively) (Table 2, Figure 3). *Diospyros lycioides* also had a larger crown diameter in the winter subplots (2.39 ± 0.11 m, $F_{2,209} = 10.55$, $P < 0.0001$) compared with continuous- and summer-grazing subplots (0.99 ± 0.12 and 0.99 ± 0.08 m,

respectively). *Searsia burchellii* was the only species that was significantly shorter in the winter subplots (1.4 ± 0.56 m, $F_{2,263} = 4.522$, $P = 0.009$) compared with continuous- and summer-grazing subplots (1.61 ± 0.07 and 1.735 ± 0.16 m, respectively).

The standardised Von Gadow mingling index (M_{sp}) indicated that the three species are highly mingled ($M_{sp} > 0.75$) except in the winter-grazing subplots, where *S. burchellii* and *D. lycioides* were indicated to occur in clusters ($M_{sp} < 0.5$).

Univariate pattern analysis

In this study, both the K function and the O -ring statistic were used because in spatial analysis a combination of two or more tests is more informative (Chen et al. 2011). In continuous-grazing subplot 1, the $L(r)$ function showed that *S. burchellii* and *D. lycioides* were significantly aggregated up to 12 m (GoF test: $p = 0.01$). However, the $O(r)$ function showed aggregation at 0–2.5 m and at 4–7 m for *S. burchellii* (GoF test: $p = 0.01$ and $P = 0.01$, respectively), whereas this function indicated that *D. lycioides* was aggregated up to 8 m (GoF test: $P = 0.01$). *Diospyros lycioides* showed a random pattern as indicated by both $L(r)$ and $O(r)$ functions, whereas *S. burchellii* and *S. erosa* showed aggregation up to 2 m and 1 m (GoF test: $P = 0.01$ and $P = 0.04$), respectively, according to the $L(r)$ function, in continuous-grazing subplot 2.

Diospyros lycioides in summer-grazing subplot 2 was aggregated up to 8 m (GoF test: $P = 0.01$) according to the $L(r)$ function, whereas the $O(r)$ showed aggregation up to 2 m (GoF test: $P = 0.03$). The $L(r)$ function showed aggregation of all three species (i.e. except *E. eriocephalus*, which did not occur in these plots) at different scales in summer-grazing subplot 2 (Table 3). However, the $O(r)$ function showed a random pattern at all scales for *S. erosa* and *D. lycioides* and a significant repulsion (i.e. competition) at 14–16 m (GoF test: $P = 0.04$) for *S. burchellii*.

In winter-grazing subplot 1, $L(r)$ indicated *S. erosa* aggregation at 2–4 m (GoF test: $P = 0.03$). In winter-grazing subplot 2, the $L(r)$ and $O(r)$ functions showed significant aggregation for *S. erosa* at 0–8 m and 6–7 m (GoF test: $P = 0.02$ and $P = 0.04$), respectively.

Bivariate pattern analysis

In continuous-grazing subplot 1, the interaction between *S. burchellii* vs *S. erosa* and *D. lycioides* showed significant attraction at all scales (GoF test: $P = 0.01$), according

to the $L_{12}(r)$ function, whereas the $O_{12}(r)$ function showed aggregation up to 7 m (GoF test: $P = 0.01$) (Table 4, Appendix 1). The *D. lycioides* vs *S. burchellii* + *S. erosa* interaction in continuous-grazing subplot 1 was significantly aggregated (GoF test: $P = 0.01$) at all scales according to the $L_{12}(r)$ function. The $O_{12}(r)$ function showed significant aggregation up to 7 m (GoF test: $P = 0.01$) (Table 4, Appendix 1). Interactions in the continuous-grazing subplot 2 were all random.

In summer-grazing subplot 1, $L_{12}(r)$ showed significant attraction between *S. erosa* vs *D. lycioides* and *S. burchellii* from 2–3 m (GoF test: $P = 0.02$). However, the $O_{12}(r)$ function showed that the pattern was mostly random. In summer-grazing subplot 2, *S. erosa* vs *D. lycioides* and *S. burchellii* showed significant attraction at 1–3 m (GoF test: $P = 0.03$) according to the $L_{12}(r)$ function, whereas the $O_{12}(r)$ indicated that the pattern was random. In summer-grazing subplot 2, the $L_{12}(r)$ function also showed a significant attraction between *S. burchellii* vs *D. lycioides* and *S. erosa* between 6–7 m (GoF test: $P = 0.03$). The $O_{12}(r)$ showed significant attraction between *D. lycioides* vs *S. erosa* and *S. burchellii* up to 3 m (GoF test: $P = 0.04$).

In winter-grazing subplot 1, *S. erosa* vs *D. lycioides* and *S. burchellii* were significantly attracted between 2 and 6 m (GoF test: $P = 0.03$) according to the $L_{12}(r)$ function. The $O_{12}(r)$ function showed attraction at 2–3 m only (GoF test: $P = 0.04$). In winter-grazing subplot 2, *S. erosa* vs *D. lycioides* and *S. burchellii* showed significant repulsion (i.e. competition) between 7 and 25 m (GoF test: $P = 0.03$), whereas the $O_{12}(r)$ index showed a random distribution.

Nearest-neighbour analysis

There was a significant positive correlation between sum of the distance to the nearest neighbour and the sum of the canopy diameters of the focal shrub and its neighbours in all of the grazing plots for all shrub species (Table 5). However, although the P -values were significant (because of the large number of data points), the relationships explained very little (<5%) of the variation in all of the grazing plots (Table 5).

Discussion

Shrub density was high in continuous- and summer-grazing plots relative to winter-grazing and continuous-rest plots. This finding supported our prediction that the timing of grazing had an effect on shrub encroachment.

Table 1: Species density of encroaching shrub species under different grazing regimes indicating that continuous- and summer-grazing plots have higher shrub densities than winter-grazing and continuous-rest plots

Grazing regime	Species density (stems ha ⁻¹)			
	Overall	<i>Searsia erosa</i>	<i>Searsia burchellii</i>	<i>Diospyros lycioides</i>
Continuous-grazing plot 1	1 624	248	768	592
Continuous-grazing plot 2	1 792	336	1 056	400
Summer-grazing plot 1	1 639	165	924	550
Summer-grazing plot 2	1 519	250	612	562
Winter-grazing plot 1	136	92	28	24
Winter-grazing plot 2	176	116	40	20
Continuous-rest plot	60	44	7	9

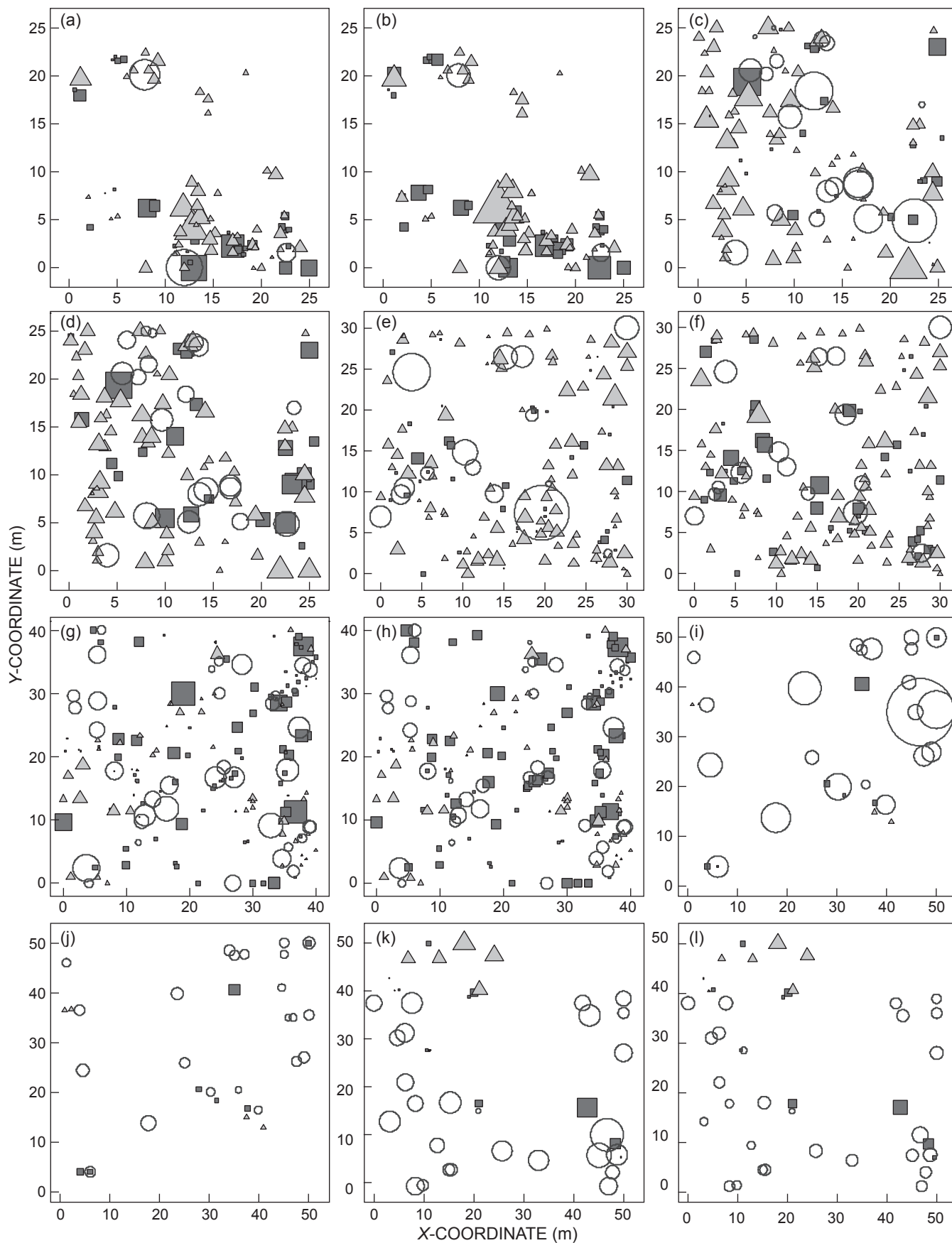


Figure 3 (for legend see facing page)

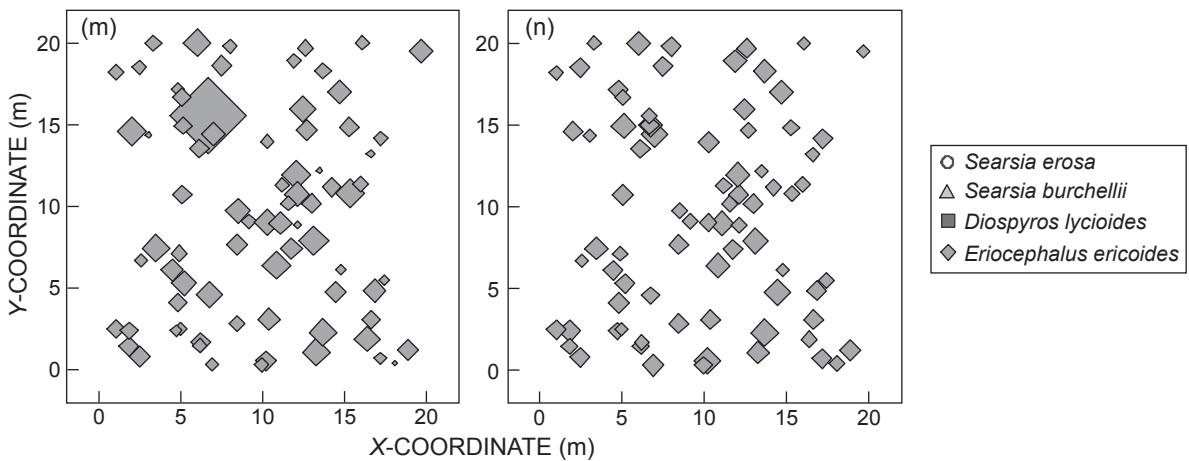


Figure 3: Maps of horizontal and vertical differentiation in the grazing subplots. Shown are horizontal (a) and vertical (b) differentiation in continuous-grazing subplot 1; horizontal (c) and vertical (d) differentiation in continuous-grazing subplot 2; horizontal (e) and vertical (f) differentiation in summer-grazing subplot 1; horizontal (g) and vertical (h) differentiation in summer-grazing subplot 2; horizontal (i) and vertical (j) differentiation in winter-grazing subplot 1; horizontal (k) and vertical (l) differentiation in winter-grazing subplot 2; and horizontal (m) and vertical (n) differentiation in the continuous-rest plot. The size of the respective symbols is proportional to mean crown diameter and height. The smallest diameter was 0.075 m and the largest was 13.5 m. The shortest shrub was 0.15 m and the tallest was 5.9 m

Table 2: Height, crown diameter (CD), height differentiation (HD), crown-diameter differentiation (CDD), species mingling index (MI), standardised mingling index (M) (see Methods) and the mean inter-shrub distance to four nearest neighbours (NND) of encroaching species in the grazing plots. All values are the mean ± SE

Plot	Species	Height	CD	HD	CDD	MI	M	NND
Continuous grazing	<i>S. erosa</i>	2.02 ± 0.15	2.13 ± 0.21	0.49 ± 0.01	0.48 ± 0.04	0.89 ± 0.15	0.96 ± 0.03	1.09 ± 0.18
	<i>S. burchellii</i>	1.61 ± 0.07	1.41 ± 0.09	0.46 ± 0.04	0.52 ± 0.04	0.41 ± 0.09	0.97 ± 0.01	1.25 ± 0.08
	<i>D. lycioides</i>	1.62 ± 0.09	0.99 ± 0.12	0.48 ± 0.07	0.36 ± 0.09	0.64 ± 0.17	0.87 ± 0.13	1.01 ± 0.11
Summer grazing	<i>S. erosa</i>	1.98 ± 0.87	2.36 ± 0.13	0.49 ± 0.06	0.54 ± 0.03	0.81 ± 0.12	0.88 ± 0.09	1.46 ± 0.12
	<i>S. burchellii</i>	1.74 ± 0.16	1.34 ± 0.08	0.46 ± 0.04	0.54 ± 0.01	0.5 ± 0.06	0.81 ± 0.04	1.42 ± 0.08
	<i>D. lycioides</i>	1.4 ± 0.54	0.99 ± 0.08	0.48 ± 0.07	0.38 ± 0.04	0.56 ± 0.12	0.97 ± 0.11	1.44 ± 0.07
Winter grazing	<i>S. erosa</i>	2.06 ± 0.09	3.69 ± 0.14	0.59 ± 0.06	0.62 ± 0.06	0.25 ± 0.01	0.80 ± 0.16	4.28 ± 0.13
	<i>S. burchellii</i>	1.4 ± 0.54	1.63 ± 0.23	0.5 ± 0.09	0.44 ± 0.06	0.67 ± 0.12	0.33 ± 0.02	3.34 ± 0.42
	<i>D. lycioides</i>	1.99 ± 0.2	2.39 ± 0.11	0.45 ± 0.06	0.43 ± 0.02	0.74 ± 0.09	0.24 ± 0.14	3.51 ± 0.28
Continuous rest	<i>E. ericoides</i>	0.58 ± 0.16	0.62 ± 0.15	–	–	1	1	1.32 ± 0.1

Table 3: Summary of univariate analysis of three shrub species under different grazing regimes showing that the encroaching species are generally aggregated. Numbers in parentheses are radii (in metres) at which the observed pattern is significantly different from the expected under the selected null hypotheses. L(r) = Ripley univariate function, O(r) = univariate O-ring function; Ag = aggregation pattern, Ra = random pattern

Plot	Species	L(t)	O(r)
Continuous-grazing 1	<i>Searsia burchellii</i>	Ag (1–12)	Ag (0–2.5) Ag (4–7)
	<i>Diospyros lycioides</i>	Ag (1–12)	Ag (0–8)
Continuous-grazing 2	<i>Searsia burchellii</i>	Ag (0–2)	Ag (0–2)
	<i>Searsia erosa</i>	Ag (0–1)	Ra
	<i>Diospyros lycioides</i>	Ra	Ra
Continuous rest	<i>Eriocephalus ericoides</i>	Ag	Ag (1–10)
Summer-grazing 1	<i>Searsia erosa</i>	Ra	Ra
	<i>Diospyros lycioides</i>	Ag (2–4)	Ag (1–2)
Summer-grazing 2	<i>Searsia burchellii</i>	Ag (3–5)	Ag (0–5), Re (14–16)
	<i>Searsia erosa</i>	Ag (4–5), Ag (14–16)	Ra
	<i>Diospyros lycioides</i>	Ag (1–13)	Ra
Winter-grazing 1	<i>Searsia erosa</i>	Ag (6–7)	Ag (0–8)
Winter-grazing 2	<i>Searsia erosa</i>	Ra	Ag (6–7)

Table 4: Summary of bivariate analysis results of three shrub species under different grazing regimes showing that the encroaching species are generally aggregated. Numbers in parentheses are radii (in metres) at which the observed pattern is significantly different from the expected under the selected null hypotheses. $L_{12}(r)$ = Ripley bivariate function, $O_{12}(r)$ = univariate O-ring bivariate function; Ag = aggregation pattern, Ra = random pattern, Re = repulsion

Plot	Pattern	$L_{12}(r)$	$O_{12}(r)$
Continuous-grazing subplot 1	<i>Searsia burchellii</i> vs <i>Searsia erosa</i> and <i>Diospyros lycioides</i>	Agg (0–12)	Agg (0–7)
Continuous-grazing subplot 2	<i>Searsia burchellii</i> vs <i>Searsia erosa</i> and <i>Diospyros lycioides</i>	Ra	Ra
Continuous-grazing subplot 1	<i>Diospyros lycioides</i> vs <i>Searsia erosa</i> and <i>Searsia burchellii</i>	Agg (0–12)	Agg (0–7)
Continuous-grazing subplot 2	<i>Diospyros lycioides</i> vs <i>Searsia erosa</i> and <i>Searsia burchellii</i>	Ra	Ra
Continuous-grazing subplot 2	<i>Searsia erosa</i> vs <i>Searsia burchellii</i> and <i>Diospyros lycioides</i>	Ra	Ra
Summer-grazing subplot 1	<i>Searsia erosa</i> vs <i>Searsia burchellii</i> and <i>Diospyros lycioides</i>	Agg (2–3)	Ra
Summer-grazing subplot 2	<i>Searsia erosa</i> vs <i>Searsia burchellii</i> and <i>Diospyros lycioides</i>	Agg (1–8)	Agg (2–3)
Summer-grazing subplot 1	<i>Searsia burchellii</i> vs <i>Searsia erosa</i> and <i>Diospyros lycioides</i>	Agg (2–7)	Ra
Summer-grazing subplot 2	<i>Searsia burchellii</i> vs <i>Searsia erosa</i> and <i>Diospyros lycioides</i>	Agg (6–7)	Ra
Summer-grazing subplot 1	<i>Diospyros lycioides</i> vs <i>Searsia erosa</i> and <i>Searsia burchellii</i>	Agg(1–7)	Agg (0–6)
Summer-grazing subplot 2	<i>Diospyros lycioides</i> vs <i>Searsia erosa</i> and <i>Searsia burchellii</i>	Agg (0–10)	Ra
Winter-grazing subplot 1	<i>Searsia erosa</i> vs <i>Searsia burchellii</i> and <i>Diospyros lycioides</i>	Agg (2–8)	Agg(2–3)
Winter-grazing subplot 2	<i>Searsia erosa</i> vs <i>Searsia burchellii</i> and <i>Diospyros lycioides</i>	Re (7–25)	Ra

High shrub encroachment in the summer- and continuous-grazing plots may indicate that water is a major limiting factor for both woody and grass species in semi-arid regions (Ward 2005). Grasses mainly use topsoil water, whereas shrubs utilise subsoil moisture (Knoop and Walker 1985; Ward et al. 2013). Removal of grass by sheep herbivory during the rainy season may allow water to percolate into the subsurface areas, thereby allowing woody species to proliferate (Cipriotti and Aguiar 2012; Ward et al. 2013). High shrub density in continuous- and summer-grazing plots indicates that grass removal in the wet season (in continuous- and summer-grazing plots) affords shrub seedlings an opportunity to germinate with less competition from established herbaceous plants (Bond 2008; Ward et al. 2013). Conversely, there was relatively little encroachment in the (dry) winter-grazed plot, presumably because, when

the aboveground grass material is dead, there is insufficient soil moisture for shrub seeds to germinate. A very low density of encroaching species was conspicuous in the continuous-rest plot, further emphasising the importance of grazing on shrub encroachment. Further experimental studies would be needed to establish whether these mechanisms are indeed functional.

Searsia burchellii and *D. lycioides* had very high densities in the continuous- and summer-grazing plots relative to the winter-grazing plot. These two species were 10 times more dense in the continuous- and summer-grazing plots than in the winter-grazing plots (Table 1). The presence of *S. erosa* in the winter-grazing plot at high density may indicate that this shrub species is highly competitive against grass and may be facilitating the other encroaching species in this region. The proposal that *S. erosa* may be facilitating the

Table 5: Summary of results from the correlations between nearest-neighbour distances and sum of canopy areas. There was only one subplot in the continuous-rest plot (see Methods). n = Number of individuals of the respective species in the plot, N/A = values were not determined because of low sample size

Grazing regime	Subplot	Species	r^2	p	n
Continuous grazing	1	<i>S. erosa</i>	N/A	N/A	3
		<i>S. burchellii</i>	0.0092	0.001*	37
		<i>D. lycioides</i>	0.0147	0.001*	76
	2	<i>S. erosa</i>	0.0094	0.185	20
		<i>S. burchellii</i>	0.0017	0.004*	66
		<i>D. lycioides</i>	0.0061	0.05*	25
Summer grazing	1	<i>S. erosa</i>	0.0525	0.001*	16
		<i>S. burchellii</i>	0.0017	0.001*	84
		<i>D. lycioides</i>	0.0015	0.062	50
	2	<i>S. erosa</i>	0.0028	0.038*	40
		<i>S. burchellii</i>	0.0082	0.0001*	49
		<i>D. lycioides</i>	0.0042	0.0001*	90
Winter grazing	1	<i>S. erosa</i>	0.0016	0.02*	23
		<i>S. burchellii</i>	0.67	0.0001*	7
		<i>D. lycioides</i>	0.134	0.26	6
	2	<i>S. erosa</i>	0.064	0.0001*	28
		<i>S. burchellii</i>	0.465	0.15	10
		<i>D. lycioides</i>	0.067	0.37	6
Continuous rest		<i>E. ericoides</i>	0.143	0.0001*	78

* $p < 0.05$

growth of *S. burchellii* and *D. lycioides* is further strengthened by examining the sizes of these plants in the grazing plots. *Searsia erosa* was the tallest and had the broadest canopy diameter in the continuous-, summer- and winter-grazing plots. The large canopy diameters of *S. erosa* may provide the seedlings of other woody species with protection against harsh temperatures, higher available soil moisture and nutrients (Flores and Jurado 2003). The high *S. erosa* mingling index in continuous- and summer-grazing plots supports the role of *S. erosa* as a facilitator in the growth of the other woody species. Although *S. erosa* appears to be highly competitive against grass, it had low densities in continuous- and summer-grazing plots, indicating that it is a weak competitor against *S. burchellii* and *D. lycioides*.

The larger canopy diameters of the three species in the winter-grazing subplots relative to the continuous- and summer-grazing subplots could be due to the low shrub density in the winter-grazing plots. Plants in a high-density stand tend to vigorously compete for light and will invest more in their height than in their crown-diameter growth (Weiner and Thomas 1992; Nishimura et al. 2010; Nagashima and Hikosaka 2011). In a low-density stand, plants have the luxury of more space and less competition for sunlight and will invest in crown-diameter growth to maximise sunlight absorption (Weiner and Thomas 1992; Nishimura et al. 2010; Nagashima and Hikosaka 2011). Therefore, plants in low-density stands (winter-grazing subplots) should be expected to have a larger crown diameter compared with high-density stands (continuous- and summer-grazing plots) (Table 2).

The species in continuous- and summer-grazing subplots had a higher degree of mingling, indicating that the species were randomly distributed. However, *S. burchellii* and *D. lycioides* in the winter-grazing plots show some

degree of aggregation around *S. erosa*. The aggregation of *S. burchellii* and *D. lycioides* around *S. erosa* in the winter-grazing subplots may indicate that the two species may benefit from higher soil-moisture content and nutrients, protection against harsh temperatures and reduced soil compaction and erosion (Tielbörger and Kadmon 2000; Flores and Jurado 2003; Schleicher et al. 2011).

Searsia erosa and *S. burchellii* showed random height and crown-diameter distribution in all the grazing subplots. *Diospyros lycioides* showed that it was generally surrounded by shrubs of larger crown diameters than itself in the continuous- and summer-grazing subplots. However, in the winter-grazing subplots, the crown diameter differentiation (CDD) of *D. lycioides* was closer to 0.5 and the diameter was much larger than in the continuous- and summer-grazing subplots (Table 2). The lower CDD of *D. lycioides* in the continuous- and summer-grazing subplots may indicate that *D. lycioides* is less competitive against the *Searsia* species and invests more in height growth at the expense of crown development to remain competitive against the other species.

In this study, the scale-dependence of point-pattern analysis showed that there was generally aggregation among the shrubs. These findings diverge from our prediction and those of several other studies that concluded that competition was predominant in arid and semi-arid environments (Skarpe 1991; Maestre et al. 2005). However, these findings are in agreement with those of Coueron and Kokou (1997), Tielbörger and Kadmon (2000) and Chen et al. (2011), who concluded that plants in semi-arid and desert communities tend to aggregate when small. Plants that exhibit an aggregated distribution may facilitate the growth of one another (Schleicher et al. 2011). Plants that grow at high density may create an 'island of fertility', enhancing the growth of surrounding plant species, as

shown in other arid environments (Ravi et al. 2010). Another reason that could lead to such aggregation is spatial heterogeneity induced by edaphic gaps (Chen et al. 2011). The gaps are formed by the removal of grass species during grazing by livestock. The period in which these gaps are formed is of particular importance. When the gaps are formed in the wet season, shrub seedlings will obtain enough moisture for their establishment (Cipriotti and Aguiar 2012), and the rate of woody encroachment will be high. This is supported by the high shrub density in the summer- and continuous-grazing plots in this study.

The observed aggregation in the grazing plots could also be due to the positive effects of one plant species on the establishment of seedlings of other species (nurse-plant syndrome), which has been reported in many semi-arid and arid regions (Callaway and Walker 1997; Bruno et al. 2003). A shrub with a large canopy diameter reduces solar radiation and moderates extreme temperatures by canopy shade. The nurse syndrome was quite apparent in winter-grazing plots, where *S. erosa* was the dominant species in terms of both density and crown size. The bivariate analysis showed that *S. burchellii* and *D. lycioides* were aggregated around *S. erosa*, which may indicate that *S. erosa* could be acting as a nurse plant.

Conclusions and recommendations

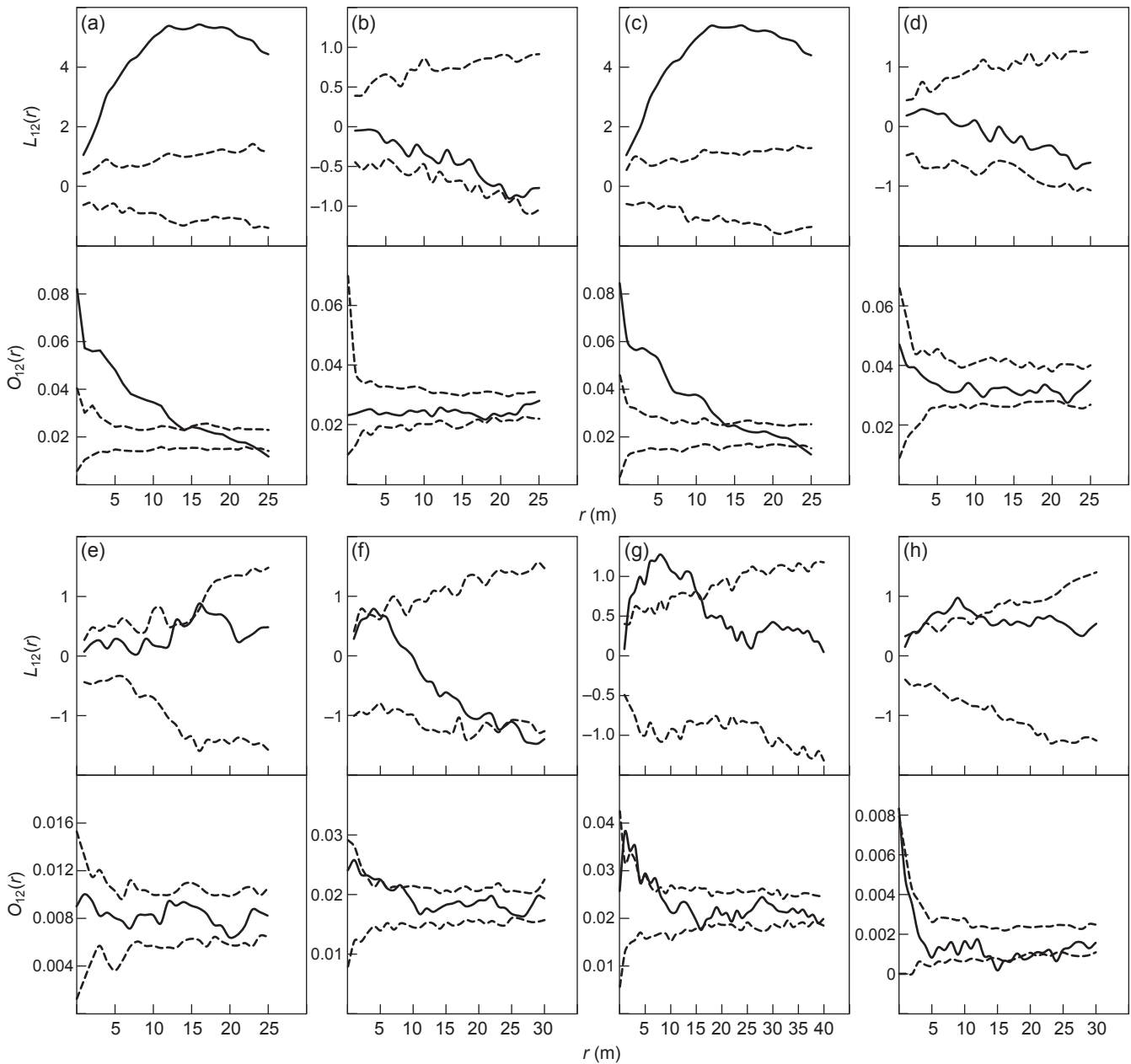
In line with our prediction, grazing in the wet season increases the density of encroaching species. This finding may imply that grazing intensity in the wet season should be reduced to minimise shrub encroachment. The presence of *S. erosa* in the winter-grazing plot may suggest that the species is highly competitive against grass compared to *S. burchellii* and *D. lycioides*. Contrary to our prediction, we generally found that there was aggregation among shrubs in the grazing plots and that *S. erosa* could be acting as a nurse plant for other shrubs. We recognise that these findings are from an unreplicated grazing trial. We suggest that a greenhouse experiment be set up to validate these findings. We propose two greenhouse experiments. One of the experiments should test whether grazing at different intensities in the wet season causes shrub encroachment. The other experiment will test whether *S. erosa* has a nurse effect on *S. burchellii* and *D. lycioides* and whether this effect is due to shading, hydraulic lift and/or differential accumulation of nutrients.

References

- Archer S, Schimel D, Holland E. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* 29: 91–99.
- Balanda M. 2013. Spatio-temporal structure of natural forest: a structural index approach. *Beskydy* 5: 163–172.
- Bertness MD, Ewanchuk PJ. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132: 392–401.
- Bond WJ. 2008. What limits trees in C₄ grasslands and savannas? *Annual Review of Ecology, Evolution and Systematics* 39: 641–659.
- Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125.
- Callaway RM, Walker LR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965.
- Chen J, Liu J, Yang X, Wang Y, Yu X. 2011. The structure and spatial patterns of three desert shrub communities in the western Ordos Plateau: implications for biodiversity conservation. *Journal of Food, Agriculture and Environment* 9: 714–722.
- Cipriotti PA, Aguiar MR. 2012. Direct and indirect effects of grazing constrain shrub encroachment in semi-arid Patagonian steppes. *Applied Vegetation Science* 15: 35–47.
- Clements FE, Weaver JE, Hanson HC. 1929. *Plant competition: an analysis of community functions*. Washington, DC: Carnegie Institution of Washington.
- Couteron P, Kokou K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology* 132: 211–227.
- Dale MRT. 1999. *Spatial pattern analysis in plant ecology*. Cambridge: Cambridge University Press.
- du Toit JCO. 2010. An analysis of long-term daily rainfall data from Grootfontein, 1916–2008. *Grootfontein Agriculture* 10: 24–36.
- Flores J, Jurado E. 2003. Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* 14: 911–916.
- Getzin S, Dean C, He F, Trofymow AJ, Wiegand K, Wiegand T. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* 29: 671–682.
- Gray L, He F. 2009. Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. *Forest Ecology and Management* 259: 98–106.
- Graz FP. 2004. The behaviour of the species mingling index M_{sp} in relation to species dominance and dispersion. *European Journal of Forest Research* 123: 87–92.
- Jeltsch F, Weber G, Grimm V. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology* 150: 161–171.
- Kgope BS, Bond WJ, Midgley GF. 2010. Growth responses of African savanna trees implicate atmospheric CO₂ as a driver of past and current changes in savanna tree cover. *Austral Ecology* 35: 451–463.
- Kgosikoma OE, Harvie BA, Mojeremane W. 2012. Bush encroachment in relation to rangeland management systems and environmental conditions in Kalahari ecosystem of Botswana. *African Journal of Agricultural Research* 7: 2312–2319.
- Knoop WT, Walker BH. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73: 235–253.
- Legendre P, Fortin MJ. 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources* 10: 831–844.
- Loosmore NB, Ford ED. 2006. Statistical inference using the G or K point pattern spatial statistic. *Ecology* 87: 1925–1931.
- Maestre FT, Valladares F, Reynolds JF. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* 93: 748–757.
- Meyer KM, Ward D, Wiegand K, Moustakas A. 2008. Multi-proxy evidence for competition between savanna woody species. *Perspectives in Plant Ecology, Evolution and Systematics* 10: 63–72.
- Mucina L, Rutherford MC (eds). 2010. *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia* 19. Pretoria: South African National Biodiversity Institute.
- Nagashima H, Hikosaka K. 2011. Plants in a crowded stand regulate their height growth so as to maintain similar heights to neighbours even when they have potential advantages in height

- growth. *Annals of Botany* 108: 207–214.
- Nishimura E, Suzaki E, Irie M, Nagashima H, Hirose T. 2010. Architecture and growth of an annual plant *Chenopodium album* in different light climates. *Ecological Research* 25: 383–393.
- O'Connor TG, Puttick JR, Hoffman MT. 2014. Bush encroachment in southern Africa: changes and causes. *African Journal of Range and Forage Science* 31: 67–88.
- Perry GLW, Miller BP, Enright NJ. 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecology* 187: 59–82.
- Pillay T, Ward D. 2012. Spatial pattern analysis and competition between *Acacia karroo* trees in humid savannas. *Plant Ecology* 213: 1609–1619.
- Punchi-Manage R, Wiegand T, Wiegand K, Getzin S, Gunatilleke CVS, Gunatilleke IAUN. 2013. Effect of spatial processes and topography on structuring species assemblages in a Sri Lankan dipterocarp forest. *Ecology* 95: 376–386.
- Ravi S, D'Odorico P, Huxman TE, Collins SL. 2010. Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. *Rangeland Ecology and Management* 63: 267–274.
- Riginos C, Grace JB, Augustine DJ, Young TP. 2009. Local versus landscape-scale effects of savanna trees on grasses. *Journal of Ecology* 97: 1337–1345.
- Sankaran M, Ratnam J, Hanan N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17: 236–245.
- Schleicher J, Wiegand K, Ward D. 2011. Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. *Journal of Arid Environments* 75: 270–278.
- Shackleton C. 2002. Nearest-neighbour analysis and the prevalence of woody plant competition in South African savannas. *Plant Ecology* 158: 65–76.
- Skarpe C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science* 2: 565–572.
- Springsteen A, Loya W, Liebig M, Hendrickson J. 2010. Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. *Plant and Soil* 328: 369–379.
- Tielbörger K, Kadmon R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81: 1544–1553.
- Trollope WSW. 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. *African Journal of Range and Forage Science* 5: 173–177.
- van Auken OW. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90: 2931–2942.
- Ward D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science* 22: 101–105.
- Ward D. 2010. A resource ratio model of the effects of changes in CO₂ on woody plant invasion. *Plant Ecology* 209: 147–152.
- Ward D, Hoffman MT, Collocott SJ. 2014. A century of woody plant encroachment in the dry Kimberley savanna of South Africa. *African Journal of Range and Forage Science* 31: 107–121.
- Ward D, Wiegand K, Getzin S. 2013. Walter's two-layer hypothesis revisited: back to the roots! *Oecologia* 172: 617–630.
- Weiner J, Thomas SC. 1992. Competition and allometry in three species of annual plants. *Ecology* 73: 648–656.
- Wiegand K, Saltz D, Ward D. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment—insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 229–242.
- Wiegand K, Saltz D, Ward D, Levin SA. 2008. The role of size inequality in self-thinning: a pattern-oriented simulation model for arid savannas. *Ecological Modelling* 210: 431–445.
- Wiegand T, Moloney AK. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104: 209–229.
- Wolfe DW, Erickson JD. 1993. Carbon dioxide effects on plants: uncertainties and implications for modeling crop responses to climate change. In: Kaiser H, Drennen T (eds), *Agricultural dimensions of global climate change*. Delray Beach: St Lucie Press. pp 153–178.

Appendix 1: Bivariate $L_{12}(r)$ function (square root transformation of the bivariate Ripley $K_{12}(r)$ function) and the bivariate O-ring statistics $O_{12}(r)$ showing the analysis of the interaction between *Searsia erosa*, *S. burchellii* and *Diospyros lycioides* in different grazing plots. r (m) is the distance scale in metres. Observed patterns (solid line) that fall above, below and within 95% Monte Carlo envelopes (dashed lines) indicate aggregation, regular or random patterns, respectively. (a) Continuous-grazing subplot 1: *S. burchellii* vs *D. lycioides* and *S. erosa*; (b) continuous-grazing subplot 2: *S. burchellii* vs *D. lycioides* and *S. erosa*; (c) continuous-grazing subplot 1: *D. lycioides* vs *S. erosa* and *S. burchellii*; (d) continuous-grazing subplot 2: *D. lycioides* vs *S. erosa* and *S. burchellii*; (e) continuous-grazing subplot 2: *S. erosa* vs *S. burchellii* and *D. lycioides*; (f) summer-grazing subplot 1: *S. erosa* vs *S. burchellii* and *D. lycioides*; (g) summer-grazing subplot 2: *S. erosa* vs *S. burchellii* and *D. lycioides*; (h) summer-grazing subplot 1: *S. burchellii* vs *S. erosa* and *D. lycioides*; (i) summer-grazing subplot 2: *S. burchellii* vs *S. erosa* and *D. lycioides*; (j) summer-grazing subplot 1: *D. lycioides* vs *S. erosa* and *S. burchellii*; (k) summer-grazing subplot 2: *D. lycioides* vs *S. erosa* and *S. burchellii*; (l) winter-grazing subplot 1: *S. erosa* vs *S. burchellii* and *D. lycioides*; (m) winter-grazing subplot 2: *S. erosa* vs *S. burchellii* and *D. lycioides*



Appendix 1 (cont.)

