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Ecology, population biology and conservation status of *Euphorbia schoenlandii* Pax, an endemic to the Succulent Karoo, South Africa

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ABSTRACT

Many threatened plant species in South Africa occur outside of protected areas and these include numerous succulent species that are traded internationally. Despite the potential impact that this may have on rare and endemic succulent species, limited population data exist to inform the non-detriment findings required by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to ensure that international trade is sustainable. A concerted effort is being made in South Africa to gather such data for threatened succulents in the Euphorbiaceae. As part of this effort, the study set out to locate the extant populations of *Euphorbia schoenlandii*, an endemic of the Succulent Karoo, and acquire a better understanding of the population biology and ecology of the species. We applied the point-centred quarter method to estimate population size and density at each locality. This first-ever comprehensive field survey allowed for the determination of the geographic distribution of the species, as well as the sizes and number of populations. Biotic and abiotic environmental variables were employed to generate a habitat profile and a species distribution model for conservation purposes. Population structure, regeneration potential, and stability of the three known populations were also assessed. According to this study, approximately 29 152 individuals remain in the wild. It was shown that the species is often associated with nurse plants. Various potential pollinators were identified, but of concern was the considerable infestation by an alien snout moth (*Nephopteryx divisella*), a known pest of euphorbias. The first adult size class contained the highest proportion of individuals, which is indicative of pulse recruitment. Seedling numbers were low, most likely because the surveys were conducted during a drought period. Overall, this study provides the first data on various aspects of the population structure and ecology of *E. schoenlandii*. It provides valuable information regarding current threats, and also highlights the vulnerability of the species to further habitat loss and degradation or future illegal or unregulated harvesting.

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1. Introduction

There appears to be a general paucity of information on the biology and ecology of succulent euphorbias in southern Africa, with most studies focused on species indigenous to the sub-tropical parts of South Africa (Raal, 1988; Pfab and Witkowski, 1999; Knowles and Witkowski, 2000; Van der Linde et al., 2017; Mhlongo et al., 2023). Quantitative studies have only recently been conducted on the locally endemic euphorbias of the arid and semi-arid parts of the winter-rainfall region of South Africa (Jabar et al., 2021). Rare, drought-tolerant succulents from the Succulent Karoo are especially prone to climate change, habitat loss, overgrazing and overharvesting (Young et al., 2016; Grace, 2019).

The Noordpol (*Euphorbia schoenlandii* Pax) is well-known for its heliotropic behaviour (positioning itself so that the apex of its stem points northwards towards the sun) and is endemic to the Succulent Karoo in the Western Cape Province of South Africa (Court, 2010). *Euphorbia schoenlandii* is currently listed as Vulnerable B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v) on the Red List of South African Plants with an Extent of Occurrence (EOO) of 1200 km^2 and known from less than 10 locations (Raimondo, 2007). The term 'location', in this sense, is defined as a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon present (IUCN, 2016).

Whilst the foremost threat to the survival of *Euphorbia* stem succulents is habitat destruction and disease (Van der Linde et al., 2017), the unsustainable harvest of wild succulents for the horticultural trade may place additional pressure on populations of rare and

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endemic taxa which are already at risk of extinction. Succulent euphorbias are popular in specialist plant collections worldwide (CITES, 2012) and international trade in these species is therefore regulated through their inclusion in Appendix II to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

CITES aims to ensure that trade in Appendix II species is sustainable. Parties to CITES that export plant species included in Appendix II are required to demonstrate that levels of export are not detrimental to the survival of the species concerned or do not hamper their role within the ecosystems in which they naturally occur (Smith et al., 2011). This is achieved through the making of a non-detriment finding (NDF) by the Scientific Authority of the exporting country. An NDF is a science-based risk analysis in which the vulnerability of a species (i.e. extrinsic and intrinsic factors that increase extinction risk) is weighed against how well it is managed (Smith et al., 2011). Factors such as the biological and ecological characteristics of the species, its national status (distribution, abundance, and threats), control and management of harvest, legal protection of the species, and trade information relating to the species are considered (SANBI, 2014). Data presented in an NDF should be recent and quantitative to enhance the confidence in the assessment (Smith et al., 2011).

Around 900 South African plant species are included in the Appendices to CITES and it would be impractical, and unnecessary, to conduct thorough NDF assessments for all 900 species. Priority species have therefore been identified by the Scientific Authority by considering the threat status of each species in relation to volumes of- and trends in legal trade, as reported in the CITES trade database. Through this process, *Euphorbia schoenlandii* was identified as a priority species, potentially at risk from international trade. The species has an IUCN Red List status of Vulnerable and is traded in moderate volumes i.e., between 250 – 999 plants exported over a 10 year period (high trade volumes range between 1 000 and 10 000 whole specimens exported over a 10 year period). Prior to this study, very little was known about the species' life history, the status of the species in the wild, or the impact of international trade on wild populations. A robust NDF could not be conducted until these crucial knowledge gaps had been addressed.

The aim of this study was to acquire current, reliable information on the population biology and ecology of *E. schoenlandii* to contribute to the NDF for the species. The following specific research objectives were addressed: (i) to ascertain the geographic distribution of the species and the number of populations, as well as plant abundance; (ii) to determine the habitat profile of the species; and (iii) to elucidate the population structure, regeneration potential and dispersal efficiency of populations. The study ultimately endeavoured to provide insight into the species' population dynamics, which is valuable information for predicting how populations may respond to climate change, habitat degradation or harvesting. It is furthermore anticipated that the study will contribute significantly to our knowledge and understanding of succulent euphorbias in arid southern African ecosystems and prove a useful addition to the rather limited body of literature on CITES-listed succulent plants.

2. Materials and methods

2.1. Species description

Euphorbia schoenlandii is a perennial, spiny stem succulent comprised of a cylindrical stem covered with prominent, spirally disposed ovoid-conic tubercles that have a triangular cavity on the upper side just below the apex. Plants are usually single-stemmed (Fig. 1a), but

Fig. 1. *Euphorbia schoenlandii* (a) individual comprised of a single stem; (b) a multi-stemmed individual; (c) woody spines protruding from uppermost portions of tubercular cavities, fertile peduncles arising directly beneath spines, and rudimentary leaves at the growing tip of the plant; (d) cyathium with toothed involucral glands; (e) ripe fruit with a deep red colour.

Table 1
Seasons during which surveys were conducted for *Euphorbia schoenlandii* and the reproductive state of plants found at the time of survey (2015 and 2016).

	Autumn	Winter	Spring
Survey period	May	June-July	September-October
Phenological state	Cyathia and fruit present	Cyathia and fruit present	Fruit present, dispersal underway

may also become multi-stemmed (Fig. 1b). Solitary, woody spines derive from modified sterile peduncles that are produced from the uppermost portion of the cavity of each tubercle (Fig. 1c). The spines are pale brown when young, turning pale grey or whitish with age and may be straight or variably curved. The species is monoecious and bisexual fertile peduncles arise from the lower portion of the tubercular cavities, directly beneath the spine (Fig. 1c), and carry cyathia singularly or in cymes of three. The five involucral glands are toothed along the outer margin (Fig. 1d) (White et al., 1941). Seed capsules are trilocular and glabrous, ripening to a deep red colour at maturity (Fig. 1e). This species is reported to flower between April and July (Goldblatt and Manning, 2000), and this was supported by the findings of this study (see Table 1).

2.2. Study area

Euphorbia schoenlandii occurs in the north-western corner of the Western Cape Province of South Africa in the southern portion of the Namaqualand Sandveld Bioregion and, to a lesser degree, in the Knersvlakte Bioregion (Rutherford et al., 2006), both bioregions within the Succulent Karoo Biome. The Sandveld is the lowest-lying of these two bioregions and occurs along the coastal plains of South Africa's west coast, from the Richtersveld in the north to the vicinity of the lower Olifants River in the south. It is bounded in the east and west by Namaqualand Hardeveld, and the Atlantic Ocean respectively. The Knersvlakte Bioregion also lies at a low altitude but occurs further inland, bordered to the east by the Bokkeveld Escarpment and to the west by Namaqualand Sandveld and Hardeveld (Rutherford et al., 2006). The landscape comprises a flat to slightly undulating coastal peneplain and low-relief hills (Van Wyk and Smith, 2001; Rutherford et al., 2006).

The strong maritime influence on this semi desert region results in an even, mild climate and the study area falls within the typical unimodal winter-rainfall region of the Succulent Karoo (Rutherford et al., 2006). The Namaqualand Sandveld Bioregion experiences the lowest mean annual precipitation (MAP) in the Succulent Karoo, receiving an average of 105 mm of rainfall per annum, while the Knersvlakte has a MAP of 132 mm (Rutherford et al., 2006). The majority of rainfall occurs between May and August. Prevailing onshore winds from the Atlantic Ocean produce fog which provides an important supplement to the low rainfall of the region (Van Wyk and Smith, 2001). Another valuable source of moisture, which may occur all year round, is the copious dewfalls that are generated by high air humidity along the coast together with relatively cool nocturnal temperatures (Rutherford et al., 2006). Frost is a rare phenomenon in these low-lying coastal regions, with 2 to 4 days of frost per year. Catabatically warmed berg winds descending from the interior plateaus of the country, especially in autumn, have been known to produce absolute temperatures of more than 44 °C in these regions, whilst the mean annual temperature ranges between 16 °C and 18 °C (Rutherford et al., 2006).

2.3. Locating populations

Euphorbia schoenlandii is said to be found in open areas with deep, red Aeolian sands, but also loamy soil on the lower slopes of hills, where they often occur in fairly dense vegetation (Raimondo, 2007). Details of known sites were acquired from locality records obtained from the National (PRE) and Bolus (BOL) herbaria, CapeNature (the provincial conservation agency in the Western Cape) and iSpot (www.ispotnature.org/communities/southern-africa), the latter a citizen science platform aimed at documenting biodiversity. Field surveys targeted these areas during the optimal flowering and fruiting times (Table 1), but finding populations was sometimes hampered by vague and outdated locality references.

2.4. Population delineation, size and density

The upright growth habit and distinctive appearance of this species makes it easy to spot in the field. However, delineation of population boundaries was somewhat challenging since plants were spread out over rather extensive areas, with both dense aggregations and sparsely scattered groups. The peripheries of populations were determined on foot and by vehicle, following population edges, while recording GPS points and notes along the way to aid mapping later and to estimate the Area of Occupancy (AOO).

Due to the larger population sizes and widespread areas occupied, total counts were not practically possible. The point-centred quarter method (PCQ) of plotless sampling (Cottam and Curtis, 1956) was therefore used to estimate population density and number of individuals. This method involves measuring distances of plants from a sampling point for a random sample of individuals, typically along a transect, and recording the characteristics of interest for each plant sampled (Mitchell, 2007).

A 100 m transect was placed within the population to encompass as much topographical variation as possible. For each transect, a list of 10 random two-digit numbers was generated from one of seven tables of random digits and used as the intervals (in metres) at which sampling would take place along each transect. Duplicates were ignored and 00 was recorded as 100. If the difference between any of the numbers was four or less, the second number was crossed out and a new one was generated. This ensured that points were at least five meters apart to avoid the same individuals being measured repeatedly.

At each predetermined random interval, a 2 m pole was laid out on the ground perpendicularly across the transect to form quadrats (Fig. 2). In each of these quadrats, the plant nearest to the sampling point (the centre of the four quarters) was located and the distance from the sampling point to the centre of the plant was recorded (Fig. 2). Population density (plants per ha) was estimated from the distance data using the equation Density = 10 000/$\overline{d}^2$ where $\overline{d}$ = mean distance between sampling points and plants (Mitchell, 2007). An estimate of the number of individuals in the population was obtained by multiplying density with area occupied.

Because the areas occupied were relatively vast (varying between 93 to > 1 400 ha), it was not possible to lay transects through entire populations. Thus, at each site, transects were laid through areas with dense, intermediate, and sparse aggregations of plants, thus ensuring a stratified sample of varying degrees of densities, and the results extrapolated for the entire area.

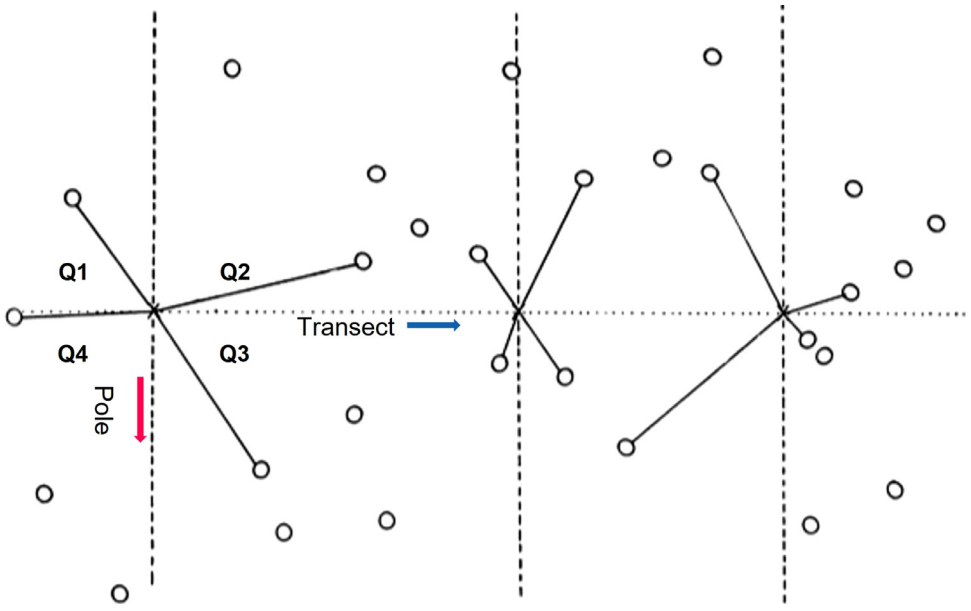


Fig. 2. Layout and approach of the point-centred quarter method. Open circles indicate the hypothetical position of plants in a population. Adapted from Cottam and Curtis (1956).

2.5. Plant measurements and observations

Stem diameter (SDr) was measured at the widest part of the stem using a Vernier Caliper, and height (H) of the stem was taken with a tape measure. In the case of multi-stemmed individuals, the number of stems was counted and SDr and H of each stem were measured separately. Given the cylindrical shape of these plants, volume (V) was calculated as $V = \pi\ r^2$ x H where r = SDr/2. For multi-stemmed individuals, the volume of each stem was calculated, and all values added to give a total volume for the plant.

The number of cyathia and fruits on each plant were counted if present. Any floral visitors observed while counting flowers were photographed and noted to ascertain the possible pollinators for the species. Dead plants encountered while sampling were noted. Any incidence of herbivory damage was recorded, however the extent of the damage was not quantified. Plants were also inspected for signs of insect damage, disease, and trampling. Signs of disturbance and habitat degradation were also documented.

2.6. Biotic and abiotic habitat features

2.6.1. Association with vegetation

An *E. schoenlandii* plant was classed as associated with succulent shrub (S) or non-succulent shrub (N), if a shrub or any part thereof occurred within a 15 cm radius of the euphorbia plant. If neither, then it was categorised as growing in the open (O).

2.6.2. Soil sampling and analyses

Soil samples were taken from five sites, two on the edges of the species' distribution and three in the core. At each site, five soil samples were collected from different patches of plants to a depth of 12–15 cm per site and pooled together.

Exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) were extracted by adding 50 ml 1 M ammonium acetate ($NH_4C_2H_3O_2$) (pH=7) to 5 g of soil, which was shaken for 15 min and then the solution filtered through Whatman 40 filter paper. Extracts were analysed by atomic absorption spectroscopy (SpectrAA 250 Plus). Soil pH was determined with a 1:2.5 extraction of soil to solution using both deionised water and 1 mol/L potassium chloride (KCl) and measured with a digital pH meter. Particle size distribution was analysed according to procedures prescribed by the Non-Affiliated Soil Analysis Work Committee (1990). After hydrating 50 g of soil to wetting point, samples were pre-treated with 10 ml hydrogen peroxide (H_2O_2) to remove soil organic matter before sieving (Jensen et al., 2017).

2.7. Mapping

Population boundary coordinates were imported into GeoCAT (Geospatial Conservation Assessment Tool – http://geocat.kew.org/) to calculate EOO and AOO according to the IUCN Red List criteria (Bachman et al., 2011).

Distances between localities were measured in Euclidean distance and averaged to determine the degree of isolation amongst populations.

2.8. Data and statistical analyses

2.8.1. Species distribution modelling

A maximum entropy approach to modelling species geographic distributions was chosen for use in this study since it utilises 'presence-only' species occurrence data and has been shown to produce robust results with the small sample sizes typical for threatened species (Phillips et al., 2006).

Environmental predictors considered for the model included a set of 19 bioclimatic variables (https://www.worldclim.org/) and three topographic variables. The bioclimatic variables were derived from monthly temperature and rainfall values to represent annual trends, seasonality and extreme or limiting environmental factors (Van Staden et al., 2020; Pradhan and Setyawan, 2021), while the three topographic variables (slope, aspect, and altitude) were derived from a SRTM (Shuttle Radar Topography Mission) Digital Elevation Model (DEM). To reduce redundancy, both the bioclimatic variables and the topographic variables were tested for correlation ($r^2 > -0.65$ or > 0.65) using the Band Collection Statistics tool in ArcMap (Merow et al., 2013; Pradhan, 2016). The eleven least correlated predictor variables were then selected for use in the model.

Species niches were modelled with the MaxEnt modelling software (v 3.4.1). To train the model, 80 % of presence data recorded in the field during surveys were used, while the remaining 20 % were used for accuracy testing. The regularisation multiplier was set to 1 to prevent over-fitting. Model replications were set to 100 using 'subsample', and 'random seed' was set to true. Model performance was

evaluated by examining the probability that a randomly chosen presence site is ranked above a random background site (Phillips et al., 2006). A random ranking will return an Area Under Curve (AUC) of 0.5 while a perfect ranking would achieve an AUC of 1. A jacknife test was applied to provide estimates of the relative contributions of the environmental variables to the model.

Model results were refined by excluding highly altered habitats mapped using the 2020 South African National Land Cover dataset (DFFE, 2021).

2.8.2. Relationship between population size and density

Linear regressions were performed in XLSTAT (v 19.6) to explore the relationship between population size and density.

2.8.3. Population structure and regeneration potential

Populations for which sufficient reproductive data (fruits and cyathia) were available were used to delimit size classes, and resulting size class distributions were then applied to all other populations. Following Condit et al. (1998), expanding size class widths were utilised. Plant volume was used to describe the population structure of *E. schoenlandii* on the premise that plant volume increases with age.

Life stage classes were taken into consideration to ensure that size classes would be biologically meaningful (Cousins et al., 2014). The seedling life stage was defined as a plant reliant on the cotyledons (seed leaves), and once it switches to external nutrient sources, it was considered to have passed to the juvenile stage (Cousins et al., 2014). Juveniles were defined as non-reproductive plants, with the transition phase to sub-adult being marked by the onset of flowering (Harris et al., 2014). No plants with cotyledons were observed in the field, therefore all non-reproductive plants were classified as juveniles. Sub-adults were defined as plants occupying the size class displaying intermediate levels of reproduction, i.e. where the proportion of non-reproductive individuals outweighed, equalled or was slightly less than the proportion of reproductive plants (Cousins et al., 2014). Adult classes were characterised as those where most plants were reproductive (typically > 75 %). Size class distributions (SCDs) based on plant volume were delimited as follows: juveniles ($\leq$ 20 cm^3), sub-adults (21–150 cm^3) and adults (151–1 150, 1 151–2 150, 2 151–3 150, 3 151–4 150, > 4 150 cm^3).

To assess population stability, quotients between successive size classes were calculated. Quotients in a stable population will approach an approximately constant value, while unstable or episodically recruiting populations are characterised by fluctuating quotients (Martins and Shackleton, 2017).

Population structure was further explored through analysing SCD slopes. Since size classes varied in width, the number of plants in each size class was divided by the width of the size class to obtain a corrected abundance per size class (N_i) (Condit et al., 1998), and because some classes contained no individuals, each class was transformed by $\ln(N_i + 1)$. A least squares linear regression was performed using the corrected abundance per size class ($\ln[N_i + 1]$) as the dependent variable and the size class midpoint ($\ln[d_i]$) as the independent variable (Condit et al., 1998; Cousins et al., 2014). Interpretation of the shape of SCDs follows Van der Merwe and Geldenhuys (2017). A negative slope indicates fewer individuals in larger size classes (good recruitment), while positive slopes are indicative of poor recruitment with more individuals in the larger size classes. According to Van der Merwe and Geldenhuys (2017), shrinking populations (decreasing plant density) will exhibit less negative SCD slopes, while growing populations display more negative slopes. The y-intercept of regressions is also reported as it is considered a useful parameter for understanding population dynamics, in that a value near zero indicates the presence of a few small individuals, whereas a high value is indicative of the occurrence of many small individuals (Van der Merwe and Geldenhuys, 2017).

Simpson's index of dominance (SDI) (λ) provides an additional measure of population structure and describes the probability that any two plants from a population are from the same size class. Lambda (λ) values close to zero indicate that individuals are relatively evenly distributed among the size classes, while values closer to 1 indicate a higher likelihood that two individuals drawn at random belong to the same size class (Cousins et al., 2014).

$$\lambda = \frac{1}{N(N-1)} \sum_{i=1}^{k} N_i(N_i - 1)$$

where N is the total number of plants, N_i is the number of plants in class i, and k is the number of size classes.

Finally, linear regressions were constructed to explore the relationship between the size of reproductive plants and the number of reproductive structures produced. All data were tested for normality (Shapiro-Wilk W test) before analysis and subjected to logarithmic transformation ($\log_{10} y + 1$) when $p < 0.05$. To compare plant size and reproductive output between populations, one-way ANOVAs were performed in Statistica v.13.3. Since data violated the assumption of homogeneity, unequal N HSD Post-Hoc Tukey tests were applied to establish statistically significant differences between populations.

3. Results and discussion

3.1. Distribution and population sizes

The field surveys located three populations varying in size from 945 to 23 839 individuals (Table 2) and in total there are an estimated 29 152 plants in the wild. S, P and E (Table 2) constitute a single, contiguous population, however since the area occupied is large (exceeding 2 000 ha), it was split into three sampling zones based on proximity to the coast. Each section was treated as a subpopulation and analysed separately. A few *E. schoenlandii* plants were noted at population H (A. Horstmann, pers. obs.), but the area could not be

Table 2
Plant abundance, density, and area occupied by surveyed populations of *Euphorbia schoenlandii* in the Succulent Karoo, Western Cape, as well as estimated mortality levels and percentage affected by herbivory and stem-boring moth larvae. S, P and E constitute a single population subdivided into subpopulations. Precise localities are withheld to protect the species from illegal harvest. [1]Distance from the coast (measured in a straight line from the centroid of each locality) is ranked from one (closest to the coast) to six (furthest from the coast). [2]Mean Euclidean distances (km) between the centroids of localities indicate the degree of isolation of a population.

Locality	No. of individuals	Density (plants/ha)	Area occupied (ha)	Mortality (% of plants)	Herbivory (% of plants)	Stem borer (% of plants)	Distance from coast [1]	Mean isolation distance [2] (km)
S	5 608	22.45	249.83	12	0	3	1	25.7
P	16 693	11.23	1 487.05	10	11	2	2	25.6
E	1 538	3.79	406.09	2	13	10	3	25.2
A	945	10.17	92.93	11	10	47	6	44.3
K	4 368	7.22	605.17	15	16	15	4	53.0
H	Not sampled	–	–	–	–	–	5	33.5

Table 3
Habitat features and climatic conditions associated with surveyed *Euphorbia schoenlandii* subpopulations in the West Coast region of the Western Cape. Locality H is excluded here since this population was not surveyed. ('Vygie' refers to iceplants (Aizoaceae); 'Strand' means beach; 'Veld' means vegetation; MAP = Mean annual precipitation; MAT = Mean annual temperature.).

Locality	Vegetation type (Mucina et al. 2006)	MAP (mm)	MAT (°C)	Altitudinal range (m)	Slope (degrees)	Predominant aspect
S	Namaqualand Strandveld	187	17.8	34–52	0.32–8.42	SW, W
P	Namaqualand Strandveld	184	17.9	10–137	0.23–5.89	SW, W
E	Namaqualand Strandveld	173	18.1	31–69	0.11–3.98	NW, W
A	Knersvlakte Dolomite Vygieveld	174	19.3	72–122	0.11–8.65	SE, SW
K	Knersvlakte Quartz Vygieveld	164	18.2	60–122	0.34–4.26	S, SE

surveyed as the locality came to light after all fieldwork was completed (the locality was however included in biogeographical analyses, see Section 3.2.2). In general, *E. schoenlandii* was found to be most abundant closer to the coast (S and P).

Linear regression revealed that there was no relationship between population size and plant density for *E. schoenlandii* ($r^2 = 0.051$; $p = 0.715$). The spatial arrangement of *E. schoenlandii* populations does not display any real geographic centre, and abundance between the two most isolated populations (A and K) varied greatly. Patterns of species abundance and distribution are not always straightforward and easy to classify (see Section 3.2.2 for further discussion of the reasons for this). Martínez-Meyer et al. (2012) suggested that it is preferable to study relationships in environmental space (the species' ecological niche) to explain abundance distributions, since these are usually much stronger than relationships in geographical space.

3.2. Habitat profile and biotic interactions

3.2.1. Habitat characteristics

Euphorbia schoenlandii occurs at altitudes of 10–137 m above sea level with plants found growing on very gentle to moderate slopes (0.1–8.7°) (Table 3). Plants occurred predominantly on south-westerly and westerly aspects (Table 3) and were often found growing on or around *heuweltjies* – large circular mounds thought to be created by termites, and which are known to be hotspots for nutrient accumulation and biogeochemical activity in the soil (Booi, 2011; McAuliffe et al., 2014). Mean annual precipitation over the distribution range of the species varied between 164 and 187 mm, along a north-south gradient (successively wetter to the south), K being the most northerly site and S the most southerly (Table 3). Vegetation type differed between populations, with the largest portion of the natural population (S-P-E population) occurring in Namaqualand Strandveld (as does the unsampled H) (Table 3).

Population A occurs on dolomite and the soil therefore has a very high calcium content, and the S-value indicates that soil fertility was also highest there (Table 4). Calcium and magnesium levels were high at P (Table 4), and S-values indicate that soil fertility across this subpopulation is higher than for the two neighbouring subpopulations (S and E). All *E. schoenlandii* populations occur on loamy sand that tends to be alkaline (Table 4).

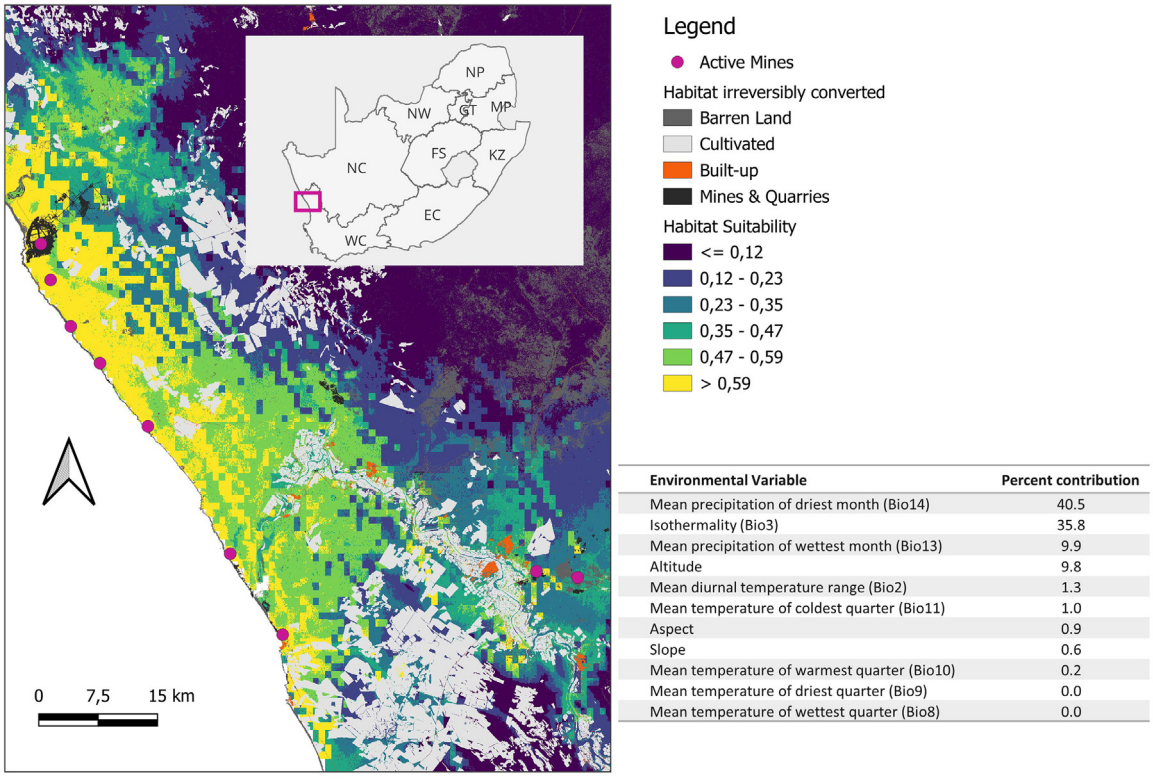
3.2.2. Species distribution model

Model performance was high with an average AUC test value of 0.991 ± 0.002 for the replicate runs. The total area of suitable habitat predicted by the model (Fig. 3) was 184 869 ha, of which 18 908 ha (10.2 %) has been irreversibly altered, particularly by mining and agriculture (vineyards and croplands). Although land cover data is useful in broadly assessing direct habitat loss, it does not detect all changes to the landscape nor does it capture degradation within natural ecosystems (Skowno et al., 2021). Examination of satellite imagery indicates that even though they are not currently under crop cultivation, certain areas of suitable habitat show evidence of having been ploughed at some point but are not classed as converted habitat within the land cover data. Surveys were conducted in these areas since there were herbarium records indicating presence of the species there, however no *E. schoenlandii* plants could be found. Historical records and accounts provide some insight. White et al. (1941) relay that William Triebner had told of a large colony of *E. schoenlandii* between Vanrhynsdorp and Vredendal, and Hall (1984) also noted that the species was formerly extremely abundant in this area but that thousands of individuals were destroyed when, following an exceptionally heavy wet spell in the 1960s, some farmers tried to grow wheat. The resulting crop was negligible and so the land was left fallow, but the strips of ploughed land were still evident some 20 years later (Hall, 1984) and are indeed still visible today on current satellite imagery for that region, as mentioned above.

The landcover data also do not fully portray the footprint of habitat disturbance from mining activities, and there are several active mines dotted along the coastal region within areas depicted as suitable *E. schoenlandii* habitat (Fig. 3). A diamond mine situated on the coast directly above the Olifants River mouth granted access to conduct a survey, but even though this area is depicted by the model as highly suitable habitat for the species, no plants could be located there. Similarly, a survey of the coastal region south of subpopulation S also did not yield any plants. The entire coast from south of S to southwest of population K has been extensively prospected and mined, not only for diamonds but also for heavy minerals found in the dark red sands characteristic of

Table 4
Soil properties of the five sampled *Euphorbia schoenlandii* subpopulations. H is excluded here since this population was not surveyed. (S-value = Sum of exchangeable alkaline cations).

Locality	Nutrient Status				Exchangeable Cations				S-Value	Particle Size Distribution (%)				pH	
	Ca	Mg	K	Na	Ca	Mg	K	Na		Gravel	Sand	Silt	Clay	H_2O	KCl
	(mg/kg)				(cmol(+)/kg)					(>2 mm)	(<2 mm)				
S	613	195	381	411	3.06	1.60	0.98	1.78	7.42	0.1	92.7	2.4	5.0	8.78	8.13
P	1744	401	522	532	8.7	3.29	1.34	3.87	17.2	0.7	81.9	11.3	6.8	8.03	7.87
E	712	147	222	42	3.55	1.21	0.57	0.18	5.51	<0.1	88.0	7.9	4.0	8.07	7.68
A	3179	207	556	825	15.86	1.70	1.43	3.59	22.6	2.5	81.6	11.4	7.0	8.52	8.18
K	650	239	211	261	3.24	1.97	0.54	1.13	6.88	0.8	83.7	9.0	7.3	7.35	7.09



Environmental Variable	Percent contribution
Mean precipitation of driest month (Bio14)	40.5
Isothermality (Bio3)	35.8
Mean precipitation of wettest month (Bio13)	9.9
Altitude	9.8
Mean diurnal temperature range (Bio2)	1.3
Mean temperature of coldest quarter (Bio11)	1.0
Aspect	0.9
Slope	0.6
Mean temperature of warmest quarter (Bio10)	0.2
Mean temperature of driest quarter (Bio9)	0.0
Mean temperature of wettest quarter (Bio8)	0.0

Fig. 3. Species distribution model output for *Euphorbia schoenlandii* displaying potentially suitable habitat. Light grey, orange and black areas represent land irrevocably altered by anthropogenic activities, and which are now regarded as non-suitable habitat. The positions of known populations are not displayed to protect the species from illegal harvest. Estimates of the relative contributions of environmental variables to the Maxent model for *E. schoenlandii* are also given and values shown are averages over 100 replicate runs.

this coastline, and inland near population A dolomite and iron have been mined, leading to high levels of disturbance and habitat destruction throughout this region (De Villiers et al., 2004).

The results of the ecological niche model for *E. schoenlandii*, along with historical information and the occurrence of the species in varied vegetation types, points to the probability that this plant was once considerably more widespread within its distribution range. It is clear though that the species has suffered extensive habitat loss and habitat degradation due to mining and agricultural activities, resulting in a high degree of isolation and fragmentation between the three remaining populations. Passive recovery of perennial vegetation following ploughing and other forms of land degradation in the Succulent Karoo may take upward of 300 years to occur (Milton and Dean, 2015). Considering this very slow rate of recovery together with *E. schoenlandii*'s short-distance ballistic seed dispersal mechanism, it is unlikely that the species would be able to recolonise previously inhabited areas without assistance.

Since availability of moisture is the most limiting factor for plants in arid environments, it is no surprise that mean precipitation of the driest month emerged as the prominent explanatory variable in the species distribution model (Fig. 3). Extreme precipitation conditions evidently influence the species' distribution range (O'Donnell and Ignizio, 2012). Since fog occurrence is greatest closer to the coast, it stands to reason that the greater abundance and density of *E. schoenlandii* plants near the coast (at S and P; Table 2) can be ascribed to the higher moisture availability. The onshore flow of air from the Atlantic Ocean creates fog and heavy dew on the west coast (Desmet, 2007), which is a far more reliable source of moisture for plant growth than rainfall in terms of frequency and predictability of occurrence (Desmet and Cowling, 1999). These forms of non-rainfall moisture may even exceed precipitation in terms of quantity (Agam and Berliner, 2006). Harvesting of fog and dew by plants is a common phenomenon in coastal semi-desert regions (Hanisch et al., 2015) and the preference of coastal populations of *E. schoenlandii* for south-western to western aspects (Table 3) could be explained by the fact that these slopes receive more fog (P. Desmet, pers. comm.). Non-rainfall atmospheric moisture is intercepted by vegetation, accruing on leaf and stem surfaces and either dripping or being funnelled by means of stem flow onto the soil below the plant, making significant amounts of water available to the roots for absorption and thereby providing an important alternative source of moisture for plants in arid environments (Desmet and Cowling, 1999; Agam and Berliner, 2006). The prominent tubercles and spines on *E. schoenlandii* plants (Fig. 1a, b, c and e) may serve to increase the surface area for intercepting fog, and the spiral arrangement of the tubercles together with the channels formed at their bases could effectively funnel water droplets down the stem. Other studies conducted in arid and semi-arid ecosystems have also reported 'moisture capture' to be a determinant factor in the amount of fog and dew deposition into the soil, and this in turn correlates with vegetation abundance (Kidron, 2005; Del Prado and Sancho, 2007).

The model further revealed that isothermality (the extent to which the diurnal temperatures fluctuate relative to the annual temperature oscillations) was the second most significant driving factor influencing the distribution of the species (Fig. 3). The climate along the west coast is ameliorated by the presence of the Atlantic Ocean (Desmet, 2007) and therefore, temperature fluctuations are generally not extreme in this region. Isothermality is often an important environmental predictor for species inhabiting coastal habitats (O'Donnell and Ignizio, 2012) and the high contribution of this variable in explaining the distribution of *E. schoenlandii* is indicative of a species reliant on a relatively even temperature regime.

3.2.3. Nurse plant effects

Most *E. schoenlandii* plants (63 %) were associated with surrounding dwarf shrub cover and there appeared to be a slight preference for non-succulent shrubs (Fig. 4). In arid environments nurse plants modify microclimatic conditions beneath their canopies, thus

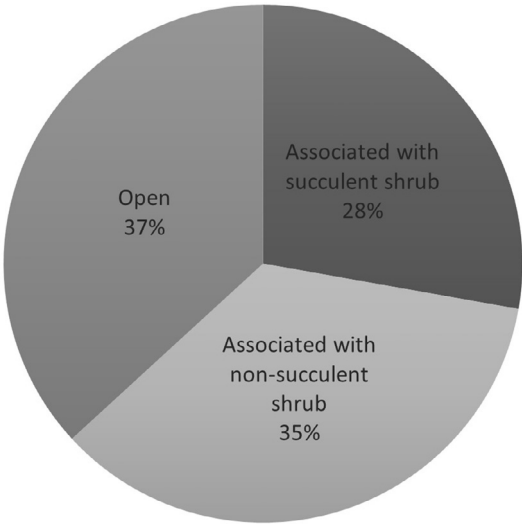


Fig. 4. Vegetation recorded within the microhabitat (inside a 15 cm radius) of sampled *Euphorbia schoenlandii* plants (Open: no surrounding vegetation).

ameliorating abiotic stress and facilitating not only germination and establishment of seedlings under them, but also promoting seedling survivorship (López et al., 2007; Munguía-Rosas and Sosa, 2008). These nurse plants provide refuges for the most vulnerable life stages of the beneficiaries by regulating soil temperatures, reducing rates of evapotranspiration, improving soil properties through input of organic material, and providing a degree of protection against herbivory (Kos and Poschlod, 2007; Adie and Yeaton, 2013). Additionally, branched structures that transmit wind, such as the canopy of a shrub, are efficient at combing non-rainfall atmospheric moisture from the air (Desmet and Cowling, 1999), and plants growing beneath these shrubs may also benefit from the moisture that is channelled down to the soil around the base.

The preferential occurrence of succulents beneath shrub canopies is reported for many spiny succulents (López et al. 2007; Munguía-Rosas and Sosa, 2008; Landero and Valiente-Banuet, 2010). *Euphorbia perangusta* (Raal, 1988) and *Euphorbia ingens* (Thrash, 1998) regenerate and grow in the shade of trees in the African savanna. Milton et al. (1999) state that all leaf- and stem-succulent plant families of southern Africa, except the Mesembryanthemaceae and Zygophyllaceae, are confined, either during establishment or throughout their lifespan, to patches of shade beneath shrubs or among rocks. It is important to note though, that not all nurse plants serve as equally suitable safe sites for seedling establishment, and that beneficiary species may show a preference for a certain set of facilitator species (Landero and Valiente-Banuet, 2010). Further examination of the possible existence of such species-specific facilitative interactions may be warranted for the study species, as declines in suitable nurse plants could potentially have negative effects on population recruitment.

3.2.4. Pollinators

Insects belonging to the Coleoptera, Diptera, Hymenoptera and Thysanoptera were observed visiting cyathia of the study species. Ants (Hymenoptera) were by far the most frequently observed visitors to *E. schoenlandii* cyathia (78 % of observations). Floral visitors included Karoo balbyter ants (*Camponotus fulvopilosus*) (Fig. 5a),

Fig. 5. Flower visitors observed on *Euphorbia schoenlandii* plants: (a) *Camponotus fulvopilosus* (note pollen on the head and forelegs); (b) *Lepisiota crinite*; (c) Order Diptera, Family Tachinidae (d) Order Coleoptera, Family Mordellidae; (e) Order Thysanoptera, Family Phlaeothripidae; (f) *Gymnetron* sp. (Order Coleoptera, Family Curculionidae).

small hairy sugar ants (*Lepisiota crinite*) (Fig. 5b), tachinid flies (Fig. 5c), tumbling flower beetles (Fig. 5d), tube-tailed thrips (Fig. 5e) and weevils (Fig. 5f).

Gómez et al. (1996) noted that plants in arid environments that have flowers with accessible nectaries, and which are located close to the ground, have a higher probability of being visited and pollinated by ants. Ants are often considered poor pollinators though, since the secretion of antimicrobial substances from their metapleural glands is thought to reduce pollen viability (Dutton and Frederickson, 2012). Furthermore, they are believed to negatively impact pollination by stealing nectar, damaging flowers, and disrupting pollination by other insects through their aggressive behaviour (Chacoff and Aschero, 2014). Most species in the genus *Camponotus*, however, have been shown to lack metapleural glands (Gómez et al., 1996; Dutton and Frederickson, 2012) and ants in this nectarivorous genus are known to successfully and effectively pollinate Euphorbiaceae (Araf et al., 2010; Martins, 2010). *Camponotus fulvopilosus* on *E. schoenlandii* were observed carrying pollen picked up during foraging (Fig. 5a) and it is likely that these ants, and maybe others, play an important role in the pollination ecology of the species. Further research, perhaps as part of a study focusing on the reproductive biology and ecology of the species, would however be required to confirm this notion.

Since they do not fit the traditional profile of effective pollinators, thrips have often been overlooked in pollination studies, however, there is evidence to support their effectiveness in pollinating Euphorbiaceae (Moog et al., 2002). Again, further examination of thrips as a potential pollinator would be required.

3.2.5. Snout moth infestation

During the field surveys, the presence of lepidopteran larvae, with concomitant webbing and frass, were observed on the apical portions of some plants in all surveyed populations. Larvae were noted on sampled plants from May to October. A single small plant infested with larvae (Fig. 6a) was collected and the larvae reared to adulthood in Potchefstroom, South Africa. The emergent imago (Fig. 6d-f) was identified as the exotic moth *Nephopteryx divisella* Duponchel (Lepidoptera, Pyralidae). This species is an oligophagous (insects that confine their feeding activity to plants belonging to one taxonomic group), multivoltine (producing more than two broods or generations per year) stem-boring snout moth indigenous to southern Europe.

Nearly half of the sampled individuals in the smallest *E. schoenlandii* population were found to be affected (Table 2). This population (A) is situated the furthest inland, and experiences hotter, drier conditions than the others (Table 3). S and P, which are close to the coast, were hardly infested. Larval damage was focused on the apex of the plant where the softest tissue is situated. Defoliation and damage to the growing tip of the plant, as well as young spines that had not yet hardened (Fig. 6b), was evident. In some cases, flowers and immature fruits had also been eaten, and latex encrusted tunnels were visible where the larvae had bored into the stems (Fig. 6c). Die-off of uneaten reproductive structures in the affected areas was also observed.

Nephopteryx divisella larvae feed exclusively on the Euphorbiaceae (Cristofaro et al., 1998) and the species has been reported as a pest on both succulent and leafy euphorbias (Singh and Harsh, 1996; Cristofaro et al., 1998; Bella et al., 2017). Although there is no literature on the current distribution of this moth in South Africa or when it was first recorded here, Raal (1988) mentions the destruction of emergent branches of *Euphorbia perangusta* (an endemic to the North-West Province - >1000 km away from the distribution range of *E. schoenlandii*) by an unidentified moth species. Judging by the two longitudinal stripes visible on the larvae pictured in his article, and the silken webbing between the spines of the plant, it appears as though the moth responsible for the damage could have been *N. divisella*. Knowles and Witkowski (2000) also identified insect larvae of the Pyralidae as a major threat to the Endangered Limpopo endemic, *Euphorbia barnardii*.

The larvae of this moth is known to have a devastating effect on Euphorbiaceae and it has been investigated as a potential biological control agent for the invasive species *Euphorbia esula* in North America (Cristofaro et al., 1998) and *Jatropha gossypiifolia* in Australia (Snow et al., 2016). The damage noted on *E. schoenlandii* plants is consistent with that reported for other host species (Cristofaro et al., 1998; Datinon et al., 2013; Snow et al., 2016; Bella et al., 2017). Further research is thus warranted to assess the level of threat posed to *E. schoenlandii* by this moth.

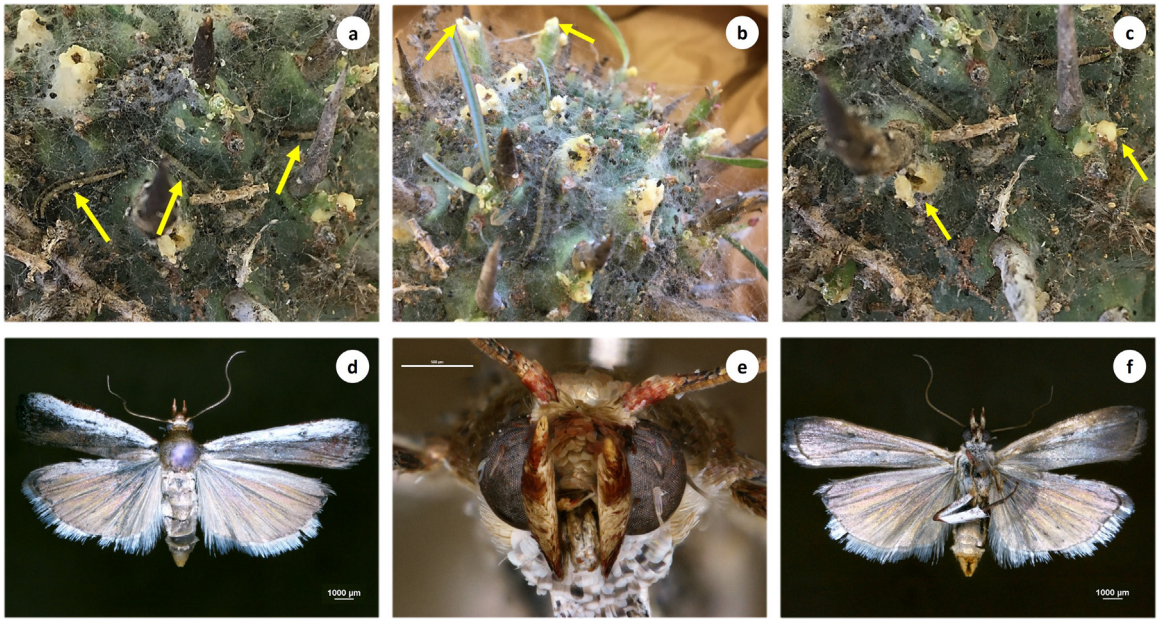


Fig. 6. (a) *Nephopteryx divisella* larvae (indicated by yellow arrows) on a *Euphorbia schoenlandii* plant; (b) immature, unhardened spines that have been consumed by larvae (indicated by yellow arrows); (c) reproductive structures beneath spines are eaten and latex encrusted tunnels are evident where the larvae have bored into the stem (indicated by yellow arrows); (d) dorsal view of imago reared from larvae in (a); (e) front view of moth face; (f) ventral view of moth.

3.2.6. Herbivory

Despite the caustic and poisonous properties of *Euphorbia* latex (Wal et al., 2013), herbivory by goats, sheep and small buck was observed. Succulent plants present a valuable source of moisture for animals in xeric environments, especially during the dry season (Heilmann et al., 2006) and it is not unusual for them to include euphorbias in their diet (Pfab and Witkowski, 1999; Knowles and Witkowski, 2000; Heilmann et al., 2006).

Euphorbia schoenlandii populations experienced relatively low overall levels of herbivory though (≤16 % of sampled individuals affected per population (Table 2)), perhaps because of the spiny nature of the plants (Fig. 1a-c). Sometimes plants were nibbled on at the base or along one side, but more often the tops were eaten. In certain instances, the entire epidermis and cortex of a plant were stripped bare by goats. Population K, which experienced the highest herbivory levels, was situated in a grazing camp (stocked with sheep) on private land, as were A and E. Although herbivory at P was not particularly prevalent overall (Table 2), the degree of damage to plants was more severe than at any of the other localities, and was concentrated in the portion of the population occurring on communal land where mostly goats, and some sheep, graze. Whilst herbivory seems not to present a direct threat to *E. schoenlandii* populations, overgrazing does appear to have caused rather considerable habitat degradation within the species' distribution range.

3.3. Population structure and regeneration potential

The first adult size class (151 – 1 150 cm^3 plant volume) dominated all populations, but more so for K (Fig. 7e) which was also the most unevenly distributed population, as indicated by the higher SDI value (Table 5). This might reflect a possible pulse of recruitment that may have occurred some years ago, and could be attributed to a period of exceptionally good rainfall. Inconstant quotients across populations support this idea as these are characteristic of episodically recruiting or unstable populations (Shackleton, 1993).

Recruitment is episodic in many arid zone plant species, and pulses of population renewal may occur at intervals of years, decades, or centuries (Milton et al., 1999; Duncan et al., 2006). Furthermore, recruitment and seedling establishment in arid ecosystems is directly related to rainfall timing and amount, with plant populations requiring sustained high rainfall episodes in successive years to regenerate (Adie and Yeaton, 2013; Milton and Dean, 2015). Since the sampling period occurred during a drought, the lack of seedlings observed in the field was expected. However, a small number of juveniles and sub-adults were observed in several subpopulations, indicating that a

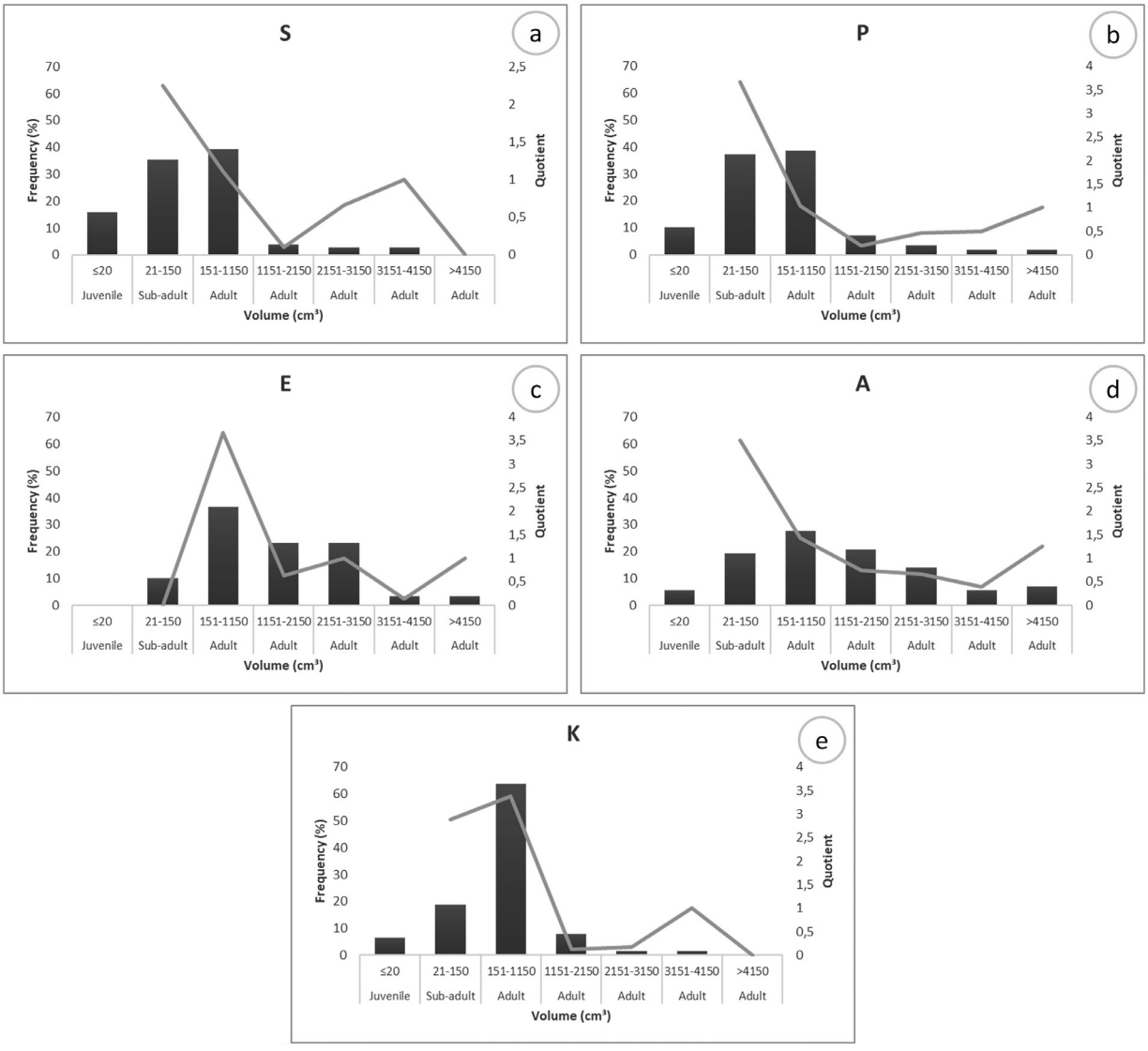


Fig. 7. Size class distributions of *Euphorbia schoenlandii* subpopulations, and quotients between successive size classes.

Table 5
Data and statistics describing the structure of *Euphorbia schoenlandii* populations. Ordinary least squares regression slopes (with standard error (SE) and p values), y-intercept and Simpson's Index of Dominance (SDI) results are presented (*significant $p < 0.05$, ** $p < 0.005$). Back-transformed values for means of log plant volume and log number of reproductive structures (from ANOVA) with standard deviation are also given (*significant $p < 0.05$, ** $p < 0.005$).

Locality	Slope	SE Slope	r^2	*p*	y-intercept	SDI (λ)	Mean plant size (cm^3)	Mean reproductive structures
S	−0.078	0.011	0.927	**0.002****	0.259	0.301	106.68 ± 17.31	26.78 ± 20.44
P	−0.143	0.013	0.969	<**0.001****	0.483	0.302	108.78 ± 18.29	**23.73 ± 20.59****
E	0.000	0.002	0.013	0.830	0.005	0.230	**190.31 ± 17.68****	27.46 ± 19.16
A	−0.031	0.003	0.963	**0.001****	0.106	0.177	**170.51 ± 19.83***	29.85 ± 19.86
K	−0.063	0.005	0.978	<**0.001****	0.214	0.449	128.27 ± 15.83	**37.05 ± 18.75****

degree of low-level recent recruitment had taken place before the onset of the drought.

The percentage of juveniles in subpopulations of *E. schoenlandii* varied between 6 and 16 %. The only locality not showing signs of recent recruitment was E (Fig. 7c), this is further demonstrated by the slope of zero and a very low y-intercept (Table 5). Significant negative slopes for all other populations indicate growing populations. Size class distribution slopes were not overly negative, though slightly more so at P (−0.143) and S (−0.078), and these negative slopes together with the higher y-intercept values, indicate healthier levels of recruitment at these localities (Niklas et al., 2003). This is attributed to the plants of these two populations occurring in closer proximity to the coast and growing predominantly on south-westerly aspects, thereby receiving more moisture input from fog. S had a higher proportion of juveniles (16 %) (Fig. 7a) than P (10 %) at the time of the survey (Fig. 7b). Despite the plants at P producing the lowest mean number of reproductive structures, the higher y-intercept value and more negative slope calculated for this population (Table 5) indicated better recruitment levels overall, which may be attributable to the higher soil fertility (Cortina et al., 2013). P is also the largest population (Table 2). The largest size class was absent from the population at K and the subpopulation at S (Fig. 7a and e).

Regression analysis of plant size and reproductive structures demonstrated a significant positive linear relationship (r^2 = 0.345; $p < 0.0001$) (Fig. 8), with larger plants generally producing more reproductive structures than smaller individuals, as has been found in other studies (Pfab and Witkowski, 1999; Cousins et al., 2013). Analysis of variance revealed that both mean plant size and mean reproductive output varied significantly between populations ($p < 0.001$). Pair-wise comparisons indicated that plants at E (which had the largest mean size (Table 5)) were significantly larger than those at P and S (Tukey: $p < 0.005$), likely owing to the presence of more individuals in the larger (>1 151 cm^3) adult size classes (Fig. 7). Plants at A were significantly larger than those at P, S and K (Tukey: $p < 0.05$), however plants in this population were not significantly more reproductive than any of the others probably due to the snout moth infestation that hampered reproduction (Pfab and Witkowski, 1999; Bisane, 2019). Plants at K possessed the highest mean number of reproductive structures (Table 5) and were significantly more reproductive than plants at P (Tukey: $p < 0.0001$). This could be ascribed to the higher total proportion of adult plants at K (75 %) than at P (53 %).

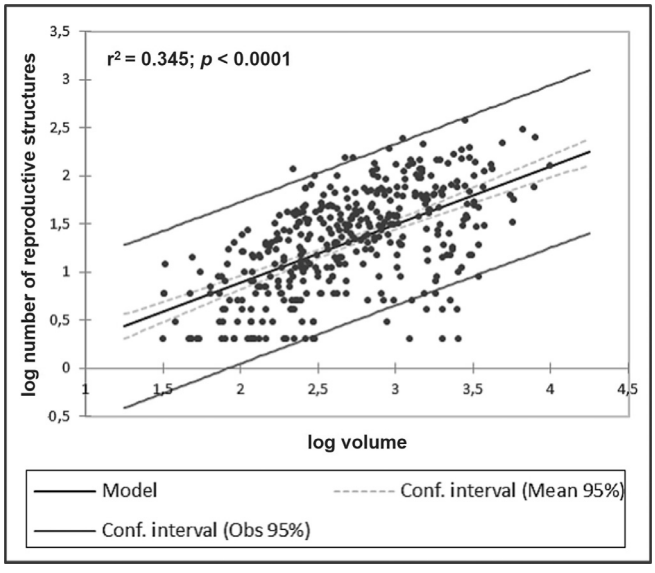


Fig. 8. Regression between log plant size (volume) and log number of reproductive structures produced by reproductive sub-adult and adult *Euphorbia schoenlandii* individuals; all plants from all populations combined.

3.4. Threat status

Populations/subpopulations were separated by distances of between 5 and 88 km, with mean isolation distances per population ranging between 25 and 53 km (Table 2) and indicating extreme isolation for populations K and A. Whilst the distance between populations resulted in a slightly larger EOO (1 682 km^2) than previously reported for the species (1 200 km^2), the AOO was found to be small (100 km^2). None of the populations occurred within a formal protected area nor in any nationally protected threatened ecosystem types. The species and its habitat are thus entirely unprotected.

Euphorbia schoenlandii has been heavily impacted by habitat loss from farming activities and mining, as well as habitat degradation due to overgrazing. Subpopulations S and P were transected by several dirt roads and off-road tracks, leaving them fragmented and disturbed. Furthermore, there were rubbish dumps and a quarry within these areas, adding to the habitat degradation and disturbance. Erosion is also a threat, particularly around P. Expansion of agricultural fields may lead to further destruction and fragmentation of habitat, especially if a proposed agricultural development (extension of existing vineyards) around subpopulation E were to go ahead. This is especially problematic as the species employs a short-distance ballistic dispersal mechanism, and visual examination of seeds revealed that no elaiosome is present to facilitate ant distribution over longer distances, so dispersal to new sites or recolonization following extirpation would be unlikely. This poor dispersal ability, along with the fact that it is a slow-growing plant, also puts *E. schoenlandii* at risk from climate change as such species cannot shift rapidly enough to remain within their suitable climatic envelopes of temperature and precipitation (Wilson and Primack, 2019).

Based on the findings of this study, the conservation status of *Euphorbia schoenlandii* should remain Vulnerable, although the criteria should be amended to B1ab(iii)+2ab(iii). It is likely that *E. schoenlandii* was formerly more widespread than today, and reintroduction into rehabilitated coastal sites would greatly improve the conservation status of the species.

4. Conclusions

This study estimates the global *E. schoenlandii* population at 29 152 individuals in three populations. It is restricted to an area less than 100 km^2 in the southern portion of the Namaqualand Sandveld. Its distribution is mainly limited by isothermality and the availability of moisture during the driest months, and the plants fare particularly well in coastal areas where moisture can be captured during frequent fog and dewfall events coming off the Atlantic Ocean. *Euphorbia schoenlandii* occurs at low altitudes on loamy sand that is alkaline, but there was no evidence to suggest that the species is an edaphic specialist. The species showed dependence on nurse plants, especially non-succulent dwarf shrubs, which likely facilitate recruitment and survival. A wide array of potential pollinators were identified, of which ants were the most prolific floral visitors. Although herbivory was present at low levels in all populations, it is rather the infestation by larvae of a destructive, alien stem-boring moth (*Nephopteryx divisella*) that is likely to pose the biggest threat, especially to the smallest population, though this does require further research.

The dominance of the first adult class within the subpopulations is indicative of pulse recruitment events which occurred an unknown number of years ago. However, even during the current drier spell of the study, juvenile plants comprised up to 16 % of the subpopulations growing closer to the coast, these being exposed to fog on western slopes. Although larger plants generally produced more reproductive structures than smaller individuals, this pattern was not clear across subpopulations and requires more in-depth research to understand the observed patterns.

This study generated a considerable portion of the quantitative data required to compile a CITES non-detriment finding (including on the biological characteristics, national status, management, and protection status of the species), whilst also providing the information needed for the conservation and management of the species. The resultant NDF produced for *E. schoenlandii* by the Scientific Authority of South Africa, found the species to have a high vulnerability and the management regime is weak. The research study assisted with reducing levels of uncertainty to virtually zero and significantly contributed to the robustness of the NDF, allowing for sensible management recommendations to be proposed. This study furthermore contributes significantly to the limited body of knowledge on the biology and ecology, in general, of succulent euphorbias endemic to arid ecosystems in South Africa.

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

L. Jabar: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **S.J. Siebert:** Supervision, Writing – review & editing. **M.F. Pfab:** Conceptualization, Project administration, Resources, Supervision, Writing – review & editing. **D.P. Cilliers:** Formal analysis, Software.

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