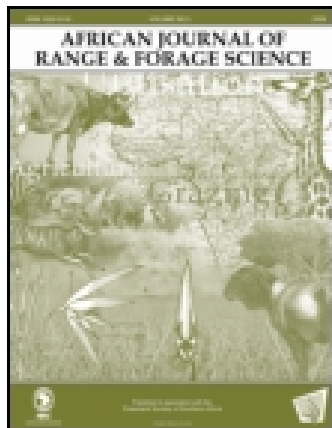


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Bush clump succession in grassland in the Kei Road region of the Eastern Cape, South Africa

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Bush encroachment is a vegetation dynamic of global interest. This study describes the pattern of succession of bush clumps in the Eastern Cape, South Africa, using a space-for-time substitution. Clumps formed following establishment of mainly *Acacia karroo* in grassland through nucleation via animal dispersal. A total of 49 tree or shrub species were recorded in 40 clumps. With increasing clump size, there was a corresponding increase in woody basal area, species richness and diversity, but not evenness. Correspondence analysis showed that the pattern of compositional variation was closely related to clump size; differences resulting from clump establishment disappeared as clumps developed. Population size structure of 20 (of 21) species was dominated by small individuals, indicating that regeneration has increased over time. *Coddia rudis* was prolific on a clump periphery; *Scutia myrtina* and *A. karroo* were dominant within clumps. Seven shrub and nine tree species were encountered more frequently within a clump than on its periphery. All species other than *A. karroo* had fruits suited to dispersal by birds or mammals. The overall pattern of bush clump succession shows close parallels with that initiated by invasion of *Prosopis glandulosa* into grassland in Texas, USA.

Keywords: *Acacia karroo*, bush encroachment, plant diversity, savanna, woody invasion

Introduction

Increase of the woody component within savanna or grassland at the expense of the herbaceous component is commonly referred to as 'bush encroachment'. It has emerged as a dynamic of global significance in tropical or subtropical regions over the past century (Archer 1995, van Auken 2000, Roques et al. 2001). Land use and management effects, such as heavy grazing or partial exclusion of fire, are reputedly main causes of bush encroachment (Walker et al. 1981, Archer 1990, 1995, Roques et al. 2001). More recent literature has singled out the apparent physiological benefit of increasing concentrations of atmospheric CO₂ for C₃ woody plants at the expense of C₄ grassland (Bond 2008). Thus encroachment may be driven by both global (e.g. CO₂) and local (e.g. grazing and fire) drivers, acting in a complementary manner. Efficacy of encroachment is further dependent on attributes of encroaching species, including dispersal (Brown and Archer 1989), establishment success (O'Connor 1995), and growth rate (Higgins et al. 2000), each of which may interact in a complex way with global and local drivers (Bond and Midgley 2012).

Patterns of bush encroachment have not been well studied (Archer 1990, 1995, Bond 2008). An increased number of case studies would contribute a broader foundation for improving understanding of underlying processes. In southern Africa, bush encroachment is most commonly associated with an increase of microphyllous species such as *Acacia* (van Vegten 1983, Friedel and Blackmore 1988, O'Connor 2001, Roques et al. 2001, Wigley et al. 2010),

which may facilitate the later entry of other woody species, including broad-leaved, bipinnate microphyllous, and evergreen species (Potts and Tidmarsh 1937, du Preez and Venter 1990, Hoffman and O'Connor 1999, Skowno et al. 1999, Smith and Goodman 1987, Jordaan 2010). Successional change may promote development of bush clumps in certain instances (Gower et al. 1992). Specifically in the Eastern Cape, South Africa, bush encroachment of savanna and grassland by *Acacia karroo* (du Toit 1967) and subsequent ingress of other species to form bush clumps or closed thicket has long been noted (Story 1952, Comins 1962, O'Connor and Crow 1999). The development of bush clumps is an example of autogenic succession through facilitation (Connell and Slatyer 1977) in which a founder individual promotes additional species through a nucleation process driven by animal dispersal (Yarranton and Morrison 1974). Rates of encroachment have been relatively rapid in the Eastern Cape, with a doubling of woody cover over 20 years following the drought-prone 1960s (O'Connor and Crow 1999).

Bush clumps are poorly studied in southern Africa. The few available descriptions of clumps suggest involvement of an *Acacia* species in their formation (Gower et al. 1992, van der Linden et al. 2005, Mucina and Rutherford 2006: 475). Degradation of termitaria was implicated in the establishment of *Acacia nilotica* and subsequent development of bush clumps in KwaZulu-Natal (Gower et al. 1992). Detailed study has been undertaken of autogenic succession of subtropical grassland to thorn woodland in southern

Texas (Archer et al. 1988, Archer 1990, 1995). Livestock grazing promoted ingress of *Prosopis glandulosa*, eventually leading to conversion of grassland to multispecies bush clumps (clusters). This pattern of change described for Texas appears to be closely similar to the perceived pattern for the Eastern Cape, in which *A. karroo* apparently fulfils the role of *P. glandulosa*.

The general aim of this study was to examine development of bush clumps in the Eastern Cape, using a 'space-for-time' substitution. The Texan case study (Archer 1990, 1995) was adopted as a working conceptual model. Evidence was sought for whether clumps are initiated by establishment of *A. karroo* in grassland, followed by an increase in clump size through establishment of animal-dispersed species. The following specific questions or predictions were addressed.

- Is *A. karroo* responsible for the initiation of bush clumps?
- As bush clumps increase in size, is there an increase in their richness, diversity and composition that is in accord with a facilitation model of succession?
- If autogenic succession is occurring, then the pattern of species turnover with increasing clump size should be reflected in the size structure of species populations. For example, early colonisers should not have regenerating individuals in large clumps; species requiring forest-like conditions should only establish in larger clumps.
- If autogenic succession is driving clump expansion, then different species should be favoured within a clump versus its periphery.
- Colonisation of a clump requires targeted dispersal through bird or mammal vectors, the identity of which might depend on fruit size and the size of mouthparts of available agents. Wind dispersal should play a minor role.

Methods

Study area

The study area was located in the Kei Road region of the Eastern Cape, South Africa (32°45' S, 27°42' E) at an altitude of 560 m above sea level. The area is mesic and frost-free, with a mean annual rainfall of 772 mm (1900–1991) (Jarvel 1996, O'Connor and Crow 1999, Mapuma 2000). Rainfall occurs mainly during summer, although mid-summer is drier than early or late summer; winter is usually dry. Mean daily temperature per month varies between 8.6 °C (minimum) in winter and 31 °C (maximum) in summer. The geology of the region consists of sandstones and shales of the Ecca and mainly Beaufort series, with associated dolerite intrusions, of the Karoo sequence (South African Council for Stratigraphy 1980). Soils are derived *in situ* from sandstone and were classified as Glenrosa 1211 (Soil Classification Working Group 1991). The soil has a sandy-clay texture and there are no free stones or boulders in the soil profile (Jarvel 1996, Mapuma 2000). Topography is undulating.

The vegetation of the region is classified as Bisho Thornveld (SVs7) by Mucina and Rutherford (2006: 513), although their description does not mention multispecies bush clumps. Acocks (1953) described the region as Eastern Province Thornveld (northern form), consisting of a mosaic of open grassland, bush clumps within a grassland

matrix (as occurred in the study area) and closed canopy woodland. The study area has been used for commercial livestock ranching using cattle and sheep for many decades. No land clearing or other disturbances are known to have occurred. Fire occurs infrequently and is rarely used as a management tool.

Field sampling and analysis

A bush clump was defined as an association of two or more woody species with contiguous canopies that were separated from other woody plants by grassland. A relatively homogeneous area within a single paddock was sampled in order to limit the influence of edaphic and management variables on clumps. The area was located on the crest and upper slopes. A total of 40 bush clumps covering the perceived range in size was sampled without bias for composition during 1992. Each clump was measured for its length along its longest axis, and breadth perpendicular to that axis. Clump area was calculated as the area of an ellipse. Each individual woody plant within a clump was identified and measured for stem circumference (above any basal swelling, below the first branch), and height. For a subset of 26 clumps, each individual was scored for whether it was positioned within a clump or on the periphery. Nomenclature of woody plant species follows the African Plants Database (2012).

In order to identify which species may initiate a clump, woody individuals within grassland between bush clumps were sampled with 20 randomly placed transects of 30 m by 2.5 m. Each woody individual was measured as described above. Assuming that the largest tree in a clump was the first to establish, the relation between clump size and its largest tree was examined in order to identify the likely clump initial. This was done separately for the sample in which *Acacia karroo*, and the sample in which another species, was the largest individual. This assumption has two important sources of error. First, the founder individual may have died; accordingly a search was made for stumps. Second, the largest individual may be faster growing than the founder, but unfortunately growth rates are not known.

For clumps, the basal area per plant was determined, from which the basal area per species per clump, and the total woody basal area per clump, were calculated. Species richness was calculated as the number of woody species recorded per clump. Diversity was estimated using the Shannon-Wiener index of $\exp(H')$, where $H' = -\sum p_i (\ln p_i)$ and p_i is the relative basal area of species i in a clump. Evenness was estimated using Alatalo's (1981) variation of Hill's ratio: $E = (N_2 - 1)/(N_1 - 1)$, where $N_2 = 1/\sum p_i^2$ and $N_1 = \exp(H')$. The relations between clump area and woody basal area, species richness, diversity and evenness were examined using regression techniques. If *A. karroo* or any other species provides the founding individual, it should be the largest tree whose size should be related to clump size. Linear regression, with clump size used as an untransformed value, proved to be the most effective form for most relations with clump area, although an inverse exponential was fitted for species richness and diversity using SAS (SAS Institute 2010). Apparent outliers (two large clumps) did not exert undue leverage on regressions.

Compositional variation among clumps was examined with a correspondence analysis (CA) ordination using CANOCO version 4.56 (ter Braak 2009). CA was chosen on account of the degree of compositional turnover evident across clumps, as most clumps shared some species. Species were represented by their proportional contribution to the total basal area of a clump, rather than by their absolute basal area, in order to downweight the effect of clump size on compositional variation. Woody species that appeared only once were excluded. Correlations were sought between compositional variation (axis scores) and clump size, species richness, diversity and evenness.

Population size structure of the main species was examined in order to infer their pattern of population growth, in particular regeneration. For example, a reverse-J size structure is indicative of a growing population with healthy regeneration; a hump-backed curve is indicative of failed recent regeneration. Individuals were assigned to the following stem diameter size class codes: 1 = ≤ 1.5 cm, 2 = >1.5 –3 cm, 3 = >3 –5 cm, 4 = >5 –10 cm, 5 = >10 –15 cm, 6 = >15 –25 cm, and 7 = >25 cm. A χ^2 test was used to examine whether a species was encountered more frequently than expected within a clump or on its periphery. For *A. karroo*, the relationship between position and plant size was examined with a contingency test. A weakness of this exercise is that the area of a clump's periphery is unknown but smaller than the area of its interior. Interpretation of preference for a clump interior is made on the basis of sample size and reported *P* value (Stewart-Oaten 1995).

The dispersal type and diameter of the fruit of each species recorded in bush clumps were summarised using literature sources (Palgrave et al. 2002, Boon 2010). Literature sources were also used to gain an idea of the birds (Hockey et al. 2005) and mammals (Skinner and Chimimba 2005) available for dispersal.

Results

Woody regeneration in grassland

A total of five tree and five shrub species was encountered in the 20 transects sampled between bush clumps (Table 1). *Acacia karroo* was three-fold more abundant

than all other species, and occurred in all transects, in support of it being the primary species responsible for clump initiation. A number of animal-dispersed shrub (*Diospyros lycioides*) and tree (*Elaeodendron croceum* and *Scutia myrtina*) species were sufficiently abundant in grassland to suggest that they may serve as a clump initial. The scarcity of the other six species suggests they were 'accidents' of establishment.

Bush clumps

The 40 clumps sampled described a range in size from 4 m² to 422 m², although the majority of clumps were less than 115 m² in size (mean = 67 m², SE = 12.9 m²). As bush clump size increased, there was a linear increase in total woody basal area (Figure 1), and a non-linear increase (inverse exponential) for species richness (Figure 2; Appendix 1 lists all species) and diversity (Figure 3). Species richness increased from two for the smallest clump to 38 for the largest clump (mean = 13.6, SE = 1.25). The lack of a relation between clump size and evenness (Figure 4) indicates that the relative abundance of species

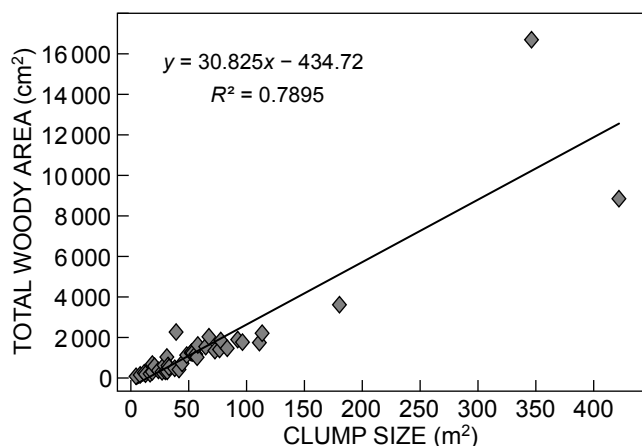


Figure 1: Total woody basal area of bush clumps ($n = 40$) in relation to clump area in the Kei Road region of the Eastern Cape

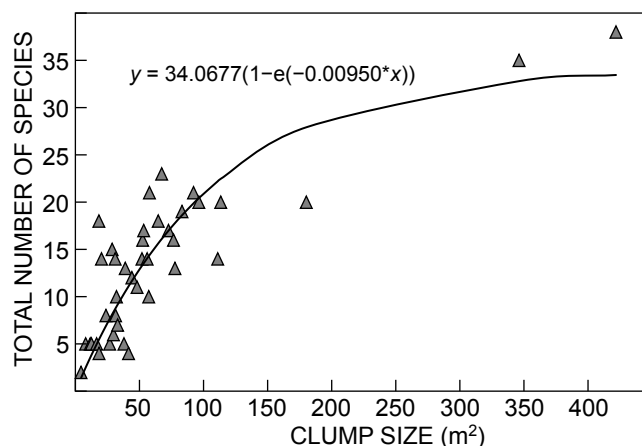


Figure 2: Total number of species in relation to bush clump size ($n = 40$; $P < 0.0001$) in the Kei Road region of the Eastern Cape

Table 1: Woody individuals encountered between bush clumps in the Kei Road region of the Eastern Cape (20 transects of 30 m \times 2.5 m)

Species	No. of plants	Frequency (%) ($n = 20$)	Total no. of plants (%)	Density (plants ha ⁻¹)	
				Mean	SE
<i>Acacia karroo</i>	209	100	76	69.5	12.52
<i>Diospyros lycioides</i>	28	50	10	9.3	4.44
<i>Elaeodendron croceum</i>	25	50	9	8.3	3.97
<i>Scutia myrtina</i>	7	20	2.5	2.3	2.70
<i>Grewia occidentalis</i>	2	10	0.7	0.7	-
<i>Coddia rudis</i>	2	5	0.7	0.7	-
<i>Canthium ciliatum</i>	1	5	0.4	0.3	-
<i>Diospyros whyteana</i>	1	5	0.4	0.3	-
<i>Gymnosporia heterophylla</i>	1	5	0.4	0.3	-
<i>Trimeria grandifolia</i>	1	5	0.4	0.3	-

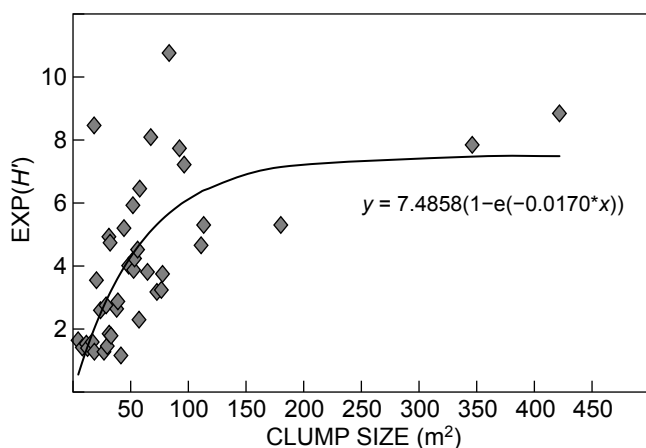


Figure 3: Shannon-Wiener diversity index of woody species per clump in relation to bush clump size ($n = 40$; $P < 0.0001$) in the Kei Road region of the Eastern Cape

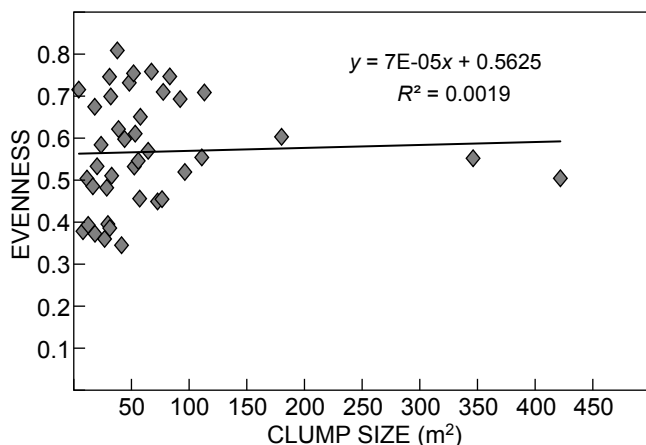


Figure 4: Woody species evenness per bush clump ($n = 40$) in relation to clump size in the Kei Road region of the Eastern Cape

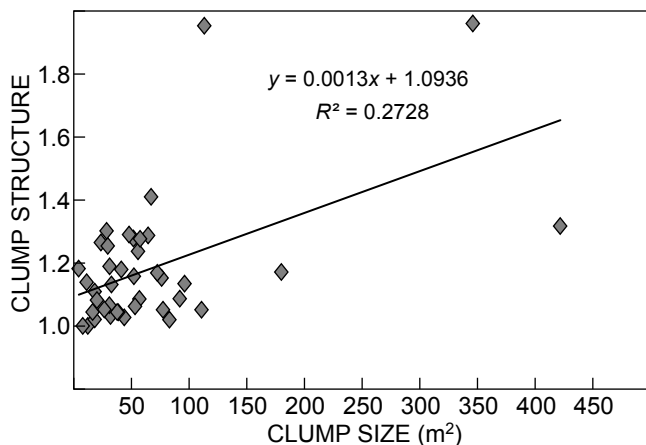


Figure 5: Geometry of clump structure, defined as the length of the longest axis divided by the length of the perpendicular axis, in relation to clump size in the Kei Road region of the Eastern Cape

remained constant as size of bush clumps increased. Clump geometry was slightly elliptical for smaller clumps, but was pronouncedly more asymmetrical for larger clumps (Figure 5). The pattern for small clumps is consistent with clump expansion through addition of new individuals on both their periphery and within the clump interior. The three largest clumps ($>180 \text{ m}^2$) had undergone coalescence of two or more clumps.

The expected relationship between clump size and the size of the largest tree was found for *Acacia karroo*, which was the largest individual for about half of the clumps, all of which were less than 85 m^2 in size (Figure 6). A similar relationship was evident for clumps in which *A. karroo* was not the largest individual (Figure 7), which included the seven largest clumps. *Scutia myrtina* was the largest individual for the majority (16 of 19) of these, whilst *Coddia rudis*, *Halleria lucida* and *Olea europaea* each accounted for one clump. A large stump of *A. karroo* was found in three of

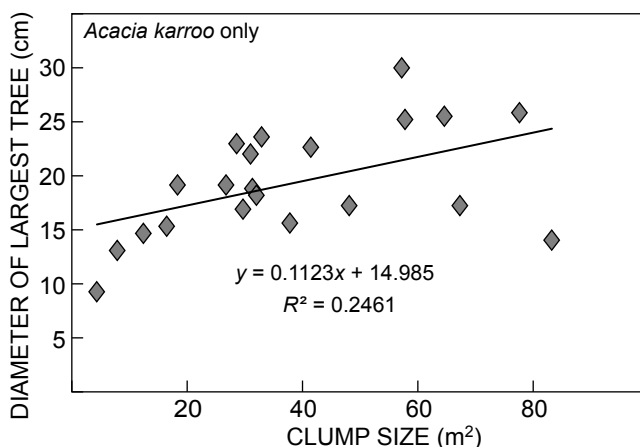


Figure 6: Relation between size of the largest *Acacia karroo* tree in a clump and size of a bush clump for clumps in which the largest individual was *A. karroo* ($n = 21$), in the Kei Road region of the Eastern Cape

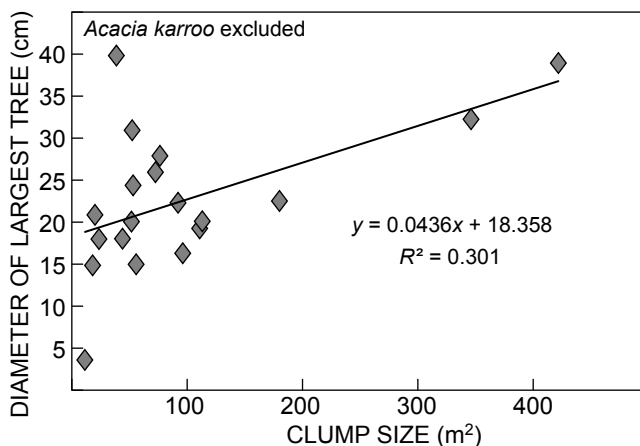


Figure 7: Relation between size of the largest tree in a clump and size of a bush clump for clumps in which the largest individual was not *Acacia karroo* ($n = 19$) in the Kei Road region of the Eastern Cape

these 19 clumps, which was considered to have been the founder individual. Stem diameter of the largest individual of *A. karroo* (Figure 6) ranged from 10 to 30 cm, whereas that of other species (Figure 7) ranged from 15 to 35 cm. *Acacia karroo* therefore appears to be the main species serving as a clump initial, although *S. myrtina* may also be important.

Correspondence analysis provided an effective description of the compositional variation of bush clumps, with axes

one and two accounting for 33.0% and 19.5% of the total species variance, respectively (Figures 8 and 9, Table 2). Subsequent axes were not interpretable and are not commented on further. Clump size was correlated with the second ($r = 0.542$; $df = 39$; $P < 0.01$) but not the first axis ($r = 0.064$; $df = 39$; $P > 0.01$) (Figure 8). The first axis described mainly a gradient for clumps in which the largest individual was *S. myrtina*, often with *A. karroo* not present, through

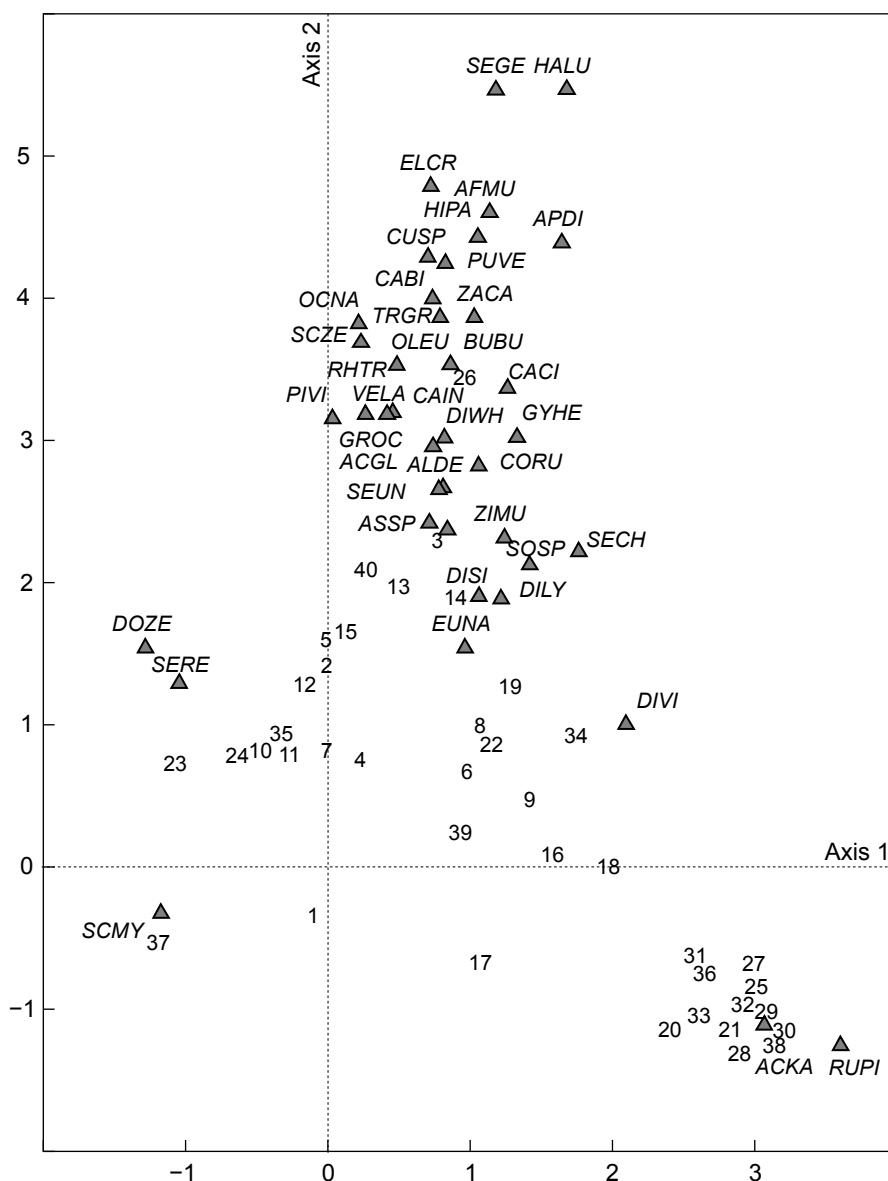


Figure 8: Biplot of a correspondence analysis of tree species composition for bush clumps ($n = 40$) in the Kei Road region of the Eastern Cape. Axes one and two account for 33.0% and 52.5% of the cumulative variance, respectively. Numerals represent bush clumps; triangles represent species. Key to species: ACKA, *Acacia karroo*; ACGL, *Acalypha glabrata*; ALDE, *Allophylus decipiens*; APDI, *Apodytes dimidiata*; AFMU, *Afrocanthium mundianum*; ASSP, *Asparagus* species; BUBU, *Burchellia bubalina*; CACI, *Canthium ciliatum*; CAIN, *Canthium inerme*; CABI, *Carissa bispinosa*; CORU, *Coddia rudis*; CUSP, *Cussonia spicata*; DILY, *Diospyros lycioides*; DISI, *Diospyros simii*; DIVI, *Diospyros villosa*; DIWH, *Diospyros whyteana*; DOZE, *Dovyalis zeyheri*; ELCR, *Elaeodendron croceum*; EUNA, *Euclea natalensis*; GROG, *Grewia occidentalis*; GYHE, *Gymnosporia heterophylla*; HALU, *Halleria lucida*; HIPA, *Hippobromus pauciflorus*; OCNA, *Ochna natalitia*; OLEU, *Olea europaea*; PIVI, *Pittosporum viridiflorum*; PRSP, *Asparagus* species; PUV, *Putterlickia verrucosa*; RHTR, *Rhoicissus tridentata*; RUPI, *Rubus pinnatus*; SCZE, *Scolopia zeyheri*; SCMY, *Scutia myrtina*; SECH, *Searsia chirindensis*; SEGE, *Secamone gerrardii*; SERE, *Searsia rehmanniana*; SEUN, *Searsia undulata*; SOSP, *Solanum* sp.; TRGR, *Trimeria grandifolia*; VELA, *Vepris lanceolata*; ZACA, *Zanthoxylum capense*; and ZIMU, *Ziziphus mucronata*.

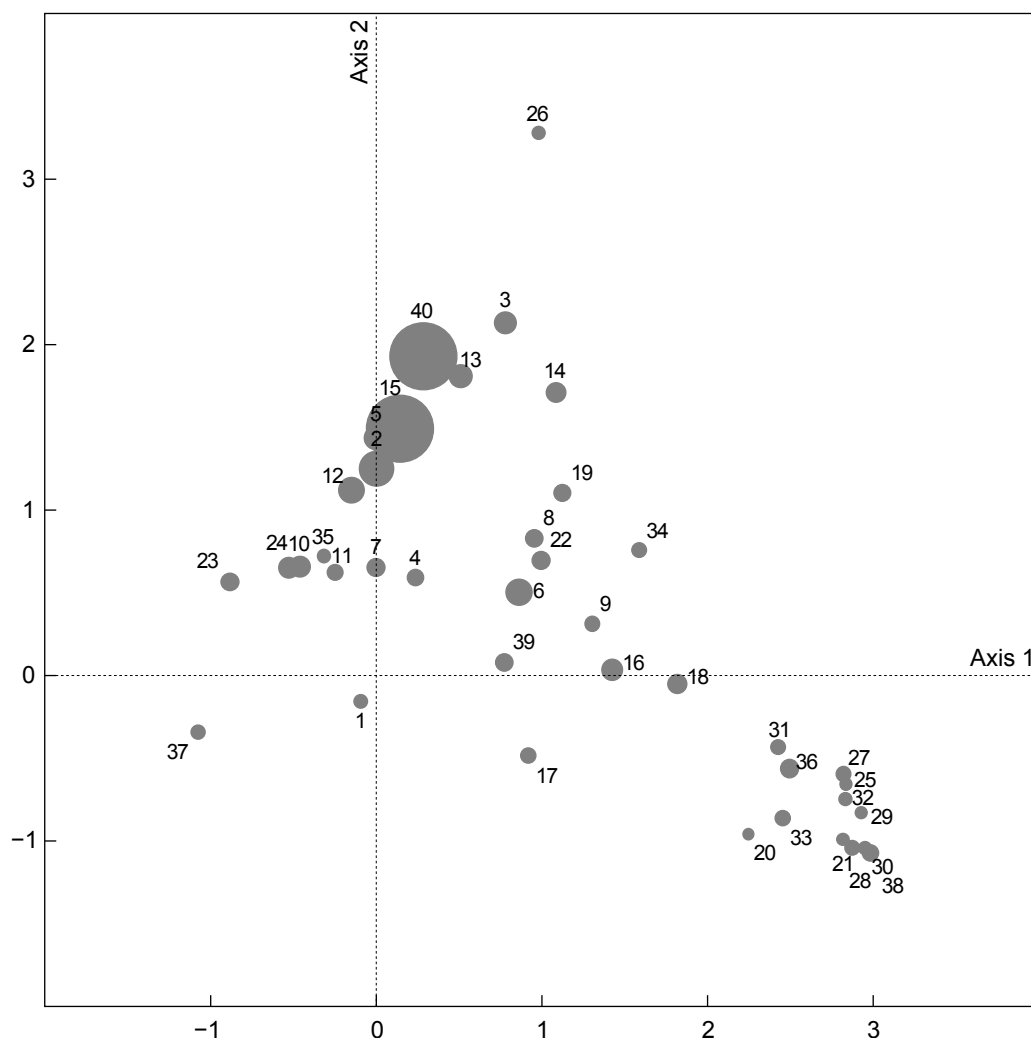


Figure 9: Axes one and two of a correspondence analysis of bush clumps ($n = 40$) in the Kei Road region of the Eastern Cape, with symbols for sites scaled to reflect the size of the bush clump

to those in which the largest individual was *A. karroo*. As most of the clumps defining the spread of the first axis were relatively small, this pattern would suggest that these two species were the initial individual of their respective clumps. The second axis captures the increase in species richness ($r = 0.810$; $df = 39$; $P < 0.001$) and diversity ($r = 0.906$; $df = 39$; $P < 0.001$) with increasing clump size (Figure 8). The triangular shape of the distribution of clumps within ordination space indicates that compositional differences among clumps were reduced with an increase in clump size. The array of species along axis 2 from bottom to top (Figure 8) describes the successional pattern of species with increasing clump size. A similar pattern can be inferred from the frequency of occurrence of species within clumps (Figure 10). Shrub species such as *Diospyros lycioides*, *Coddia rudis*, *Gymnosporia heterophylla*, *Grewia occidentalis* and *Euclea natalensis* were among the first species to appear within clumps (i.e. frequent). Tree species such as *Afrocanthium mundianum*, *Allophylus decipiens*, *Pittosporum viridiflorum* and *Apodytes dimidiata* appeared when clumps were well established (i.e. infrequent).

Table 2: Summary table of the performance of the correspondence analysis of compositional variation among bush clumps ($n = 40$)

	Axis				Total inertia
	1	2	3	4	
Eigenvalues	0.660	0.390	0.260	0.178	2.001
Cumulative percentage variance of species data	33.0	52.5	65.4	74.3	

The composition of the periphery of a clump was distinct to that of the clump interior (Table 3). *Coddia rudis* was the dominant species of the periphery; *S. myrtina* and *A. karroo* were subdominants, and three shrub species were conspicuous. Clump expansion was therefore driven mainly by regeneration of *C. rudis*. For the clump interior, *S. myrtina* was dominant, *C. rudis* and *A. karroo* were subdominant, with the shrubs *G. occidentalis* and *G. heterophylla* conspicuous. A number of species were non-randomly positioned in respect of clump periphery versus its interior (Table 3). The position of *A. karroo* individuals depended

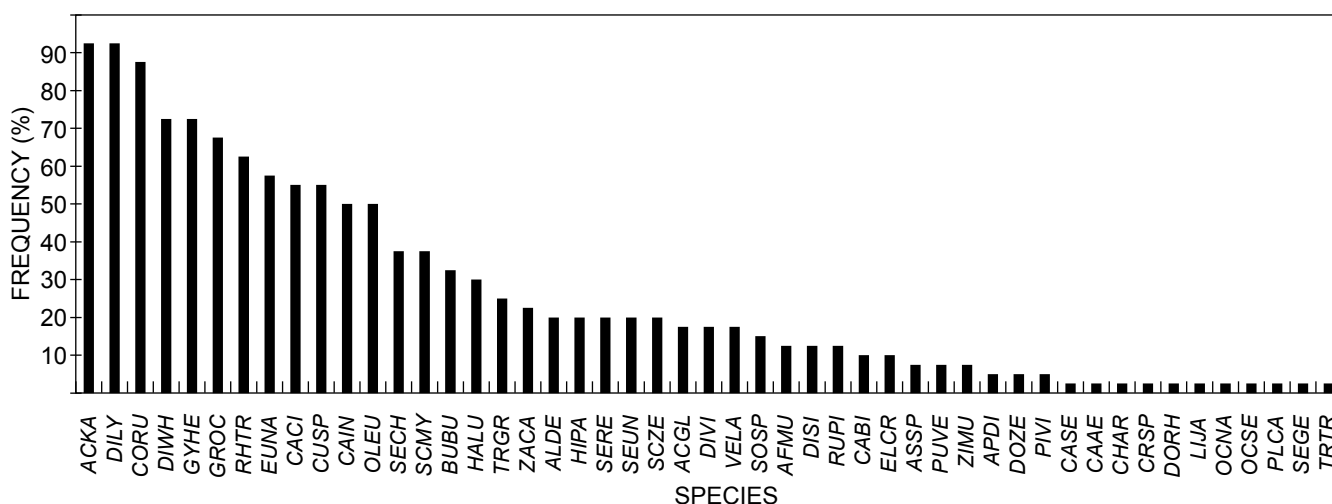


Figure 10: Frequency (%) of species in bush clumps ($n = 40$) at the Kei Road region of the Eastern Cape. Species names are the first two letters each of genus and species; refer to Appendix 1 for the full names

Table 3: Frequency of individuals occurring within the periphery versus the interior of a clump, and contribution to total number recorded and to total basal area for the main shrub and tree species

Species	n	Periphery (%)	Interior (%)	χ^2 test P	Percentage of interior number	Percentage of periphery number	Percentage of interior basal area	Percentage of periphery basal area
Shrub species								
<i>Burchellia bubalina</i>	22	36.4	63.6	0.2008	0.5	0.5	0.2	0.1
<i>Carissa bispinosa</i>	12	0.0	100.0	0.0006	0.5	0.0	0.2	0.0
<i>Coddia rudis</i>	1267	12.5	87.5	<0.0001	42.7	52.9	16.3	31.9
<i>Diospyros lycioides</i>	197	42.5	57.5	0.0368	4.8	10.4	7.1	6.9
<i>Diospyros simii</i>	10	20.0	80.0	0.0578	0.3	0.1	0.1	0.0
<i>Diospyros villosa</i>	9	0.0	100.0	0.0032	0.3	0.0	0.1	0.0
<i>Diospyros whyteana</i>	76	59.2	40.8	0.1083	5.0	2.7	1.6	0.9
<i>Euclea natalensis</i>	180	40.6	59.4	0.0113	4.1	4.4	0.4	1.1
<i>Grewia occidentalis</i>	386	22.8	77.2	<0.0001	11.9	5.3	4.2	1.8
<i>Gymnosporia heterophylla</i>	243	41.1	58.9	0.0058	5.5	6.0	1.7	3.5
<i>Rhoicissus tridentata</i>	63	79.4	20.6	<0.0001	1.9	0.8	1.6	0.4
Tree species								
<i>Acacia karroo</i> <5 cm	44	9.1	90.9	<0.0001 ¹	0.9	2.7	17.8	21.2
<i>Acacia karroo</i> >5 cm	24	79.2	20.8	<0.0001 ¹				
<i>Afrocanthium mundianum</i>	41	2.4	97.6	<0.0001	1.5	0.1	1.4	0.0
<i>Allophylus decipiens</i>	10	10.0	90.0	0.0114	0.3	0.1	0.3	0.0
<i>Canthium ciliatum</i>	69	44.9	55.1	0.3994	1.5	1.9	0.3	2.1
<i>Canthium inerme</i>	34	30.3	69.7	0.0236	0.9	0.6	1.1	1.2
<i>Cussonia spicata</i>	72	4.4	95.6	<0.0001	2.7	0.2	3.9	0.2
<i>Hippobromus pauciflorus</i>	20	5.0	95.0	<0.0001	0.7	0.1	0.1	0.0
<i>Olea europaea</i>	23	30.4	69.6	0.0606	0.6	0.4	3.0	0.1
<i>Scolopia zeyheri</i>	27	7.4	92.6	<0.0001	1.0	0.1	1.3	1.0
<i>Scutia myrtina</i>	339	46.8	53.2	0.2735	7.4	8.9	33.2	26.3
<i>Searsia chirindensis</i>	22	27.3	72.7	0.0330	0.6	0.4	0.1	0.1
<i>Trimeria grandifolia</i>	40	7.5	92.5	<0.0001	1.4	0.2	0.4	0.0
<i>Vepris lanceolata</i>	12	0.0	100.0	0.0006	0.5	0.1	0.2	0.0

¹ Contingency test of position by size

on their size, with small individuals found primarily on the periphery and large individuals primarily within a clump. Of the 11 shrub species examined, only *Rhoicissus tridentata* was encountered more frequently than expected on a clump periphery; seven species showed the converse, while

three species showed no pattern. Of the 12 tree species tested, three showed no trend and the others were encountered more frequently within a clump. Tree species preferring a clump interior included *Cussonia spicata*, as well as species characteristic of forest rather than bushveld

such as *Acalypha glabrata*, *A. decipiens*, *A. mundianum*, *Hippobromus pauciflorus*, *Scolopia zeyheri*, *Trimeria grandifolia* and *Vepris lanceolata*. Individuals within a clump were twice the height of those on the periphery (1.1 m [SE = 0.09] vs 0.6 m [SE = 0.04]; *t*-test: $P < 0.001$; paired *t*-test with clumps as observations: $P < 0.001$).

Population size structure was plotted for 21 tree or shrub species (Figure 11). A consistent pattern for 20 species was their abundant regeneration, as shown by the proportion of individuals in the smallest size classes. Of these, population size structure of seven shrub (*C. rudis*, *D. lycioides*, *D. whyteana*, *G. occidentalis*, *G. heterophylla*, *H. lucida* and *R. tridentata*) and five tree species (*Canthium ciliatum*, *O. europaea*, *Searsia chirindensis*, *S. myrtina* and *S. zeyheri*) approximated a reverse-J structure. This was interpreted as increasing regeneration with time, as the paucity of dead stems in general did not support an alternative that this size structure had resulted from a relatively constant mortality risk with growth. Populations of all other tree and shrub species except one consisted mostly of small recruits, with sparse representation of larger sizes, suggesting that they had all established recently within clumps. All uncommon forest tree species (not graphed) were also only represented by small individuals. *Canthium inerme* was an exception, regeneration of which had peaked some time back.

Fruits of all species other than *A. karroo* are dispersed by birds. Species known to be dispersed by mammals as well include *Carissa bispinosa*, *D. lycioides*, *E. croceum*, *E. natalensis*, *G. occidentalis*, *O. europaea* and *S. chirindensis*. No species were potentially wind dispersed. Most fruits were approximately spherical, whose diameter ranged from 3 mm for *Acalypha glabrata* to 38 mm for *Diospyros villosa*, with a mean of 12 mm ($n = 41$) (Figure 12).

Discussion

Clump initiation

Acacia karroo was confirmed as the main species serving as the individual around which nucleation occurred. It was the most common species in grassland (Table 1) and the largest (assumedly oldest) individual in about half of the clumps (Figure 6). This species was not the largest individual of most of the larger clumps (Figure 7). As some of the largest clumps were evident in the earliest aerial photographs in 1937 (O'Connor and Crow 1999), and the fact that an *A. karroo* individual lives for about 40 years (Barnes et al. 1996), the oldest (largest) *A. karroo* individuals may already have died before this study. This is an inherent weakness of a space-for-time substitution study. It is tentatively concluded that *Scutia myrtina* may have served as the founder individual for some larger clumps, as it was encountered as a solitary individual in grassland (Table 1) and was the largest individual for 40% of clumps (Figure 7). Knowledge of growth rates would improve the strength of this conclusion. Compositional variation along the first axis of the CA was consistent with small clumps being dominated by either *A. karroo* or *S. myrtina*. *Diospyros lycioides* was identified as a possible initial of clumps (Table 1), but it is unlikely to be encountered as the largest individual within clumps on account of its shrub

growth form. The apparent founder role of animal-dispersed species may only become evident when clumps are already well established in the landscape. Certainly, *A. karroo* was the only woody species invading true grassland in this region (Story 1952, Comins 1962; TGO pers. obs.).

The successful invasion of grassland by *A. karroo* in the Eastern Cape (Story 1952, Comins 1962, O'Connor and Crow 1999) is considered to relate to attributes of its seed ecology (O'Connor et al. 2010a) and seedling dynamics in response to changes in fire and grazing regime (O'Connor 1995), possibly in combination with the effects of increasing atmospheric CO₂ concentration on the growth of C₃ woody plants in C₄ grassland (Bond and Midgley 2012). This species develops a seedling bank within grassland (O'Connor 1995), which should allow it to exploit infrequent opportunities for growth.

Establishment of an animal-dispersed species such as *S. myrtina* may promote a greater rate of initial clump development than establishment of *A. karroo*, because trees with fleshy fruit, such as *S. myrtina*, are a natural site for visitation by frugivorous birds and mammals (Guevara et al. 1986). By contrast, *A. karroo* offers an unattractive perch site to passing frugivorous birds because it does not offer fleshy fruit, although trees of this nature are used (Archer 1995). It does, however, offer shade and forage for small mammalian herbivores, such as grey duiker *Sylvicapra grimmia* or even vervet monkeys *Cercopithecus pygerythrus*. Closer attention should perhaps be paid to the role of mammals that consume fruit in bush clump development in this region. Some of the larger fruits on offer (Figure 12) could possibly prove difficult for most frugivorous birds to process, but would be easily consumed by grey duiker or monkeys.

Development of bush clumps

Development of bush clumps proceeded as expected. There was a consistent increase in woody biomass (Figure 1), species richness (Figure 2), and diversity (Figure 3) as clump size increased. Species richness and diversity tended toward an asymptote at the largest clump sizes. Addition of new species to clumps were initially species characteristic of savanna, but culminated in species characteristic of forest scrub or margin vegetation (Figures 8 and 10, Appendix 1). The size of individuals of *A. karroo* in relation to clump size for all except the smallest clumps, and its absence from many larger clumps, indicates that it does not exert any influence on successional change subsequent to clump initiation, analogous to *P. glandulosa* in Texas (Barnes and Archer 1999).

Increase in clump area requires an expanding front rather than addition of individuals within the clump interior. The small *A. karroo* individuals along a clump periphery (Table 3) were considered to include regenerating individuals in grassland (Table 1), i.e. a seedling bank (O'Connor 1995), that were engulfed by an expanding bush clump, and individuals whose establishment was promoted by the edge environment. The dominance of *Coddia rudis* along a clump periphery (Table 3) indicates that it was one of the main species responsible for clump expansion, ostensibly through input by animal vectors. Its dominance within a clump interior is attributed to continuing clump expansion.

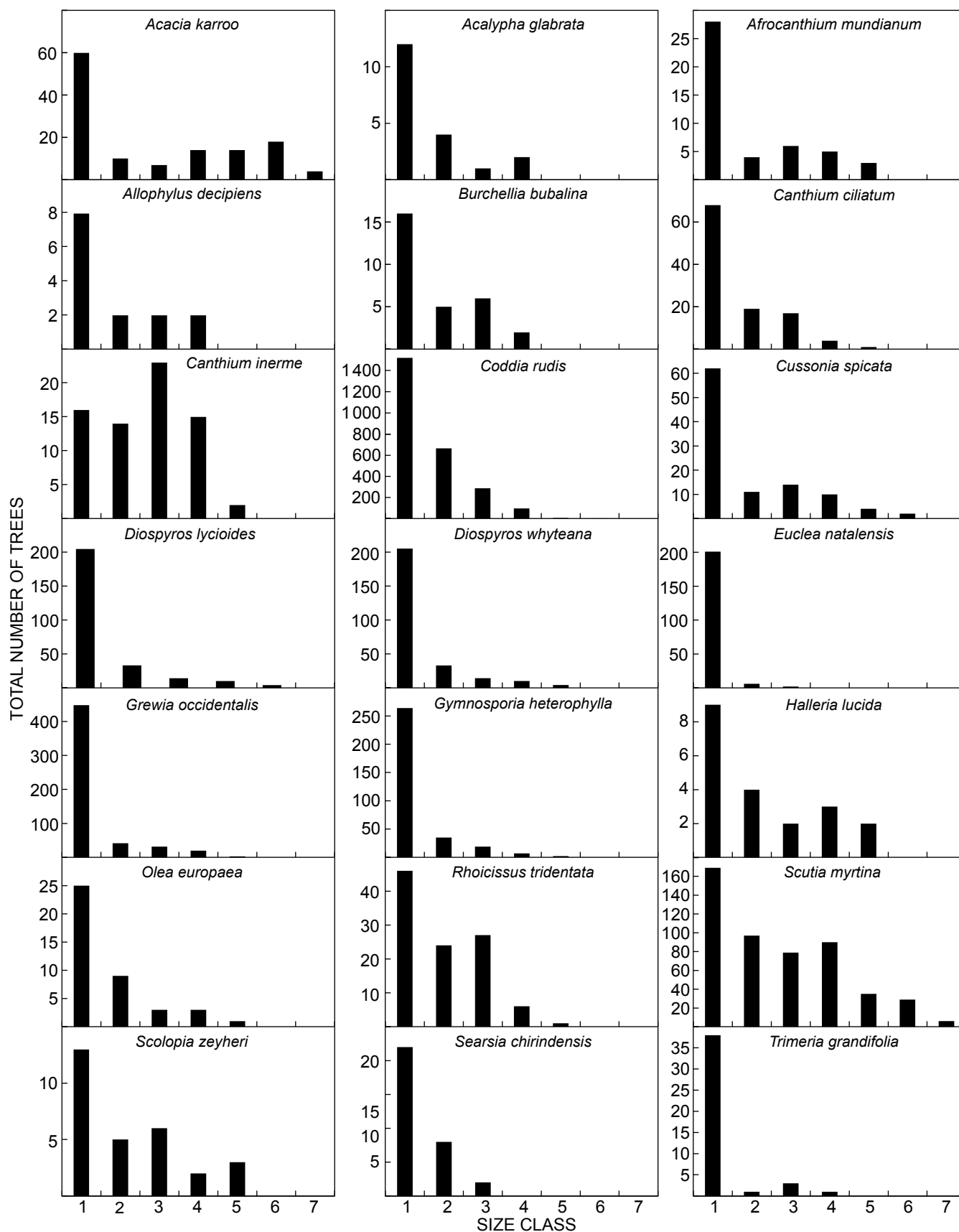


Figure 11: Total number of trees of stem diameter size classes in 40 clumps for 21 species in the Kei Raod region of the Eastern Cape. The stem diameter size class codes are: 1, ≤ 1.5 cm; 2, $>1.5-3$ cm; 3, $>3-5$ cm; 4, $>5-10$ cm; 5, $>10-15$ cm; 6, $>15-25$ cm; 7, >25 cm

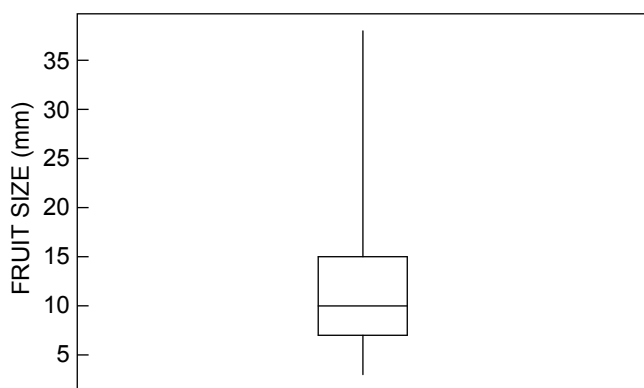


Figure 12: Box-and-whisker plot of fruit size diameter (mm) for woody species ($n = 41$) found in bush clumps ($n = 40$) in the Kei Road region of the Eastern Cape

Although a palatable shrub species, it is tolerant of defoliation (Hester et al. 2006). It was expected that other shrub species would also be best positioned on a clump's periphery in order to gain adequate irradiance, but only one species showed a non-random preference for the periphery (Table 3). Clumps were in an expanding phase as evidenced by the high proportion of small individuals (Figure 10), which accords with the doubling in woody cover between 1963 and 1986 in the Eastern Cape (O'Connor and Crow 1999).

It was expected that the pattern of bush clump development described for this study site would closely approximate the pattern recorded for savanna parkland in Texas. The similarities are striking, although there are some nuances of difference. In Texas, the microphyllous legume *Prosopis glandulosa* is effectively the only species that serves as a clump initial (Archer et al. 1988); *A. karroo*, also a microphyllous legume species, is the main initial species of clumps in the Eastern Cape, but some animal-dispersed species apparently also serve this role (Table 1). The size of clumps was similar, with most at either locality $<100 \text{ m}^2$ in size. Clump area was related to the size of the initial tree. Clump development showed a well-defined successional sequence in both cases. Species richness and diversity of clumps increased with increasing clump size in both cases; evenness showed this trend in Texas but not in this study. The total number of species recorded in larger clumps was, however, higher in the Eastern Cape (20% of clumps contained >20 species, maximum = 38) than in Texas (maximum = 15) (Archer et al. 1988). In both cases, species other than the clump initial were characterised by a high density of small individuals. Clump development occurred primarily during sequences of above-average rainfall years in the Eastern Cape (O'Connor and Crow 1999) and Texas (Archer et al. 1988, Archer 1989; Scanlan and Archer 1991). Clumps at both sites were young and expanding (Archer 1989). Birds were considered to be the only agent for dispersal of fruits in Texas (Archer 1995), but mammals were possibly important agents in the Eastern Cape.

A similar pattern of bush clump development has been described for a comparable environment in KwaZulu-Natal, South Africa (Gower et al. 1992). In this case, degrading

termitaria provided a site for establishment of *Acacia nilotica*, a well-known bush encroachment species, that in turn facilitated a nucleation process involving a number of species recorded in this study, such as *Burchellia bubalina*, *Cussonia spicata*, *Dovyalis zeyheri*, *Ehretia rigida*, *Grewia occidentalis*, *Gymnosporia heterophylla* and *Ziziphus mucronata*. Although there were odd mounds of *Trinevitermes* sp. present in the study area, there was no indication that mounds (past or present) were the cause of clump formation.

Facilitation

The pattern of bush clump development recorded in this study is consistent with a facilitation model of autogenic succession (Connell and Slatyer 1977), but a descriptive study cannot reveal the nature of environmental change that has facilitated individual species. Bush clumps in the Eastern Cape have a moderating effect on microclimate compared with inter-clumps: maximum air temperatures are lower and minimums are higher, humidity is higher, and irradiance is reduced by 80–90% (Jarvel and O'Connor 1999). These factors would all improve water balance and thereby promote water-demanding species providing they are tolerant of low irradiance conditions. A large proportion of the clump species are known to be forest-edge species (Appendix 1) of surrounding forests that occur in areas of higher rainfall (Story 1952). Clumps improve soil fertility through inducing higher concentrations of soil carbon, nitrogen, phosphorus and potassium, and increasing pH and cation exchange capacity (Mordelet et al. 1993, Jarvel and O'Connor 1999). Although improved soil fertility would promote plant growth in general, it is not known which species would gain an advantage. Clumps reduce herbaceous production considerably (Archer 1995, Mordelet and Menaut 1995, Jarvel and O'Connor 1999), thereby reducing competition and excluding or weakening fire (Hochberg et al. 1994). This should promote forest-scrub species, which are well recorded to be fire intolerant (Westfall et al. 1983, Titshall et al. 2000). Individuals growing within the interior of a clump are protected from browsing (Hester et al. 2006). This is expected to benefit mainly palatable browse species such as *Cussonia spicata*. Palatability of many of the forest edge species is not known, but casual observation suggests that few of the forest-related species recorded in this study are sought by mammalian herbivores. This suggests that these species benefit from altered microclimate and/or soil conditions.

Why bush clumps?

In southern Africa, bush encroachment is generally associated with invasion or increase of microphyllous species that may transform grassland or savanna to open or closed woodland. There are many examples of other, e.g. broad-leaved, species becoming established through mainly bird dispersal under, but not extending much beyond, the canopy of an *Acacia* (Potts and Tidmarsh 1937, du Preez and Venter 1990, Smith and Goodman 1987, Skowno et al. 1999, Jordaan et al. 2004, Jordaan 2010). In these examples, closed canopy woodland apparently forms if *Acacia* individuals form a closed canopy. The pattern reported for this study is distinct in that spatially discrete

bush clumps form through nucleation around an *Acacia* (or other) initial, with the clump attaining a size well in excess of the size of the initial tree. A spatial pattern of bush clumps of this nature is apparently not commonplace in South Africa. Apart from this study, bush clumps have been described in South Africa for a few mesic localities (van Rooyen 1983, Gower et al. 1992, van der Linden et al. 2005). Other examples of bush clumps in mesic environments are from Texas, USA (Archer et al. 1988) and Côte d'Ivoire in West Africa (Mordelet et al. 1993), although clumps also occur in non-grassland or savanna environments (e.g. Chilean matorral; Fuentes et al. 1984). Primary requirements are a suitable species to serve as a clump initial and one to promote clump expansion; in this study these roles were served by *A. karroo* and *C. rudis*, respectively. The small number of described locations in southern Africa precludes any other comment than noting commonalities of a mesic environment, an apparently relatively rich pool of bird-dispersed species that benefit from clump conditions, and possible disruption of the fire regime. Texas, USA, is the only case with a well-investigated history of bush clump development, in which their proliferation owes to anthropogenic perturbation of landscape-level disturbance regimes of fire and grazing (Archer 1990, 1995). Superficially, this would apply to the Eastern Cape. Bush clumps are therefore postulated to be primarily a transient vegetation form between grassland and closed woodland.

Management implications

The most common management objective for livestock ranching in the Eastern Cape savannas is to control bush in order to increase grass production, although an alternative of utilising bush for production of browsers has gained increasing recognition (Smit et al. 1999). Efforts to control bush encroachment would have to contain the initiation of clumps through preventing regeneration of *A. karroo* and contain the expansion of clumps. The success of using fire and goats together in order to achieve the latter has been well demonstrated in the Eastern Cape (Trollope 1980, Trollope and Tainton 1986). Traditional management approaches of mechanical or chemical clearing also require subsequent use of fire and browsing to ensure long-term effectiveness (Trollope et al. 1989). Even browsing on its own may contain clump expansion (Watson 1999, Hester et al. 2006). Preventing seedling regeneration of *A. karroo* would appear difficult (Story 1952, O'Connor 1995) unless fire is used regularly.

Biodiversity conservation is beginning to emerge as an additional objective of livestock ranching systems (O'Connor et al. 2010b). Development of bush clumps within former grassland could add 40 or so additional plant species, plus create habitat for a number of frugivorous or woodland-dependent bird species and browsing mammals. This should increase local biodiversity and habitat heterogeneity markedly. It is, however, obviously at the expense of grassland biodiversity, a number of whose less common species are potentially threatened by habitat loss through bush encroachment (e.g. Skowno and Bond 2003). Owing to a need for increased conservation of grassland in South Africa (Reyers and Tosh 2003), bush encroachment cannot be justified on biodiversity grounds.

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Appendix 1: List of woody species encountered in bush clumps in the Kei Road region of the Eastern Cape

Species	Growth form	Habitat
<i>Acacia karroo</i>	Tree	Savanna
<i>Acalypha glabrata</i>	Small tree	Forest
<i>Afrocanthium mundianum</i>	Tree	Forest margin
<i>Allophylus decipiens</i>	Tree	Forest margin
<i>Apodytes dimidiata</i>	Tree	Forest
<i>Asparagus</i> sp.	Shrub	Bushveld
<i>Burchellia bubalina</i>	Shrub	Grassland–forest margin
<i>Canthium ciliatum</i>	Small tree	Scrub forest
<i>Canthium inerme</i>	Tree	Bushveld–forest margin
<i>Capparis sepiaria</i>	Scrambling shrub	Bushveld–forest
<i>Carissa bispinosa</i>	Shrub	Scrub forest
<i>Chaetacme aristata</i>	Tree	Woodland–forest
<i>Coddia rudis</i>	Shrub	Bushveld–forest margin
<i>Croton</i> sp. (<i>sylvaticus</i> ?)	Tree	Forest margin
<i>Cussonia spicata</i>	Tree	Bushveld–forest margin
<i>Diospyros lycioides</i>	Shrub–small tree	Bushveld–forest margin
<i>Diospyros scabrida</i>	Shrub	Bushveld–forest margin
<i>Diospyros simii</i>	Shrub	Forest margin
<i>Diospyros whyteana</i>	Shrub	Scrub forest
<i>Dovyalis rhamnoides</i>	Shrub	Bushveld–forest margin
<i>Dovyalis zeyheri</i>	Tree	Woodland–forest margin
<i>Elaeodendron croceum</i>	Tree	Forest margin
<i>Euclea natalensis</i>	Shrub	Bushveld–forest margin
<i>Grewia occidentalis</i>	Shrub	Bushveld–forest margin
<i>Gymnosporia heterophylla</i> subsp. <i>heterophylla</i>	Shrub	Bushveld–forest margin
<i>Halleria lucida</i>	Shrub–small tree	Forest margin
<i>Hippobromus pauciflorus</i>	Small tree	Forest margin
<i>Jasminum angulare</i>	Climber	Bushveld–forest
<i>Lippia javanica</i>	Small shrub	Grassland–bushveld
<i>Ochna natalitia</i>	Shrub–small tree	Bushveld–scrub forest
<i>Ochna serrulata</i>	Shrub	Bushveld–forest margin
<i>Olea europaea</i> subsp. <i>africana</i>	Tree	Bushveld–forest margin
<i>Pittosporum viridiflorum</i>	Tree	Forest margin
<i>Pleurostyliia capensis</i>	Tree	Bushveld–forest
<i>Putterlickia verrucosa</i>	Shrub	Bushveld
<i>Rhoicissus tridentata</i> subsp. <i>tridentata</i>	Scrambling shrub	Forest margin
<i>Rubus pinnatus</i>	Shrub	Scrub
<i>Searsia chirindensis</i>	Small tree	Forest margin
<i>Searsia rehmaniana</i> var. <i>glabrata</i>	Small tree	Bushveld, forest margin
<i>Searsia undulata</i>	Shrub	Bushveld–forest margin
<i>Scolopia zeyheri</i>	Tree	Bushveld–forest margin
<i>Scutia myrtina</i>	Small tree	Forest margin
<i>Secamone gerardii</i>	Climber	Forest
<i>Solanum</i> sp.	Small shrub	Disturbed
<i>Trimeria grandifolia</i>	Small tree	Forest margin
<i>Trimeria trinervis</i>	Small tree	Scrub forest–forest
<i>Vepris lanceolata</i>	Tree	Forest
<i>Zanthoxylum capense</i>	Tree	Bushveld–forest margin
<i>Ziziphus mucronata</i> subsp. <i>mucronata</i>	Tree	Bushveld