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Ecological drivers of *Seriphium plumosum* encroachment: Implications for management and conservation

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ABSTRACT

Seriphium plumosum is recognised as a highly encroaching species in the Grassland and Savanna Biomes of South Africa, particularly in degraded areas. This study investigated the impacts of biotic and abiotic factors on the density, height, and population structure of *S. plumosum* across two sites: Amathole Hogsback Plantation (HP, Eastern Cape) and Klipriviersberg Nature Reserve (KNR, Gauteng), which are both subjected to significant disturbances. Field sampling using the Point-Centered Quarter method along 9 (100 m) transects at each site identified 928 plants. At the HP site, *S. plumosum* density was the highest in recently burned middle slopes, followed by less recently burned bottom and top slopes. In contrast, at KNR, shrub density peaked in the middle slope with intermediate grazing, followed by slopes with heavy and minimal grazing, respectively. The population structure at KNR consisted predominantly of mature plants with few juveniles, whereas the HP site exhibited high densities of juveniles and young adults, indicating recent disturbances facilitating shrub proliferation. Our findings highlight the significant influence of disturbance (i.e., fire and grazing) on the distribution patterns of *S. plumosum* by creating favourable 'open niches'. Structural equation modelling identified disturbance and tree cover as critical factors at HP, while grass biomass dominated at KNR, highlighting site-specific biotic and abiotic influences on shrub proliferation. This study provides valuable insights into the dynamics of *S. plumosum* in response to varying environmental conditions, which is essential for informing effective land management strategies aimed at mitigating shrub encroachment and preserving biodiversity in similar ecosystems.

1. Introduction

Seriphium plumosum L. (Asteraceae), formerly known as *Stoebe vulgaris*, is a notorious encroacher in South African grassland and savanna biomes (Jordaan and Jordaan, 2007; Snyman, 2012a). Commonly known as 'Bankrupt bush' due to its association with financial distress among farmers (Snyman, 2010; Baltimore et al., 2017; Marquart et al., 2023), *S. plumosum* poses a significant threat to both farmers' livelihoods and ecosystems (Jordaan and Jordaan, 2007; Marquart et al., 2023). Over the past two decades, the rapid spread of *S. plumosum* has raised ongoing concerns, prompting it to be classified as an encroacher under the CARA legislation (Regulation 16 of the Conservation of Agriculture Resources Act 43; Snyman, 2010). Many factors, such as unregulated veld fires, soil degradation, and land mismanagement, have been shown to promote the proliferation of this encroaching shrub (Baltimore et al., 2017; Marquart et al., 2023). While landowners and farmers have tried to implement management practices to control the spread of *S. plumosum*, these practices have largely been unsuccessful (Snyman, 2012a).

The presence of *S. plumosum* significantly diminishes grazing capacity in affected areas by up to 80 % (Marquart et al., 2023). This is attributed in part to the ability of *S. plumosum* to secrete volatile oils, which serve as a defence mechanism, rendering the shrub unpalatable to animals (Snyman, 2010; 2012b). These chemicals, through allelopathy, also inhibit the germination and growth of its own seedlings as well as the spread of new propagules from the co-occurring plants in the vicinity of the *S. plumosum* (Dakshini et al., 2023; Marquart et al., 2023; Snyman, 2010). The seeds of this shrub can remain dormant in the soil for up to five years, awaiting favourable conditions for germination (Snyman, 2012a; Dakshini et al., 2023). The seedlings are also known to be highly susceptible to harsh environmental conditions and direct sunlight (Cohen, 1935; Snyman, 2010). However, once the seedlings have established, the shrub typically grows beneath the canopy of other shrubs or grasses to shield itself

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from direct sunlight until reaching maturity (Snyman, 2010; Dubula et al., 2016).

The slope position preferences of *S. plumosum* have been extensively studied (Snyman, 2010; 2012a). According to Snyman (2012a), the shrub thrives in heavily disturbed rocky environments with a rainfall range of 620 to 750 mm. While earlier research by Davidson (1962) and Hattingh (1953) attributed the encroachment of *S. plumosum* more to low soil fertility than to overgrazing, recent studies by Adepoju et al. (2020) suggest that it tends to proliferate in regions characterised by low rainfall, high diurnal temperature variation, and heavy grazing pressure. Despite these differences, disturbed slopes appear to provide opportunities for the proliferation of this shrub. *S. plumosum* appears to prefer sandy soils with low pH (Snyman, 2012a) but can also thrive in clay soils with good drainage (Wepener et al., 2007). The shrub is rarely found in wet, fertile areas and commonly inhabits rocky hill slopes, initially establishing on southern slopes, which typically exhibit higher soil fertility (and are generally cooler), before spreading to the valleys (Snyman, 2010; 2012b; Pule et al., 2018). Over time, *S. plumosum* forms dense stands, which is characteristic of typical wind-pollinated plants (Burgoyne et al., 2005), and many Asteraceae weeds.

The prolific encroachment of *S. plumosum* poses significant challenges for South African farmlands, as the shrub lacks natural enemies (Marquart et al., 2023). This encroachment has far-reaching consequences, especially for regions reliant on livestock farming. The invasion not only diminishes grazing capacity but also affects the economic viability of affected areas (Snyman, 2012a). Consequently, there is a pressing need for effective control measures that strike a balance between economic sustainability and ecological integrity. Various studies have explored methods for managing the shrub, yet none have proven entirely effective (Snyman, 2012a; Marquart et al., 2023). While herbicides can curb its growth, the shrub often regenerates despite treatment, and herbicides generally have deleterious, non-target effects, on the plant community (Goodall et al., 2022). Research has shown that fires do not completely eradicate *S. plumosum*, as dormant seeds can germinate post-burn (Snyman, 2012a). However, the effectiveness of fire in controlling this shrub is still debatable, with some studies suggesting that the interactive effects of fire and livestock grazing can reduce its height and canopy cover (Clark et al., 2020). The manual removal of *S. plumosum* has had some success; however, it presents additional challenges due to financial constraints and the risk of residual plant remnants sprouting under favourable conditions (Marquart et al., 2023). Although chemical methods are also commonly used to control woody shrubs like *S. plumosum*, they can be expensive and may have unintended environmental consequences (du Toit, 2012; du Toit and Sekwadi, 2012). Therefore, finding sustainable solutions to mitigate the encroachment of this shrub is imperative to protect both the economic interests and environmental stability in South Africa.

Without proper monitoring and management, the unchecked spread of this aggressive encroaching shrub could lead to significant economic losses in the farming industry and the displacement of natural vegetation. Studies by Snyman (2010; 2012a) have highlighted the potential consequences of *S. plumosum* encroachment, including declines in biodiversity and disruptions to ecosystem functioning. Therefore, this study aims to (i) assess the density, size (height) structure, and distribution of *S. plumosum* across different slopes and (ii) identify the key biotic and abiotic factors driving the variation in shrub density, height and distribution. We hypothesised that (i) *S. plumosum* density and height will be higher in middle slopes compared to bottom and top slopes, as middle slopes often exhibit more favourable conditions for shrub growth, such as moderate soil moisture, better drainage, and low nutrient availability. We also hypothesised that (ii) abiotic factors, such as rock cover and disturbance, play a more substantial role in determining shrub density than biotic factors, such as grass and tree competition. These ecological insights could aid in developing more effective control measures of the shrub that may be implemented by both landowners and farmers.

2. Materials and methods

2.1. Study area

Data was collected at two sites within South Africa. The first site, Klipriviersberg Nature Reserve (KNR), is located in Gauteng, while the second site, the Amathole Hogsback Plantation (HP), is located in the Amathole Mountains of the Eastern Cape Province. KNR, the largest nature reserve in Johannesburg, covers 680 hectares at an altitude of 1712 m a.s.l. (26.289467° S, 28.011° E; van Rooyen and van Rooyen, 2014). This reserve was selected as a study site due to its known heavy grazing. The vegetation at KNR is characterised as *Themeda triandra - Acacia karroo* microphyllous woodland, situated within the Andesite Mountain bushveld of the central bushveld bioregion of the Savanna Biome (Mucina and Rutherford, 2006; Cousins et al., 2014). The landscape includes hills, rocky ridges, valleys, grassy plains, and drainage lines (van Rooyen and van Rooyen, 2014). The mean annual rainfall is 660 mm (ranging from 550 mm to 750 mm), primarily occurring from October to March, with a dry season from June to August (van Rooyen and van Rooyen, 2014). Temperature ranges from 5.6 °C to 35 °C, and frost is common from April to October (Cousins et al., 2014).

In contrast, HP (32.5833° S, 26.9500° E) has a high prevalence of non-native tree plantations, and it was chosen due to the frequent fires associated with timber harvesting. Specific slopes are targeted for timber harvests, followed by intentional fires to clear the remaining vegetation for new plantation cycles. These frequent fires and plantation cycles are disturbances that likely contribute significantly to the proliferation of *S. plumosum* in this area. HP includes both human-modified and natural slopes dominated by indigenous Afromontane Forest vegetation and alpine grasslands within the Maputaland–Pondoland–Albany key biodiversity conservation area (Mucina and Rutherford, 2006). Covering a total area of 1378 hectares at an altitude of 1200–1300 m a.s.l., HP experiences significant human disturbances due to tourism and has been a centre of the South African timber industry for over a century (Xulu et al., 2019). The area consists of non-native timber plantations: with 50 % pine (including other conifers such as *Cedrus*, and *Cupressus* species), 43 % Eucalyptus, and 7 % wattle (commercial plantations of *Acacia mearnsii* and small areas of other alien *Acacia* species) (Xulu et al., 2019) tree species. These tree plantations cause major environmental disturbances as the herbicides and fertilisers used in these areas harm indigenous species and contaminate the natural forest ground cover and soil (Xulu et al., 2019), with some studies indicating that herbicides have an even greater impact on soil pollution (Marin-Morales et al., 2013; Singh et al., 2020). Ambient temperatures in Hogsback range from below freezing between June and August to over 30 °C on hot summer days in February (Mucina and Rutherford, 2006). The area receives an average annual rainfall of 974 mm, mostly during summer, which is often accompanied by thunderstorms.

2.2. Field sampling

2.2.1. Plant density

To establish an initial framework for our sampling approach, one slope at each site where *S. plumosum* was observed to be abundant was chosen. The slopes were then further divided into three main slope positions: top, middle and bottom, providing distinct sampling locations within each study area. Field sampling comprised 9 (100 m) transects parallel to the slope (3-top ridge, 3-middle ridge, 3-bottom ridge) at each site, and the Point Centered Quarter method (PCQ) was used as the main sampling technique. Transects at the HP site were established within plantations that varied in their burning histories.

PCQ points were spaced every 5 m along each 100 m transect, and the distance from the PCQ point to the centre of the closest *S. plumosum* within each quarter was measured. Each quarter had a restriction distance of 10 m from the point where the transect was laid, and a plant was not sampled twice by marking the sampled plants with red tags. Although this should yield 80 plants per transect, there were some empty quarters (plants > 10 m away) which were recorded as blanks (Warde and Petranka, 1981). In order to account for the empty quarters where individuals were absent, a correction factor was used, and the density of *S. plumosum* was calculated as:

$$\text{Total density } (plant.ha^{-1}) = \frac{1}{\text{mean distance } (m)^2} X\ CF\left(\frac{n_o}{n_k}\right) X\ (10\ 000) \quad (1)$$

Where CF was the correction factor, n_0 was the number of quadrants in which data were missing, and n_k was the total number of sample quadrants (Warde and Petranka, 1981). Values of the correction factor (CF) are provided in Table 1 of Warde and Petranka (1981), where CF is based on the percentage of quarters in which data are lacking.

2.2.2. Canopy area and reproductive stage

Within each quarter of the PCQ, at each 5 m point along the 100 m transect, each plant considered had its height and canopy diameter measured (using a measuring tape), as well as its stage class determined. To determine the stage and size structures of the populations of *S. plumosum,* growth was assessed by measuring the canopy sizes (crown) of mature adults, young adults and juveniles. Canopy area was calculated by measuring the widest canopy diameter ($diameter_1$) and the widest diameter at 90° ($diameter_2$; Witkowski and Garner, 2008). Canopy area was then determined using the formula presented by Pfab and Witkowski (1999):

$$\text{Canopy area} = \pi \frac{Diameter_1}{2} X \frac{Diameter_2}{2} \quad (2)$$

Stage classes at each site were classified as mature adults, young adults, and juveniles. Mature adults were plants with a woody and grey stem base, which is evidence of surviving at least one year of winter, while juveniles had a green stem base (Avenant, 2015). On the other hand, young adults were neither mature nor juvenile plants, with a relatively low proportion of a grey base and a thin semi-green stem. The canopy area size classes were delimited in 0.2 m^2 increments as follows: 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.2, 2.4 and lastly >2.4. Larger canopy areas were expected in mature plants, while juveniles had smaller canopies, with young adults being intermediate.

2.2.3. Biotic and abiotic factors promoting the density of S. plumosum

In addition to the density and canopy area of *S. plumosum*, the level of disturbance, rock cover, grass biomass and tree cover at each 5 m point along the transect were determined. To determine the disturbance levels, a scale ranging from 0 to 5 was utilised, where 0 indicated no disturbance or minimal tree and rock cover, and 5 represented significant disturbance or extensive tree and rock cover (Supplementary Material). Specifically, the disturbance levels were determined based on the presence of litter (from humans), animal dung, animal footpaths, as well as any evidence of plants being trampled or rooted out (Supplementary Material). For the rock cover assessment, we considered the composition of soil and rocks, with scores ranging from 0 (very fine soils, with no rocks) to 5 (mainly large rocks), whereas, for tree cover level, we considered the proportion of *S. plumosum* covered by tree shade, with 0 being no trees around *S. plumosum* and 5 being completely shaded by trees (Supplementary Material). Grazing was categorised into low, intermediate, and heavy levels while burning history was classified into recently burned, less recently burned, and longest time since burned (Supplementary Material). These categories were used to determine the dominant disturbances across each slope. These details were obtained from site management.

Herbaceous biomass was estimated using Disc Pasture Meter (DPM) height readings, following the methodology described by Zambatis et al. (2006). Grass height was also measured in situ using a measuring tape to complement the DPM height readings and ensure accurate height measurements for comparison across sites. The DPM height readings were categorised into two groups as those with heights ≤ 26 cm and those with heights > 26 cm. Biomass for DPM readings less than or equal to 26 cm were estimated using the following equation:

$$\text{Grass Biomass } (kg\ ha^{-1}) = \left[31.7176\left(0.3218\frac{1}{x}\right)x^{0.2834}\right]^2 \quad (r^2 = 0.951; P < 0.0005) \quad (3)$$

For DPM readings greater than 26 cm, biomass was estimated using the following equation:

$$\text{Grass Biomass } (kg\ ha^{-1}) = \left[17.3543(0.9893^x)x^{0.5413}\right]^2 \quad (r^2 = 0.882; P < 0.0005) \quad (4)$$

Where x is the mean DPM height in cm of a site.

2.3. Data analysis

Data analysis was performed using R Studio version 4.0.5 (Team, 2015). A Kolmogorov-Smirnov test was conducted on canopy area size classes to determine if the distributions of *S. plumosum* in different slopes differed both within and between sites. To assess the association between slope position and the distribution of different stage classes within each site, a chi-squared test was conducted to determine whether there was a significant association between the observed frequencies under the assumption of independence between the two categorical variables (slope position and stage class distribution). To examine potential differences between *S. plumosum* as well as grass height across sites, a one-way analysis of variance (ANOVA) was conducted with $p < 0.05$. We performed two-way ANOVAs to examine the effects of slope position and site on

Table 1
Numbers (and % per stage class) of *Seriphium plumosum* individuals per habitat with transect sampling at Amathole Hogsback Plantation (HP) and the Klipriviersburg Nature Reserve (KNR), with altitude and dominant disturbance.

Site	Habitat	Mature adults (n)	Young adults (n)	Juveniles (n)	Total plants sampled (n)	Altitude (m.a.s.l)	Dominant disturbance
HP	Top	202 (96)	7 (3.5)	1 (0.5)	210	1187	Burned (>5 years)
	Middle	176 (84.2)	3 (1.4)	30 (14.4)	209	1166	Burned (<1 year)
	Bottom	78 (38.1)	87 (42.4)	40 (19.5)	205	1140	Burned (<3 years)
KNR	Top	179 (80.6)	28 (12.6)	15 (6.8)	122	1780	Heavy grazing
	Middle	122 (79.7)	29 (19.0)	2 (1.3)	153	1612	Medium grazing
	Bottom	28 (96.6)	1 (3.4)	0 (0)	29	1542	Low grazing

disturbance, tree cover and rock cover. The model included the interaction term between slope and site to explore potential combined effects on each variable. Additionally, a factorial ANOVA was used to analyse the effects of slope, site, and level of disturbance (grazing pressure and fire intensity) on the density of *S. plumosum*, including interaction terms for potential combined effects. Lastly, a structural equation model (SEM) was performed using the 'piecewiseSEM' library (Lefcheck, 2016) to identify the biotic and abiotic factors that promote the proliferation of *S. plumosum* at Klipriviersberg Nature Reserve and the Amathole Hogsback Plantation. The dependent variable was the density of *S. plumosum*, while the independent variables included the percentage of rock cover, disturbance, grass biomass, and percentage of tree cover. The model also examined the influence of rock cover and disturbance on grass biomass and tree cover, which serve as intermediate variables in the model. This was done to assess the direct and indirect effects of these abiotic and biotic factors on the density of *S. plumosum*. The formulation of the SEM was based on prior ecological knowledge regarding the key factors influencing the density of *S. plumosum*. The relationship between grass biomass and tree cover, as well as between rock cover and disturbance, were not computed as these links were considered less ecologically relevant based on previous studies. Models were selected based on their overall goodness of fit using AIC values.

3. Results

The two sites exhibited distinct patterns of dominant disturbances (Table 1). At the HP site, burning was the primary disturbance factor, with distinct patterns observed across slope positions. The top slope had the longest period without a controlled burn, followed by a recent burn in the middle and a less recent burn in the bottom slope (Table 1). Conversely, at KNR, grazing intensities played a more significant role, with heavy grazing observed at the top, medium grazing in the middle, and low grazing at the bottom slope (Table 1). These findings suggested that the ecological dynamics at each site were influenced by distinct factors, highlighting the importance of considering both biotic and abiotic factors in ecosystem management and conservation efforts.

3.1. Patterns of population structure

Chi-squared analyses revealed significant differences in the distribution of *S. plumosum* across and within sites. At the HP site, there was a highly significant association between slope position and the distribution of different stage classes ($\chi^2 = 231.1$, df = 4, $p < 0.001$; Table 1). This indicated that the proportion of mature adults, young adults, and juveniles varied considerably across the top, middle, and bottom slopes. The young adults and juveniles were particularly more prevalent at the bottom slope, which had experienced a burn less than three years ago (Table 1), than at the top slope (juveniles: $\chi^2 = 37.1$, df = 1, $p < 0.001$; young adults: $\chi^2 = 68.1$, df = 1, $p < 0.001$), which burned >5 years ago. However, there was no significant difference in the prevalence of young adults between the bottom and middle slopes ($\chi^2 = 1.43$, df = 1, $p = 0.23$), though juveniles were still significantly more prevalent at the bottom than the middle slope ($\chi^2 = 37.1$, df = 1, $p < 0.001$) which had burned less than one year ago. Similarly, at the KNR site, there was a significant, though less pronounced, association between slope position and stage class distribution ($\chi^2 = 13.719$, df = 4, $p = 0.008$). At this site, there was no significant difference in the distribution of young adults between the top and middle slopes ($\chi^2 = 0.018$, df = 1, $p = 0.89$), likely due to high levels of grazing. However, the proportions of young adults in both the top and middle slopes was higher than the bottom slope, which experienced lower grazing levels ($\chi^2 = 26.103$, df = 2, $p < 0.01$). There were also more juveniles at the top slope than at the bottom ($\chi^2 = 15$, df = 1, $p < 0.001$). These findings suggested a difference in the distribution of stage classes across the three slope positions within both the HP and KNR sites. However, stage classes at the HP site were more substantially associated with slope position. At the HP site, adults were predominantly found in the higher-lying areas, while juveniles were mainly distributed across the lower and middle slopes, with young adults showing a preference for the bottom slope. In contrast, at the KNR site, mature adults and juveniles were more common in the top and middle slopes, with juveniles only being associated with the top slope. Overall, the results indicated that slope position and disturbance level influenced the distribution of *S. plumosum* stage classes, with the HP site showing a stronger association (Table 1).

In addition to the population structure, further evidence illustrated how slope and disturbance influenced the distribution and dynamics of *S. plumosum* populations (Fig. 1). All populations within and between the sites exhibited left-skewed distributions, indicative of an inverse-J size class distribution (SCD), which is often associated with high levels of recent recruitment. This pattern suggests that while each site displayed an inverse-J distribution, the extent of this distribution may be influenced by specific slope characteristics and disturbance history. The results of the Kolmogorov-Smirnov (KS) tests highlighted significant differences in size class distributions between certain KNR slopes and their corresponding HP slopes. Comparisons of the top slopes at the KNR and HP sites ($D = 0.28205$, $p = 0.04859$) and the bottom slopes at both sites ($D = 0.28205$, $p = 0.009954$) revealed significant differences, indicating distinct variations in size class distributions between these corresponding sites. Within the KNR slopes, notable differences were also observed. The top and middle slopes at the KNR site showed a difference ($D = 0.33333$, $p = 0.009863$), as did the middle and bottom slopes ($D = 0.23077$, $p = 0.03659$). The most pronounced difference was between the bottom and top slopes ($D = 0.53846$, $p < 0.001$), indicating substantial variation in size class structure. In contrast, comparisons among the HP slopes yielded non-significant results (top and middle slopes: $D = 0.20513$, $p = 0.1565$; middle and bottom slopes: $D = 0.076923$, $p = 0.937$; bottom and top slopes: $D = 0.17949$, $p = 0.2646$), suggesting similar size class distributions across these slopes. These findings highlight that while the overall recruitment pattern of *S. plumosum* followed an inverse-J distribution, subtle variations in the size-class distributions suggested site-specific differences in population structure.

In the KNR, populations showed a high proportion of mature adults alongside significant recruitment of juveniles (Fig. 1). Conversely, the HP site generally exhibited a higher proportion of juveniles compared to the KNR site ($\chi^2 = 350.59$, df = 1, $p < 0.001$). This balanced distribution of mature and juvenile individuals suggested a stable and well-established community, with continuous recruitment and a higher proportion of juveniles at the HP than at the KNR site. This pattern further supported the observation that topography and disturbance levels significantly influenced stage class distribution and population dynamics across both sites.

3.2. Impact of biotic and abiotic factors

Biotic and abiotic factors both generally impacted the distribution of *S. plumosum*. Among the biotic factors analysed, grass height positively correlated with the height of *S. plumosum* at both the HP and KNR sites. The results showed a statistically significant difference in grass height between the sites ($F(1,254) = 36.78$, $p < 0.001$), with HP having taller grasses than KNR (Fig. 2A). Additionally, regression analyses revealed that the competition between *S. plumosum* and grasses was higher at KNR ($R^2 = 0.63$, $p < 0.001$) compared to HP ($R^2 = 0.19$, $p = 0.03$; Fig. 2A). These findings indicate that the height of *S. plumosum* at both sites did not suppress grass height. Tree cover, another biotic factor analysed, was measured as the proportion of *S. plumosum* covered by tree shade. Similar to grass height, tree cover also

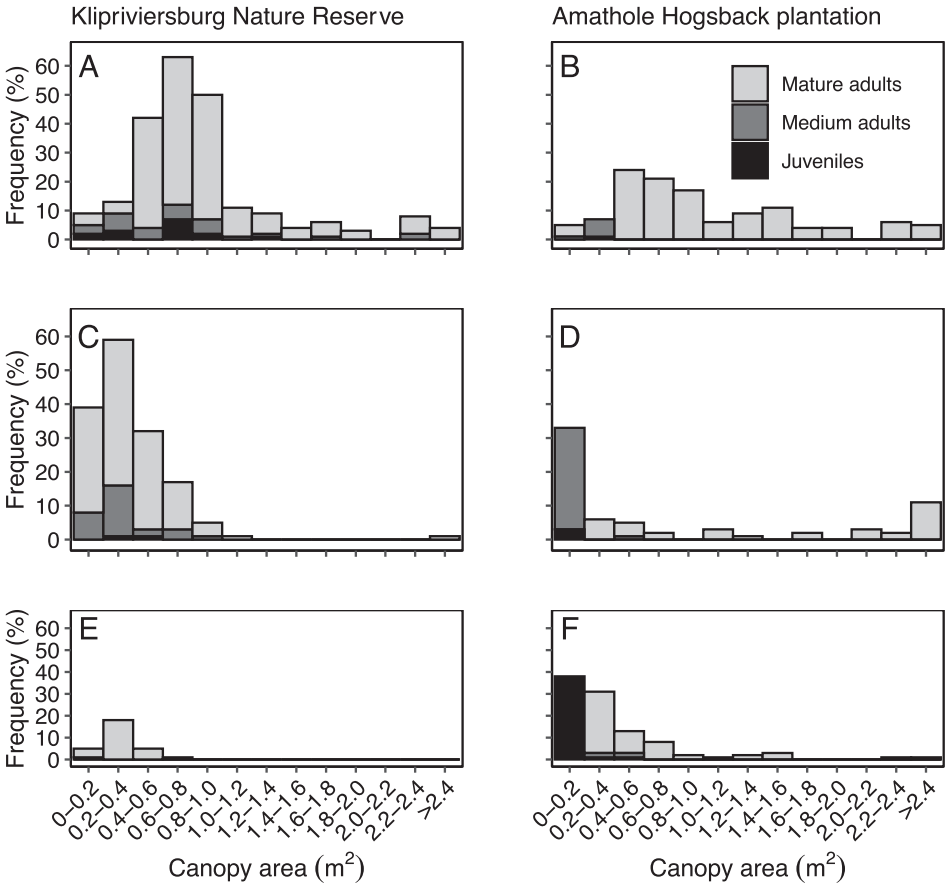

Fig. 1. Canopy area (m^2) size frequency distribution of *Seriphium plumosum* at the top (A, B), middle (C and D) and bottom (E and F) ridge at the Klipriviersburg Nature Reserve (A, C and E) and Amathole Hogsback plantation (B, D and F).

showed significant differences across slope positions (F (2,254) = 14.257, $p < 0.001$) and between the sites (F (1,254) = 5.877, $p = 0.016$), with KNR having higher tree cover than HP. Within HP, tree cover was highest at the top (12 %), and very low at the other two slope positions (<1 %; $p < 0.05$; Fig. 2D). In contrast, within KNR, the bottom (10.7 %), middle (6.7 %) and top slopes (7.7 %) showed no significant difference in tree cover ($p = 0.99$; Fig. 2D). This indicates that while tree cover had minimal impact on *S. plumosum* at HP, it had no significant effect at KNR.

Abiotic factors also had contrasting effects on the distribution of *S. plumosum*. Rock cover, a crucial abiotic factor largely associated with the prevalence of *S. plumosum*, varied significantly across the three slopes (F (2,254) = 15.49, $p < 0.001$) and between the sites (F (1,254) = 279.01, $p < 0.001$). Within HP, the bottom slope had the highest rock cover (25 %; $p < 0.01$) compared to the middle (4.23 %) and top slopes (0.034 %) which showed no significant difference ($p > 0.05$; Fig. 2C). The high rock cover at the bottom slope within HP was largely associated with the high number of juveniles found at the bottom slope (Fig. 2C). Conversely, at the KNR site, rock cover was higher at the top slope (49.2 %; $p < 0.001$), compared to the middle (24.2 %) and then bottom slopes (26.8 %) which were not significantly different ($p > 0.05$; Fig 2C). The high rock cover at the top slope in KNR was also strongly associated with the observed high growth of *S. plumosum* (Fig. 2). Similarly, the level of disturbance observed at each slope affected the prevalence of the shrub. The level of disturbance, as an abiotic factor, varied considerably between slopes (F (2,254) = 4.982, $p < 0.01$) and sites (F (1,254) = 31.162, $p < 0.001$). Within HP, disturbance levels were not very variable, with relatively higher levels at the top slope (21.8 %), followed by the middle (21.4 %) and then the bottom slope (20 %; $p < 0.05$; Fig. 2B). At the KNR site, there was no significant difference in disturbance levels between the slopes ($p > 0.05$; Fig 2B). Thus, the local disturbance within each slope did not strongly affect the prevalence of *S. plumosum*. Between the sites, the level of disturbance was significantly higher in HP, which experiences frequent burns, compared to KNR ($p < 0.001$), which is heavily impacted by grazing pressure. Therefore, both biotic and abiotic factors differentially promoted the proliferation of *S. plumosum* across slope positions and sites.

The density of *S. plumosum* also differed significantly across slope positions (F (2,254) = 4.088, $p = 0.0179$) and between sites (F (1,254) = 22.342, $p < 0.0001$) depending on the main disturbance (Fig. 2E). There was a significant interaction between slope position and site (F (2,254) = 4.436, $p = 0.0128$). Within the HP site, the middle slope had a significantly higher mean density than the bottom and top slopes ($p < 0.001$), while the top and bottom slopes showed no difference in density ($p = 0.94$). At KNR, there was no significant difference in density between the top, middle, and bottom slopes ($p = 0.57$, $p = 0.09$ and $p = 0.971$, respectively). These findings suggested that the differences in abiotic factors across slopes did not significantly affect the density of *S. plumosum*. However, the type of disturbance significantly influenced the density of *S. plumosum*, with higher density observed at HP, where previous burns were implemented, and lower densities at KNR, where grazing was the main disturbance.

Using structural equation modelling (SEM), the impact of biotic and abiotic factors on the distribution of *S. plumosum* between the sites was analysed (Fig. 3). At the HP site, rock cover negatively affected both grass biomass ($p < 0.001$) and tree cover ($p < 0.005$), but it did not significantly affect the density of *S. plumosum* ($p = 0.08$; Fig 3). Conversely, the level of disturbance at the HP site negatively

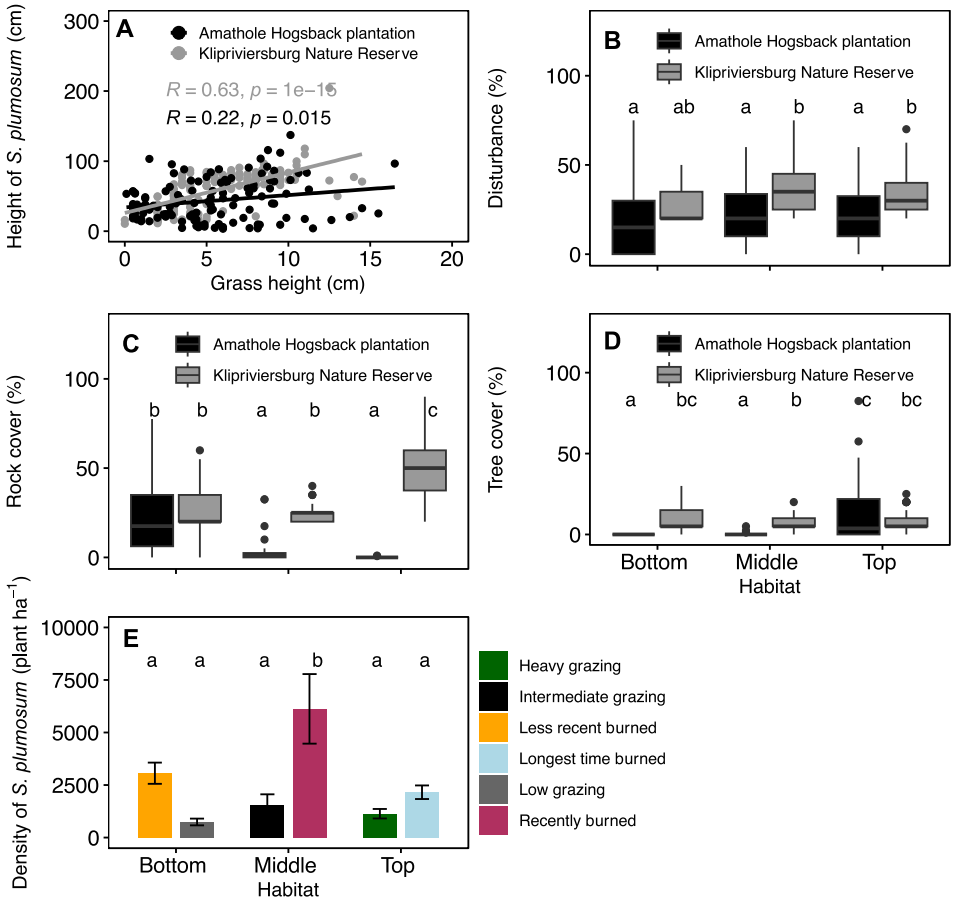

Fig. 2. Relationship between the height of *Seriphium plumosum* and grass height (a), level of disturbance (b), rock cover (c), tree cover (d) and the type of disturbance (e) prevalent at each habitat within the Klipriviersburg Nature Reserve and Amathole Hogsback plantation. Each point represents the number of sampled plants in each habitat within a site. Black represents measurements at the Amathole Hogsback Plantation (frequent fires), while grey represents the Klipriviersburg Nature Reserve (grazing pressure). Letters a to c show the levels of significance between habitats and across sites using the Tukey post hoc test.

affected grass biomass ($p < 0.001$) but positively affected both tree cover ($p < 0.005$) and the density of *S. plumosum* ($p < 0.001$). This indicated that disturbance levels were positively associated with the density of the shrub. Biotic factors had a similar influence on the density of *S. plumosum*. While grass biomass negatively affected the density of the shrub, this effect was not significant ($p > 0.05$). However, tree cover had a significant positive effect on shrub density ($p < 0.005$). Although direct relationships between shrub density and both rock cover and grass biomass were not evident, the positive association between disturbance and tree cover suggested potential indirect effects on the growth of *S. plumosum*. At the KNR site, grass biomass was the only factor that significantly affected the density of *S. plumosum* ($p < 0.01$). Neither rock cover ($p > 0.05$), level of disturbance ($p > 0.05$), nor tree cover ($p > 0.05$) significantly affected the

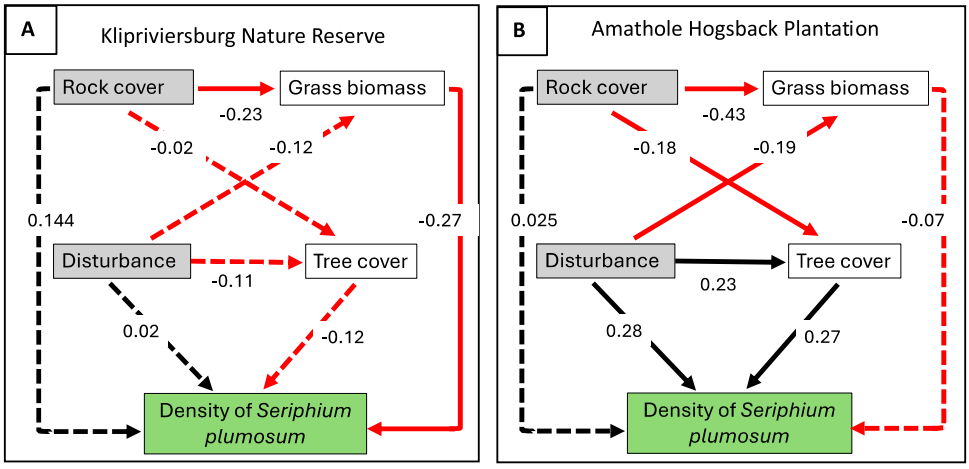

Fig. 3. Structural equation modelling (SEM) depicting the factors affecting the density of *Seriphium plumosum* at the Klipriviersburg Nature Reserve (A) and Amathole Hogsback Plantation (B). Path coefficients represent the strength and direction of relationships between variables. Solid arrows indicate significant paths, while dashed arrows indicate non-significant paths. Red arrows are negative paths, while black arrows are positive paths.

shrub's density. These findings highlighted the complex interactions between biotic and abiotic factors that influence the distribution of *S. plumosum* and suggested that site-specific conditions should be considered in management strategies.

4. Discussion

This study assessed the influence of biotic and abiotic factors on the density, height and population structure of *S. plumosum*, focusing on how these factors vary across different slope positions. Our findings revealed distinct differences between the two sites, HP and KNR, regarding the factors driving shrub proliferation. At the HP site, we observed tall grasses, high rock cover and disturbance levels, as well as short, dense *S. plumosum*. In contrast, the KNR site had short grasses and tall, less dense *S. plumosum*. This suggested that different combinations of environmental factors lead to distinct growth patterns of *S. plumosum* at different sites. The structural equation model indicated that disturbance and tree cover were the most significant factors affecting shrub density at the HP site, demonstrating the crucial role of both biotic and abiotic factors in shaping the population structure of *S. plumosum*. However, grass biomass emerged as the only significant factor at the KNR site in the model, highlighting the dominant influence of biotic factors. Our results did not support our second hypothesis, which proposed that abiotic factors like rock cover and disturbance would have a greater influence on shrub density than biotic factors. Instead, we found that both biotic and abiotic factors affected *S. plumosum* slope preferences, with biotic factors such as grass biomass and tree cover having a greater overall impact. More importantly, while both types of factors shaped shrub density, their effects were site-specific.

Building on these findings, our results provided critical insights into how biotic and abiotic factors shape the density, height, and population structure of *S. plumosum*. At the KNR site, higher grass biomass negatively impacted shrub density, likely due to competition for water and nutrients. This finding aligns with Snyman (2012a), who observed a strong correlation between grass phytomass production and *S. plumosum* density, attributing it to resource competition. Additionally, Snyman (2010; 2012a) reported that *S. plumosum* seedlings establish better under shade, possibly benefiting from reduced sun-induced stress. However, our findings at the KNR site, where tree cover was higher, suggest that while shading may aid seedling establishment, it does not promote dense shrub proliferation. The shrubs at KNR were less dense but grew much taller, contrasting with the HP site, where lower tree cover and disturbance led to shorter, denser clumps of the shrub. This pattern suggests that although tree cover may support initial seedling growth, other factors, such as competition from grasses and resource limitations, may ultimately restrict shrub density.

Additionally, abiotic factors such as higher rock cover and disturbance levels at the HP site likely create protective microhabitats that enhance juvenile establishment and growth (Pule et al., 2018). Our findings support this, as we observed greater juvenile establishment in areas with higher rock cover and disturbance at the HP site, with high rock cover associated with protection from fire (Arena et al., 2015; Kremer-Kohne et al., 2020). The contrasting environmental conditions between the HP and KNR sites highlight the importance of site-specific factors in determining the growth patterns of *S. plumosum*. The HP site favours the establishment of more juveniles and young adults, while the KNR site supports taller and more mature plants. This means that frequent fires have a higher effect on the establishment of juveniles (HP site) than grazing pressure (KNR site). This adaptability to diverse conditions highlights the resilience of the plant. Therefore, understanding these dynamics is crucial for informing targeted management strategies, such as managing grass biomass by minimising grazing pressure and reducing land disturbances that promote the growth of *S. plumosum*.

Despite the differences in biotic and abiotic factors across the sites, both exhibited an inverse J-shaped population structure, indicating high recruitment rates and favourable conditions for juvenile plants. A left-skewed distribution means that there were more individuals in the younger stage classes (e.g., juveniles and young adults) than in the older classes (Cousins et al., 2014). Such a distribution is often characteristic of a growing population, suggesting that the population has recently experienced a period of high levels of seedling establishment or successful recruitment (Cousins et al., 2014; Helm and Witkowski, 2012; Mwavu and Witkowski, 2009). If the young individuals survive to adulthood and reproduce, the population size is likely to increase (Cousins et al., 2014). With a large base of young individuals, the population has the potential to expand significantly and densify, provided the environmental conditions remain favourable and the individuals successfully mature and reproduce. Thus, the population at the HP site is likely to expand due to the frequent fires that disturb the soils and native plants. Similarly, if management practices at the KNR site do not improve, heavy grazing pressure will also promote the expansion of this shrub.

At the HP site, the highest shrub densities were observed in the middle slope, which had recently experienced a burn, followed by the bottom slope and then the top slope, which had the longest time since the last burn. At the KNR site, the highest shrub density was in the middle slope, where grazing was intermediate, whereas the top slope experienced heavy grazing. The bottom slope, where grazing was minimal, had the lowest shrub density. These observations indicate that both topography and the main disturbance factors within a site, such as fire and grazing, play crucial roles in the distribution and occurrence of shrubs. Similar findings were reported by Snyman (2012b), who noted a strong preference of *S. plumosum* for elevated slopes and rocky terrain, with the initial establishment on ridges before spreading to valley bottoms. Additionally, Snyman (2010) noted that *S. plumosum* thrives in infertile soils with low organic matter content, making the nutrient-poor rocky ridges (Huang et al., 2023) more conducive to its dominance compared to the relatively fertile slopes. Our findings are consistent with these observations, highlighting the preference for higher, more nutrient-poor ridges, which facilitate shrub dominance in specific slopes.

Snyman (2012a) previously observed that *S. plumosum* thrives in areas experiencing disturbances, where open niches with limited competition provide favourable conditions for the shrub to establish and spread. This opportunistic distribution pattern suggests that the plant often occupies areas affected by overgrazing or other land disturbances, where "empty" niches devoid of competition are available (Pule et al., 2018). Therefore, our study adds to the growing body of evidence that both fire and grazing significantly influence shrub distribution patterns by creating or maintaining these open niches. The combination of *S. plumosum*'s adaptability to diverse environmental conditions, with its preference for disturbed, nutrient-poor environments and its ability to establish in areas with reduced competition, highlights the complexity of implementing management strategies to control this shrub. This suggests that landowners and farmers must carefully consider the impact of disturbance (i.e., fire and grazing) when trying to effectively control the encroachment of S. *plumosum* throughout South Africa.

5. Conclusion

In confirming the notion that *S. plumosum* thrives in heavily disturbed environments, both sites in this study exhibited high densities of the shrub due to previous significant disturbances. The population structure at the KNR site predominantly consisted of mature plants, with a notable scarcity of juveniles. In contrast, the HP site showed high densities of juveniles and young adults, indicating that recent disturbances have promoted the proliferation of the shrub. These observations underscore the influence of disturbance regimes on the demographics of *S. plumosum* populations. The prevalence of juveniles at the HP site highlights how high levels of disturbance, such as frequent fires, facilitate the establishment and spread of the shrub. This study provides valuable baseline data on the population

structure of *S. plumosum* and identifies the key disturbances that promote its proliferation. Our results emphasise that overgrazing and frequent fires are the primary drivers of *S. plumosum* encroachment. This finding underscores the need for improved land management policies to control shrub encroachment and preserve existing biodiversity. By informing management recommendations for farmlands and similar rangelands, this study contributes to the development of strategies aimed at mitigating the adverse effects of these disturbances on plant community structure.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Edith J. Singini: Writing – review & editing, Writing – original draft, Data curation. **Bridgette M. McMillan:** Data curation, Methodology. **Solomon W. Newete:** Supervision, Project administration, Investigation, Conceptualization. **Ed T.F. Witkowski:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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Supplementary materials

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