

# Population structure and survival of the critically endangered cycad *Encephalartos latifrons* in South Africa

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## Highlights

- At least one wild *Encephalartos latifrons* population is capable of natural recruitment.
- At least one *E. latifrons* population is increasing under present environmental conditions.
- Plants in the seedling stage experience the highest levels of mortality.
- Of the reproductive individuals present in the population, females outnumbered males.
- All stages were significantly clustered in their spatial pattern.

## Abstract

This study investigates the population structure and life history traits of the Critically Endangered cycad, *Encephalartos latifrons*. Populations of *E. latifrons* have been considered functionally extinct because no natural recruitment has been observed in the wild for almost 30 years. The discovery of a previously undocumented population of *E. latifrons* has made it possible to build on previous research into the life history and regeneration capabilities of the species. This new population was censused annually over 5 years; between 2013 and 2017. Population characteristics of this 'new' population were compared to earlier studies in 2010 of a well-known and intensively managed population. Results of the censuses show that the newly discovered population of *E. latifrons* appears to be increasing under current environmental conditions through natural recruitment. The discovery of a 'new' *E. latifrons* population has uncovered many more questions and further research is needed. Information on the life history of *E. latifrons*, particularly its response to fire, should be used to inform conservation management decisions at a time where the impact of climate change is predicted to have a major influence in the Fynbos Biome.

**Keywords:** Life-history; Fire; Fynbos; Resprouter; Demography; Endangered; Cycad

## 1. Introduction

Cycads are the most threatened group of organisms with approximately 70% of known species threatened with extinction worldwide (Hoffmann et al., 2010). The cycad group comprises 3 families, 10 genera and 344 species with hotspots of cycad phylogenetic diversity in southern Africa, Australia, Indo-Pacific and Mexico (Yessoufou et al., 2017). Cycads are not only threatened by a high risk of extinction but are also at risk of losing a significant proportion of evolutionary diversity (Yessoufou et al., 2017). Main threats today include, among others, habitat destruction and trade in wild collected plants (TRAFFIC, 2003). Originating about 300 million years ago and once widespread in the Mesozoic era (Schneider et al., 2002), most cycad species are now known to have small populations with restricted distributions (Crosiers and Malaisse, 1995, Wilson, 2002, Donaldson, 2003, Octavio-Aguilar et al., 2009, Ogwal, 2017). Rare species with small populations are at greater risk to extinction from a number of threats such as changes to the environment, disruption of mutualisms and genetic threats. (Oostermeijer, 2003, Matthies et al., 2004).

Cycads are generally long-lived, slow-growing and dioecious woody perennials. They are found in a range of habitats from closed canopy tropical forests (Lopez-Gallego and O'Neil, 2010), open grasslands (Suinyuy et al., 2013), semi-arid scrublands (Krishnamurthy et al., 2013) and tropical dry forests (Álvarez -Yépiz et al., 2014). In general, cycads fit the conventional description of an S-selected life history typically conforming to a Deevey type III survivorship curve (Deevey, 1947, Grime, 1977, Pérez Farrera and Vovides, 2004, Yáñez-Espinosa and Sosa-Sosa, 2007, Octavio-Aguilar et al., 2017). Donaldson (1995) classified the genus *Encephalartos* into four different life-history types. At the one extreme there are Persisters, long-lived species reproducing largely asexually, but tend to mast seed in response to environmental cues, for example, *Encephalartos cycadifolius* (Jacq.) Lehm. At the other end of the spectrum are the Reproducers, relatively short-lived cycads with limited to no asexual reproduction relying heavily on recruitment from seed (e.g. *Encephalartos villosus* Lem.). Many cycad species display clumped distributions often as a result of poor seed dispersal (Watkinson and Powell, 1997, Pérez Farrera and Vovides, 2004, Perez-Farrera et al., 2006, Octavio-Aguilar et al., 2008, Álvarez-Yépiz et al., 2011, Álvarez -Yépiz et al., 2014), possibly owing to the extinction of megafaunal dispersers and/or range contraction of present day dispersers. This results in germination under, or close to, the female plant, which in turn ensures a suitable microhabitat for germination and increased seedling survival from drought or stress (Hall and Walter, 2013). This advantage is offset by an increase in higher intra-specific density-dependant mortality due to the clustering of seedlings in this way (Octavio-Aguilar et al., 2008, Álvarez-Yépiz et al., 2014).

Cycads are common in fire-prone habitats throughout the world (Tang, 1990, Griffiths et al., 2005, Preece et al., 2007) surviving fire by sprouting, a tolerance trait considered responsible for driving persistence at the plant level (Clarke et al., 2013). Cycads are apical sprouters (and not resprouters in strictest sense), protecting the apical meristem with tightly packed leaf bases of the mature leaves (Clarke et al., 2013).

Threats to wild cycad populations in the Eastern Cape Province of South Africa are likely to have started around 1910 when settler farmers adapted their farming methods to favour crops, livestock and plantations that would suit the environmental conditions at the time

(Somerset Payne, 1910-1911). Pineapple farming in the Bathurst district was particularly environmentally destructive where up until 1957, farmers would plough pristine land rather than use old fields to replant their crops (Departement van Landbou, 1957). After 1957, areas of unspoiled land started becoming less available and farmers started using fertilisers to plant pineapples using lands previously ploughed. The extent of land under cultivation at the time extended over a large part of the natural distribution range of *Encephalartos latifrons* Lehm. shown in a map published by the Department of Agriculture in 1957 (Departement van Landbou, 1957).

Populations of *E. latifrons* were always thought to be small with a highly restricted distribution compared to most other *Encephalartos* species (Chamberlain, 1919) but this has been exacerbated over the years by a rise in threats to the species. Besides habitat destruction resulting from destructive farming practices, new threats in the form of harvesting of wild plants began in the 1960s with an increase in the interest of cycads as horticultural plants (Swart, 2017). Permit archives and inspection reports (held at the Department of Economic Development and Environmental Affairs) show that many *E. latifrons* mature individuals disappeared from private and state land between 1960 and 1990 (Swart, 2019). The rapid destruction of in situ populations of *E. latifrons* prompted the first formal survey of all cycad species in the Eastern Cape including *E. latifrons* (Basson, 1991). The resulting survey reports a total of 63 adult *E. latifrons* individuals found in five populations within the natural distribution area (Basson, 1991). According to the report, three of the 'populations' had a single plant at each locality. Of the two larger populations, one is the subject of this study (Population A). The second population recorded in the 1991 survey was not included in this study because access to the site was not granted by the landowner over the study period. Individuals in this second population remain relatively scattered, with only one female and no natural regeneration recorded in the 1991 survey (Basson, 1991). Although the first formal survey of all populations was undertaken in 1991, Population A has been and continues to be monitored by the landowner on whose property the population exists. Population A has a history of intensive management since the 1980s and apart from the natural seedlings found in 1991, the landowner reports no further natural seedlings found in the population since (Daly et al., 2006; *E. latifrons* landowner, pers. comm.). Another once-off census of the population was undertaken in 2010 (Snow, 2010) where plants were tagged and measured. Apart from the 1991 and 2010 basic surveys, no demographic study of this or any other population had been undertaken.

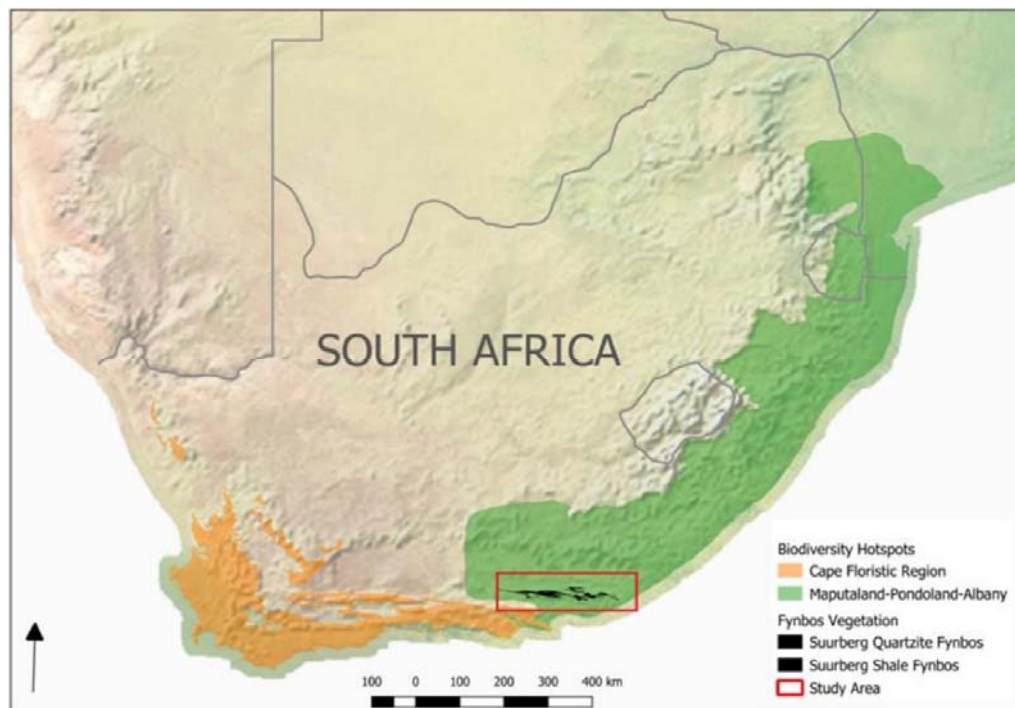
Until 2013, it was thought that all *E. latifrons* populations were known and that there were less than 100 individual plants surviving in natural habitat (DEA, 2011). It was also widely accepted that no natural pollination appeared to be taking place in known wild populations, and there was no evidence of natural recruitment (DEA, 2011). It was therefore fortunate that another *E. latifrons* population was discovered in 2013 (Swart, 2019; Population B). This has allowed research into the general life history, population structure, response to fire and survival of a wild unmanaged *E. latifrons* population. This is important information needed prior to undertaking a Population Viability Analysis for the species as well as making robust non-detriment findings in terms of CITES (Convention on International Trade of Endangered Species of Wild Fauna and Flora).

This study aims to: (1) offer insight into the demography of a wild *E. latifrons* population which may be used to guide conservation strategies to ensure long term persistence of the species; (2) increase our understanding on the population structure, response to fire and spatial patterns in wild *E. latifrons* populations for which there is limited information; (3) contribute to the knowledge of the life-histories of long-lived cycad species.

## 2. Materials and methods

### 2.1. Climate and vegetation of study area

The study area for this paper is confined to the eastern extreme of the Fynbos Biome (Rebelo et al., 2006). The area falls within the meeting point of two important biodiversity hotspots: The Cape Floristic Region (CFR) and the Maputaland–Pondoland–Albany (M–P–A) hotspots (Mittermeier et al., 2011), considered an exceptionally diverse area where six of South Africa's eight major vegetation types converge (Gibbs Russell and Robinson, 1981) (Fig. 1). This area is sometimes referred to as the south-eastern Greater Cape Floristic Region (GCFR) (Bergh et al., 2014). Vegetation types of the GCFR typically burn on a 5–50-year cycle averaging 15–25 years (Rebelo et al., 2006). Fire is generally more frequent in the eastern extreme of the GCFR (averaging 4–6 years between fires) as a result of more fertile soils with a higher summer rainfall (Cowling and Richardson, 1995). Fires in the eastern extreme of the GCFR are also often associated with ‘berg winds’ (hot dry winds flowing from the interior) occurring mostly in winter (May–August) (Cowling and Richardson, 1995, Kraaij and van Wilgen, 2014), but are generally less seasonal than in the west (Van Wilgen, 2013).



**Fig. 1.** Map showing the two biodiversity hotspots relevant to this study: Cape Floristic Region (CFR) and the Maputaland–Pondoland–Albany (M–P–A) hotspots ([www.cepf.net/our-work/biodiversity-hotspots](http://www.cepf.net/our-work/biodiversity-hotspots) accessed on the 30 April 2018). The red rectangle shows the part of the CFR that extends into the M–P–A, considered the Greater Floristic Region representing the study area.

The climate of the study area reflects bimodal to aseasonal rainfall with spring (September and November) and autumn (March and April) peaks. The mean annual precipitation (MAP) for Suurberg Quartzite Fynbos ranges from 220 to 820 mm (mean = 545 mm). The study area is classified as Cfb (Warm-summer Mediterranean climate) according to the Köppen–Geiger Climate Classification System (Kottek et al., 2006, Engelbrecht and Engelbrecht, 2016) with a low number of frost days per annum (only 5) (Rebello et al., 2006).

### 3. Study species

*Encephalartos latifrons* (Zamiaceae) is a cycad that is endemic to the Eastern Cape Province of South Africa. The species is listed as Critically Endangered (CR) – A2acd; B2ab (ii, iii, v); C1 + 2a(i) (Donaldson, 2010) with reportedly less than 100 individual plants remaining in the wild (Department of Environmental Affairs, 2011). It is an arborescent species able to reach heights of 3 m. It is one of the slowest growing species and thought to have the longest coning interval of all cycads (Kemp, 1986). Wild plants, easily recognised standing out in the mostly tree-less Quartzite Fynbos, grow in clusters on rocky outcrops with other fynbos tree species such as *Oldenburgia grandis* (Thunb) Baill. and *Loxostylis alata* Spreng. ex Rchb. These clusters sometimes occur on forest margins but are always associated with Quartzite outcrops. The glossy dark green leaves form a distinguishable ‘skirt’ around the stem. The leaflets are broad, often leading to the species being confused with *Encephalartos arenarius* R.A. Dyer, having numerous triangular pungent lobes curving strongly downwards and inwards. Like all cycads, *E. latifrons* is dioecious; male and female cones develop on separate plants. Female cones are much larger than the male cones reaching a height of 600 mm and a circumference of up to 570 mm (Giddy, 1974, Grobbelaar, 2004; pers. obs.). Seeds are large consisting of a woody kernel surrounded by a bright red fleshy sarcotesta. Pollen shedding takes place during the winter months between June and August. The female cone disintegrates spontaneously during the summer months of December and January yielding approximately 275–790 omnules (sensu Grobbelaar, 2004). There is a minimum seed resting period of approximately six months where the embryo continues to develop after fertilisation (Giddy, 1974). Cycads therefore experience a form of Non-Deep Morphophysiological dormancy associated with a poorly developed embryo at the time of seed shedding (Xaba, 2014).

### 4. Study sites

Only three *E. latifrons* populations containing more than two individual plants are currently known to exist. This paper focuses on two of these populations located at either extreme of the species distribution. Excluded from this study are individual plants that remain scattered where larger populations once existed.

The populations included in this study are referred to as Population A and Population B. Population A was included in the Population and Habitat Viability Assessment (PHVA) assessment (Daly et al., 2006) as well as in the 1991 survey (Basson, 1991). Population B is undocumented and recently discovered and has not been included in any previous assessment of the species. Population A is situated closer to the coast in an area regarded as the eastern-most outlier of the GCFR. Fynbos in this area remains in small patches interfaced with other vegetation types such as Kowie Thicket and Albany Coastal Belt

vegetation (Hoare et al., 2006). The fire climate of this site is considered as the far eastern coastal zone (Kraaij and van Wilgen, 2014). Low to moderate fire danger conditions are the norm for this area with a Fire Danger Index (FDI) rarely reaching above 2 on the FDI scale (Kraaij and van Wilgen, 2014). Population A exists in clusters across two properties divided by a game fence. One property keeps livestock and crops (site A1), while the other property is a game reserve (site A2). Population B lies further west associated with larger areas of Suurberg Quartzite Fynbos adjacent to regions of Suurberg Shale Fynbos and Bhisho Thornveld of the Savanna Biome (Rebelo et al., 2006, Rutherford et al., 2006). Fires are known to be frequent in this area. A history of fire occurrences for the neighbouring property from 1996 recorded 11 very large fires in 20 years leading up to 2016. This is approximately a fire every second year, some years with more than one fire event. The fires occurred predominantly in winter (June) and late winter to early summer (August–December). Fire return times for each site was not available at the time this study was undertaken.

Population A and B both occur within the Suurberg Quartzite Fynbos (SQF) vegetation type, but environmental conditions experienced by both populations differ in terms of fire regime, land use, conservation management, climate, altitude and disturbance history (Table 1).

## **5. Population censuses**

A once-off census of Population A was undertaken by an inspecting officer of the conservation authorities in December of 1991 (Basson, 1991). All plants in the population were counted but only measurements of plants at site A2 were included in the inspection report. An additional once-off population census of Population A at sites A1 and A2 was undertaken in 2010 where all plants were measured and tagged. No further studies have been undertaken at this site and access to the plants remains relatively restricted.

An annual census (in each of 5 years) of Population B was undertaken from 2013 to 2017 in which all plants found were tagged, stem height and circumference measured, number of stems counted, number of mature cones (if any) recorded, whether the plants had burnt in recent fires leading up to each census noted, the emergence of new seedlings documented and the co-ordinates of each plant stored in a Geographic Information System (ESRI, 2012). Plants were tagged with an aluminium label punched with a hole and attached to the plant using binding wire. This was done to enable the monitoring of survival/fire response/fecundity for each individual plant over the five-year study period. Metal tags were used to ensure that the plants could be identified if burnt in a fire.

After an extensive search of the property (and reliance on local knowledge of the area) it was assumed that all plants within the population were included in the sample. Due to the mountainous terrain and difficulty accessing the entire area, a few plants may have been missed. Survival of individual plants was recorded over the 5 years. As *E. latifrons* is regarded as one of the slowest growing cycads, growth was difficult to determine due to the small increments and high potential for measurement error.

**Table 1.** Sites within population A and B included in this study. Locality information is not revealed to protect the remaining plants from theft.

	Population A			Population B				
	Site A1	Site A2	Site B1	Site B2	Site B3	Site B4	Site B5	Site B6
<b>Altitude (masl)</b>	115–176	115–176	660–725	620–630	625–635	515–520	480–485	480–495
<b>Aspect</b>	SW	S	N	E	N	E	SW	NE
<b>Disturbance level</b>	High	High	Low	Low	Low	Medium	Low	Medium
<b>Disturbance type</b>	Intensive management of plants including artificial pollination, off-site seedling propagation and restoration	Theft of plants from site in 1993	None	None	None	Trampling and clearing for hiking path; bark harvesting	Light grazing by indigenous game	Bark harvesting
<b>History</b>	Population intensively managed for 40 + years. Male and female plants uprooted and planted closer together in 1980	Natural seedling recruitment in 1991 (Basson, 1991)	Not known	Not known	Not known	Site moderately invaded by alien and invasive vegetation but now clear	Site lightly invaded by alien and invasive vegetation but now clear	Site heavily invaded by alien and invasive vegetation now mostly cleared.
<b>Land use</b>	Livestock and crop farm	Game Reserve since 2003 – previously a livestock farm	Informally protected area with light recreational use					
<b>Fire Frequency</b>	> 15 years		1–3 years					
<b>Fire climate zone</b> (Kraaij and van Wilgen, 2014)	Far Eastern Coastal Zone		Eastern Inland Zone					
<b>Mean Annual Precipitation (Puttick et al. 2011; R. Rowsell pers. comm)</b>	720 mm		767 mm					
<b>Survey history</b>	Basson (1991); Snow (2010); informal monitoring by landowner from at least 1980 for Site A1 and post 1993 for Site A2. Landowner reports no natural seedling recruitment (Daly et al., 2006).		Population ‘discovered’ in 2013. Surveys for PhD research project in 2013, 2014, 2015, 2016 and 2017, (Swart 2019)					

Seedlings in Population B were without a measurable stem; therefore, seedling height was recorded as the size of the plant from the ground, measuring the vertical distance to the tip of the largest leaf without disturbing the leaf. The number of leaves for each seedling was counted but this did not characterise the size of the seedlings accurately due to the high variability of dead and/or burnt leaves found on the plants. The annual census was planned to coincide with the coning season for *E. latifrons* (June/July). If there had been a fire, additional visits to the sites to record survival and sprouting response were undertaken. Plants with female cones were also monitored and additional visits timed to coincide with the disintegration of the cone in January/February.

## 6. Determining stage classes

For studies on long-lived woody tree species, the use of morphological characteristics that describe stage rather than age is the preferred method in determining categories for analysing population structure in demographic analysis (Octavio-Aguilar et al., 2008, Álvarez-Yépiz et al., 2014, Cousins et al., 2014). Life history traits such as persistence and reproduction are more likely to be associated with stage of an individual rather than age in long-lived woody species (Caswell, 2001). The assumption in this study is that individuals belonging to the same stage experience similar survival, growth and reproductive rates making the use stage biologically meaningful when analysing the demographics of *E. latifrons* (Brigham, 2003). Stage classes were determined for both populations in order to compare population structure and to construct survivorship curves. Seedlings were plants without a measurable stem and divided into two categories, se1 and se2. Se1 plants included the shortest individuals with leaf lengths of 5–20 cm which were easily distinguished from the other stages as young plants with smaller leaf size differing in leaf shape – usually toothed on both margins of the leaflet. Se1 seedlings were plants in the youngest stage class having germinated within the last 2 years with between 1 and 4 leaves on each plant. These are the smaller leaves before ‘true’ leaves develop (Giddy, 1974).

Se2 plants were considered older seedlings between 21 and 80 cm leaf length having developed the larger true leaves. Se2 seedlings had between 1 and 7 leaves per plant and the leaflet margins were similar in appearance to the adult plants. Juvenile plants were also divided into two categories, juv1 and juv2. Juv1 plants had a measurable stem of between 1 and 9 cm with only one stem per plant. Juv2 were also single stemmed individuals between 10 and 34 cm in stem height. Adults were again divided into two categories a1 and a2. All adult plants had the potential to reproduce by coning. The shortest stem height recorded where an adult female *E. latifrons* coned for the first time was 35 cm (*E. latifrons* landowner, pers. comm.). An assumption was therefore made that any individual with a stem height over 35 cm had the potential to reproduce. Individuals in the a1 category reached a maximum stem height of 160 cm with between 1 and 4 suckers, each over 10 cm in stem height. Plants in the a2 category had a stem height > 160 cm where the number of suckers over 10 cm in stem height varied between 1 and 8. Plants in the a2 category tended to be multi-stemmed and therefore had a greater potential to bear cones and reproduce. Cumulative stem height (i.e. the sum of individual stem height for each plant) was used to construct the survivorship curve to reflect the difference between the smaller single-stemmed plants and the larger multi-stemmed individuals.



A two sample Kolomogorov–Smirnov test was used to test whether the stage-distribution of Population A and B differed significantly. Data were analysed using the Real Statistics Resource Pack software (version 4.14) (Zaiontz, 2017).

## 7. Data analysis

A static life table was constructed for Population B based on female numbers according to Krebs (1978). A life table was not constructed for Population A because it contained only 10 females which was considered too low to give a realistic representation of the population, particularly since 15 adult plants and/or stems had been removed from the population by illegal harvesting. It was also not possible to determine the average number of seedlings per female in the a1 and a2 stage class in Population A as this is artificially manipulated by manually pollinating cones, harvesting seed and propagating seedlings before re-planting them in the wild. For plants in Population B where the sex of individual plants was unknown, the sex ratio of known-sex plants was used to estimate the total number of females in the population. The observed number of females in each stage class ( $n_x$ ) and the proportion surviving to stage  $x$  ( $l_x$ ) was calculated as  $n_x/n_0$ . The probability of reproduction ( $m_x$ ) was calculated as the average number of seedlings per female plant in the a1 and a2 stage classes. We considered that it was possible to calculate this because seedlings near the female were assumed to be her offspring due to their tendency to form groves (Hall and Walter, 2013). The finite rate of mortality ( $q_x$ ) was calculated as  $(n_x - n_{x+1})/n_x$  and killing power ( $k_x$ ) as  $\log_{10}n_x - \log_{10}n_{x+1}$  to reflect the mortality intensity which can be summed across stages (Varley and Gradwell, 1970). Information from the life table was then used to solve the Euler-Lotka equation expressed as  $\sum e^{-rx}l_xm_x = 1$  to obtain values for the intrinsic rate of increase ( $r$ ) and net reproductive rate ( $R_0$ ), assuming a closed population with no immigration or emigration. The seedling (se1 and se2) and juvenile (juv1 and juv2) stages were pooled for this analysis.

Survival analysis for Population B was based on 5 years of right-censored data where survival and mortality of each individual was monitored and recorded annually over the study period. Whether an individual survived (0) or died (1) at the end of each annual census was recorded as a binary number. The Kaplan–Meier estimator was used to calculate the non-parametric estimates of the survivor function,  $\hat{S}(t)$ , for the two stages experiencing mortality over the study period, namely se1 and se2 (Bland and Altman, 1998).

Potential environmental influences on seedling mortality in Population B such as slope (estimate of degrees), aspect, soil moisture and distance to the nearest rock over 1 m in length and or height were estimated using exact regression analysis. Exact regression analysis caters for small sample sizes as was the case in this study. The R package ‘elrm via MCMC’ was used for this analysis (Zamar et al., 2013). Whether the seedling died (yes = 1; no = 0) was analysed as the dependent variable with aspect, slope, soil moisture and distance to the nearest rock taken as the independent variables. The number of Markov Chain iterations was set to 2000. Stages se1 and se2 were again pooled for this analysis.

Distance between plants of different sexes was calculated by means of a distance matrix using a Geographic Information System (Quantum GIS Development Team, 2015) including correlations between the number of seedlings a female produced and her proximity to the

nearest two males. The average distance to the two closest males was calculated for this analysis and tested for significance using the Pearson's Correlation Coefficient.

To determine the spatial patterning of individuals in Population A, average nearest neighbour analysis (ANN) and Ripley's K(t) function (Haase, 1995, Mitchell, 2005) were used. ANN uses a nearest neighbour index to calculate the average Euclidean distance of each individual to its nearest neighbour testing the null hypothesis of an evenly dispersed, non-clustered population. An index value of less than 1 indicates a clustered pattern in the distribution of individuals throughout the population. The disadvantage of ANN is that it is not able to describe the relationship between two or more point patterns such as the relationship between seedlings, juveniles and adults and to describe these characteristics at varying distance scales (Dixon, 2002) therefore the Ripley-K function was also used. ANN was calculated using the Spatial Statistics ArcGIS toolbox (ESRI, 2012). The z-score and p-value are sensitive to the change in size of the study area which was therefore fixed at six square kilometres for this analysis. ANN index was calculated for the entire population as well as for the individual stage classes. The Ripley's K function was used to analyse spatial patterning and dependence between stage classes at different distances. The bivariate form of Ripley's K function (L function or Besag's transformation) was used to determine spatial associations of the seedling and juvenile stages with the adult stages (Besag and Diggle, 1977). This transformation stabilises the variance of the estimator making L(r) more appropriate for use in simulation envelopes (Baddeley et al., 2015). The R package 'spatstat' was used for the analysis (Baddeley and Turner, 2005).

## 8. Results

The stage-distributions of plants in Population A and B did not differ significantly  $D(N = 6;6) = 0.67$ ,  $p = .07$  despite Population A having no seedlings. Seedlings in Population B made up 55% of the population. The juv1 stage of Population A is similar to that of Population B, with the number of juv2 plants substantially lower in Population A. Survivorship curves were constructed indicating a Deevey Type III curve for both populations.

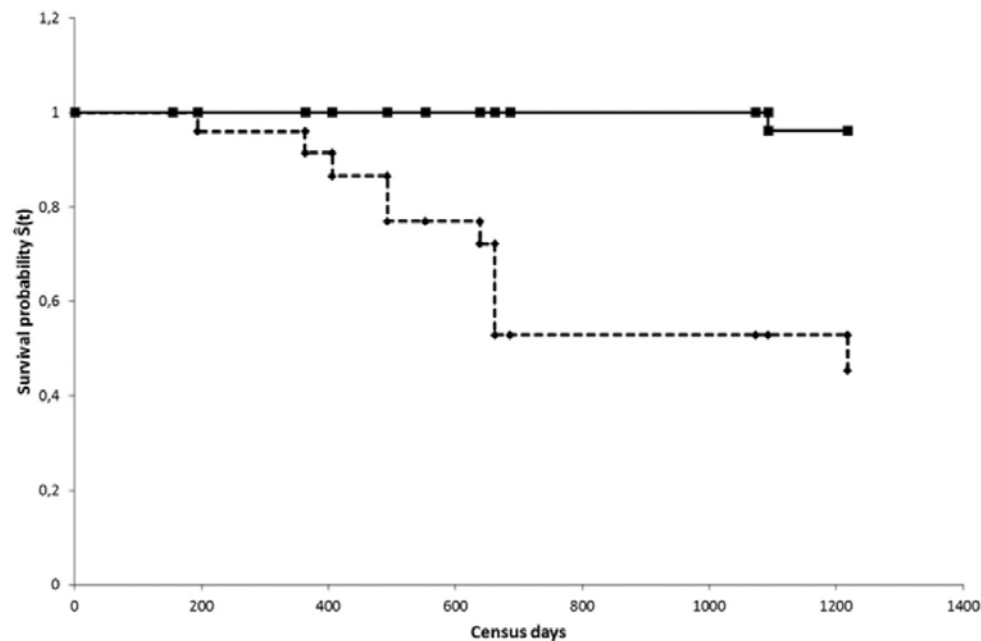
A female-based life table for Population B is shown in Table 2. The highest rate of death ( $q_x$ ) occurs in the early stage of the plant's life cycle i.e. 55% of individuals die in the seedling stage compared to the later stages. This is also reflected in the intensity of mortality or killing power ( $k_x$ ). The net reproductive rate (or replacement rate) per generation ( $R_0$ ) indicates that the population is increasing on average by two female offspring per female over each generation. The intrinsic population growth rate ( $r$ ) of 0.47 indicates an increasing population under environmental conditions at the time of the study.

**Table 2.** Static life table based on the stage classes for Population B including female plants only. The observed numbers per stage ( $n_x$ ) reflect the population at the final census in 2017. Fecundity rate ( $m_x$ ) reflects the average number of seedlings a female produced over the study period. The proportion surviving to stage  $x$  ( $l_x$ ), finite rate of mortality ( $q_x$ ) and killing power ( $k_x$ ) to reflect the mortality intensity, intrinsic rate of increase ( $r$ ), net reproductive rate ( $R_0$ ) and annual instantaneous growth rate ( $\lambda$ ) are shown.

$x$ (stage class)	$n_x$	$l_x$	$m_x$	$q_x$	$k_x$
se1 + se2	22	1.00	–	0.55	0.34
juv1 + juv2	10	0.45	–	0.30	0.15
ad1	7	0.32	6	0.43	0.24
ad2	4	0.18	2	–	–
$r$	0.38				
$R_0$	2.27				
$\lambda$	1.47				

## 9. Survival analysis

No individuals within the juvenile or adult stage classes died over the study period. The seedling stage experienced the highest mortality with 21% of seedlings (se1 + se2) dying over the 5-year study period. The Kaplan–Meier survivor function values differ significantly between the se1 and se2 stages ( $Z = 14.98$ ;  $p < .0005$ ). Fig. 2 shows the difference between the survivor function for se1 and se2 individuals with a decreasing probability of se1 surviving over the census period. The se1 stage experienced the highest seedling mortality at 41% whereas the se2 stage only contributed 3% to overall mortality. Of the seedlings that died, 33% of deaths were directly attributed to fire (i.e. they had not experienced a leaf flush after being burnt in a fire where the other seedlings had).



**Fig. 2.** Kaplan–Meier probability of survival for the se1 (dashed line) and se2 (solid line) stage plants during the study period for Population B. Survival probability for juvenile and adult stages remains at 1 (not shown in this figure).

All other stages displayed a high resilience to fire with no mortality over the study period. The production of leaf flushes after a fire was synchronous in all stages in the population occurring approximately 3 months after the fire. A higher percentage of seedling deaths (63% of the total) tended to be associated with sites where the vegetation was more closed and denser such as sites B2 and B5 on wetter slopes. Sites on drier, open slopes experienced fewer (27% of the total) deaths such as site B1 and B3. Clearing vegetation for a hiking path at the B4 site resulted in the remaining 10% of total deaths. Exact binomial regression analysis of seedling survival after fire suggests that distance to the closest rock positively affected whether a seedling survived the fire or not (coefficient = 0.03;  $p < .05$ ; se (0.015); lower = 0.0017; upper = 0.834). Survival against other environmental variables did not show any significant correlation.

## 10. Fecundity

There was a difference in the sex ratio between Population A and B where males in Population A outnumbered females by 2.6:1. The opposite was true for Population B with a ratio of two females for every male. Information on coning frequency was not available for Population A. Proportion of coning individuals during the study period for Population B is shown in Table 3.

**Table 3.** Proportion of males and females coning (relative to all adults of the same sex in the population) including sum of cones from each sex over the census period (2013–2017) in Population B. Total male and female numbers change as additional plants were found in later years.

Year	2013	2014	2015	2016	2016
Proportion of males coning in population	0.33	0.80	0.40	0	0.40
Proportion of females coning in population	0	0.56	0.22	0	0
Total male cones in population	2	8	3	0	4
Total female cones in population	0	7	2	2	2
Total number of males in population	5	9	9	9	9
Total number of females in population	3	5	5	5	5

Given the infrequent nature of coning in *E. latifrons*, an exceptionally good coning year was seen in 2014/2015, both in the proportion of coning individuals as well as the total number of cones within the population. This appeared to be a mast-seeding year with 56% of females and 80% of males coning. One adult male plant produced five cones on one stem in this year. Some plants did experience scorching in a fire while in cone. In one instance, a female plant was burnt on the one side of the stem and cone. The plant experienced localised sprouting on the charred side of the stem and cone. In another instance, a female plant with three cones was infected with a pathogen (i.e. an unidentified fungus growing on all three cones, each on a mature stem). The female plant, nevertheless, survived. All three cones turned black and remained on the stem without disintegrating. The seeds on all these cones were malformed and nonviable.

The number of offspring per female in Population B ranged from 0 to 17 seedlings. Site B6 consisted of two females with two males at a distance of 8 and 17 m from the females respectively forming a close cluster of plants. The site had no seedlings, however. Other

sites with female plants, such as site B4, had only one mature female plant with the closest male at 1439 m and six seedlings at the site. The stage structure of different sites for Population B showing proportion of individuals per stage at each site is shown in Table 4. Other sites were very productive with 17 seedlings found at site B5. Proximity of females to males did not relate to significantly higher levels of recruitment ( $r(8) = 0.23$ ,  $p = .28$ ).

**Table 4.** Stage structure of different sites for Population B showing proportion of individuals per stage at each site.

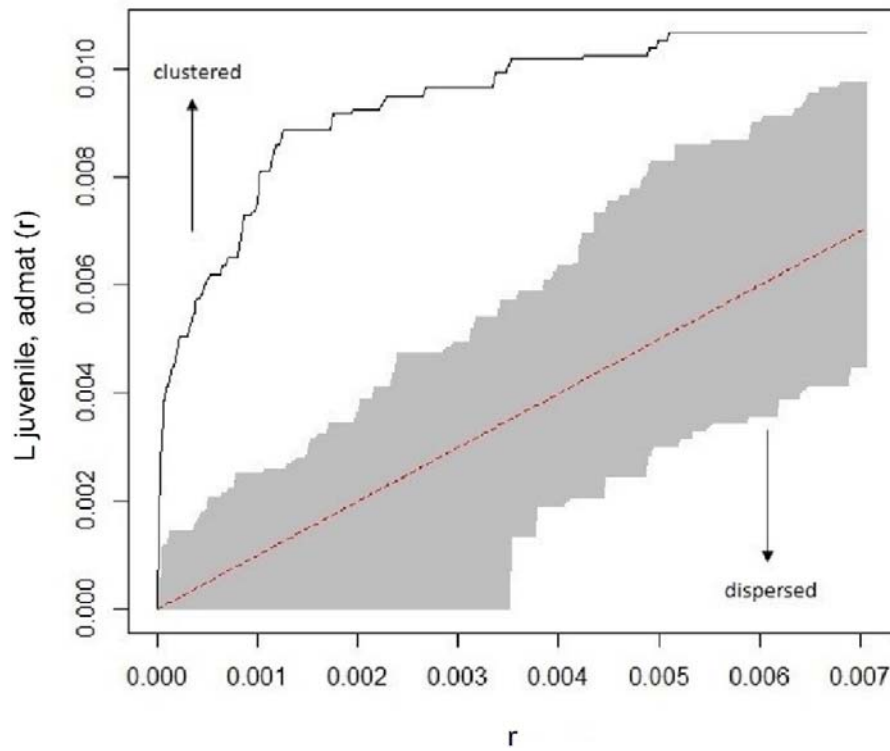
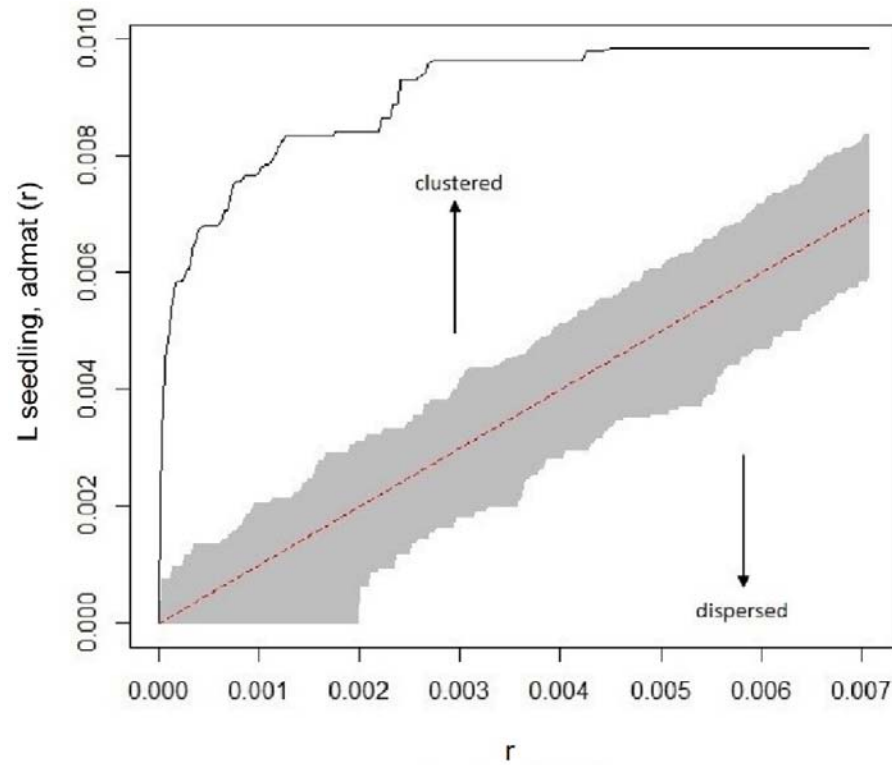
	se1	se2	juv1	juv2	ad1	ad2	N
Site B1	0.13	0.38	0.15	0.18	0.13	0.05	40
Site B2	0.44	0.13	0.06	0.06	0.25	0.06	16
Site B3	0.38	0.38	0.00	0.00	0.13	0.13	8
Site B4	0.38	0.38	0.13	0.00	0.00	0.13	8
Site B5	0.43	0.38	0.00	0.05	0.14	0.00	21
Site B6	0.00	0.00	0.00	0.00	0.25	0.75	4
Total							97

## 11. Spatial pattern

Overall, the ANN index value for Population B was 0.07 (z-score = - 20.33,  $p < .0001$ ) indicating a significant clustered pattern of individuals in Population B. Seedlings displayed the strongest clustering. As the stage classes increased, crowding became less pronounced but remaining significantly clustered (Table 5). Seedling and juvenile plants were strongly associated with the adult stages at all distances as shown by the Ripley K analysis in Population B (Fig. 3).

**Table 5.** ANN index of the different stage classes, z-score, and significance with observed and expected mean distances.

Stage class distance (m)	ANN index	z-score	p-value	Observed mean distance (m)	Expected mean distance (m)
Seedlings (se1 + se2)	0.005	- 18.8	< 0.0001	0.8	161.6
Juveniles (juv1 + juv2)	0.101	- 9.9	< 0.0001	28.1	277.1
Adults (ad1 + ad2)	0.305	- 6.9	< 0.0001	93.4	303.4



**Fig. 3.** Bivariate  $L(r)$  plots to evaluate the spatial relationship between seedlings (a) and juveniles (b) and the adult stages.  $L(r)$  function (solid line) relative to the 95% random simulation envelope (grey shading).  $L(r)$  above the simulation envelope indicates a positive spatial association.  $r$  values on the x-axis refers to distance in decimal degrees.

## 12. Discussion

Results of the life table analysis reveal that one population of *E. latifrons* is capable of natural recruitment, is stable and increasing under current environmental conditions (although still critically small). The average number of female offspring ( $R_0$ ) produced by each female over each generation (the time from the birth of a female to the production of that female's first offspring) (2.27 female offspring per female) is lower than other endangered cycad species such as *Ceratozamia mirandae* Vovides, Pérez-Farr. & Iglesias at between 5.85 and 8.2 (Perez-Farrera et al., 2006) but higher than populations of the Critically Endangered Mexican cycad *Ceratozamia zaragozae* Medellín-Leal at 1.06 (Castillo-Lara et al., 2017). Similarly, intrinsic rates of increase for the *E. latifrons* population at 0.38 was lower compared to 0.57 and 0.84 for *C. mirandae* (Perez-Farrera et al., 2006) and 0.89 for *C. zaragozae* (Castillo-Lara et al., 2017). This contrasts with the endangered *Dioon sonorensis* (De Luca, Sabato & Vázq.Torres) J.Chernick, T.J.Gregory & S.Salas-Mor. where all populations are showing signs of decline ( $r < 1$  and  $< 0$ ) (Álvarez-Yépiz et al., 2011). The crucial difference between *E. latifrons* and these three species is that *E. latifrons* has only one functional population where natural seedling recruitment is occurring. This puts *E. latifrons* (and other species such as *Zamia inermis* Vovides, J.D.Rees & Vázq.Torres where only one population is known) at greater risk of extinction through either deterministic factors (altering population growth rate such as habitat loss, illegal harvesting, alien and invasive species) or from demographic stochasticity, environmental stochasticity, genetic stochasticity, or natural catastrophes (Gilpin and Soule, 1986, Given, 1994, Brook et al., 2002).

The *E. latifrons* populations reported in this paper conform to a Deevey Type III population structure with a life history typical of a persister/reproducer (Donaldson, 1995). Other cycad species with similar population structures include *Dioon edule* Lindl. (Vovides, 1990, Octavio-Aguilar et al., 2008), *C. mirandae* (Perez-Farrera et al., 2006), *Zamia pumila* L. (Negron-Ortiz and Breckon, 1989), and *Dioon purpusii* Rose (Yáñez-Espinosa and Sosa-Sosa, 2007) among others. Population A did not have any plants in the se1 stage at the time of the census and according to the landowner, the plants in the se2 stage were artificially propagated and planted out in 2004 and 2009 (including an additional 30 since the census in 2010; the size at which they were planted is not known). There were four natural seedlings recorded at site A2 as documented in 1991. The estimated age of the seedlings was one year old ( $n = 3$ ) and an older seedling at approximately 3 years old ( $n = 1$ ). Other long-lived species such as *Kumara plicatilis* (L.) G.D. Rowley (= *Aloe plicatilis* (L.) Mill), a succulent tree endemic to the Cape Fynbos and restricted to rocky outcrops, show considerable variation in population structure across the species distribution range (Cousins et al., 2014). Cousins et al. (2014) suggest that a population structure deviating from an inverse J shape, especially in long-lived, slow-growing species does not necessarily indicate an unhealthy, declining population. They did find that populations displaying reverse J-shaped population structures were more likely to be found in areas with higher rock cover, compared to populations with fewer young plants found in areas with comparatively less rock cover (Cousins et al., 2014). Larger populations with reverse J-shaped population structures also tended to offer favourable microsites for seedling establishment compared to populations with fewer seedlings (Cousins et al., 2014).

Fire survival strategies in *E. latifrons* in Population B can be compared to those of *K. plicatilis* in that both species display morphological characteristics that suggest fire tolerance and are not resprouters per se but apical sprouters (Cousins et al., 2016). It is suggested that *K. plicatilis* has a dual fire strategy by avoiding fires in rocky refugia and tolerating fires with well-protected apical meristems, a thick corky bark and a persistent dead leaf 'skirt'. The presence of a 'skirt' consisting of dead leaves is a distinguishing characteristic displayed in *Aloe* and *Aloidendron* taxa found in fire-prone environments (Bond, 1983). This distinctive characteristic is also found in *E. latifrons*. In much the same way, *E. latifrons* populations are restricted to rocky habitats displaying high levels of survival after fire comparable to other Cape Fynbos resprouter species (Marais et al., 2014, Treurnicht et al., 2016). The *E. latifrons* seedling stages were most vulnerable to fire, but survival improved with an increased proximity to rock. Similarly, Cousins et al. (2016) found that postfire mortality of *K. plicatilis* increased with a decreasing percentage of rock cover within populations sampled. On the rocky outcrops where *E. latifrons* occurs it is often associated with another resprouting endemic fynbos tree species, *Oldenburgia grandis*. Individuals of *O. grandis* are more likely to survive fire if growing on or close to a rocky outcrop (Swart, 2008), especially plants in the seedling stages that did not have the ability to resprout. Seedling survival and proximity to rock has also been shown to be important for other cycad species where rocks act as nurse objects promoting seedling establishment and survival (Álvarez -Yépiz et al., 2014). Rocks also appear to have positive nurse effects on the establishment of woody plants in other southern African biomes (Fujita and Mizuno, 2015).

Research on resprouting fynbos shrubs found that plants resprouting earlier after a fire had better chances of survival than those resprouting later (Marais et al., 2014). The same study found that, on average, obligate resprouters in Mountain Fynbos shrubland took 45 days to resprout after fire. Sprouting response in *E. latifrons* after fire took approximately 90 days across all stages. An early sprouting response is important for carbon-replacement (via photosynthesis) where the metabolic demands of resprouting depletes carbon stores (Marais et al., 2014). The ability to resprout early after a fire also suggests a competitive advantage (in replacing canopy space lost in the fire) possibly more important in environments where competition is higher in Mountain Fynbos compared to rock outcrops in Grassy Fynbos where inter-specific competition is typically lower (Linder and Ellis, 1990).

Population A has experienced a substantially different fire regime to Population B in the recent past. According to the landowner, the last fire at the Population A site was over 15 years ago – a typical fire frequency in the far eastern coastal zone where patches of fynbos are small and fragmented (Rebelo et al., 2006, Kraaij and van Wilgen, 2014). It is not known how this population responds to fire and future monitoring is needed to determine the resilience of *E. latifrons* under a range of fire regimes. Resprouting species such as *O. grandis* displayed different adult survival rates under a range of fire regimes. Increased fire intensity due to a build-up of biomass in Mountain Fynbos, combined with berg winds, resulted in high mortalities where 43% of mature *O. grandis* plants at a site perished in a fire, compared to negligible mortalities under a fire regime similar to that experienced by Population B in Grassy Fynbos (Swart, 2008). Similar differences in mortality rates under different fire intensities were recorded in the Australian cycad *Cycas armstrongii* Miq. Liddle (2004) found that *C. armstrongii* populations were resilient to a wide range of low intensity fire frequencies. Areas of the grassy woodland invaded by exotic grasses, however,



increased the fuel load around some populations and in turn the fire intensity, resulting in adult mortalities of *C. armstrongii* of up to 50%. Likewise, increased fire intensity threatened the persistence of *O. grandis* populations (Swart, 2008) and is expected to have a similar detrimental effect on *E. latifrons* populations.

Sex ratios differ remarkably between and within cycad populations and are often difficult to determine over short study periods due to infrequent and unpredictable coning events (Clark and Clark, 1987, Tang, 1990, Mora et al., 2013, Octavio-Aguilar et al., 2017). The sex ratio of Population A in 1991 before the theft was 2 males:1 female (Basson, 1991). This is close to the current sex ratio of the population. It is likely that individual stems rather than entire multi-stemmed individuals were removed from the population retaining the sex ratio of the original population (plants stolen from site A2 ranged between 0.5 and 1.74 m in stem height). The seedlings recorded at this site in 1991 are likely not to have survived the disturbance and no natural seedlings have been recorded in Population A since. The difference in sex ratios between populations of the same species is reported for other cycad species such as the Australian cycad *Macrozamia riedlei* (Gaudich.) C.A. Gardner where all populations (and the species as a whole) were thought to be male-biased but further studies found some populations also had a strong female bias (Ornduff, 1985, Gerlach, 2012). Reasons for sex ratios deviating from a 1:1 sex ratio are not certain. In some instances, male-bias is attributed to the targeting of female plants by poachers as they are more valuable (Donaldson, 2008, Yeld, 2014). Studies also suggest male-biased coning ratios in some populations are influenced by less favourable environmental conditions given the reproductive effort needed to produce a much larger and energy expensive female cone (Ornduff, 1985, Ornduff, 1987).

The sex ratio of known plants in Population B is female-biased. This is unusual for many cycad populations as well as many dioecious flowering plants (Clark and Clark, 1987, Ornduff, 1990, Pickup and Barrett, 2013). Female-biased sex ratios are recorded in some wind-pollinated plants such as *Rumex* species where pollination intensity (larger pollen loads deposited on female plants) has been suggested to promote female bias ('gametophyte selection hypothesis') although this is likely to influence annual species rather than longer-lived perennial plants (Stehlik et al., 2008, Pickup and Barrett, 2013).

The number of offspring per female was variable with some productive sites and other sites with females completely devoid of seedlings. Distance between male and females did not appear to influence levels of seedling recruitment in Population B and it is uncertain why some females were productive while others were not. The only observable difference between the unproductive sites and the other sites with more productive females was that the site with no seedlings was once heavily invaded by alien and invasive vegetation. It has been reported that high fire intensities associated with increased fuel loads caused by alien invasions may have severe hydrological effects on the soil in the environment (Mills and Fey, 2003, Kraaij and van Wilgen, 2014) and further investigation is needed to conclude if this is the case for *E. latifrons*. Successful coning, seed development and seed recruitment are most likely to occur between fire intervals much like recruitment strategies observed in *K. plicatilis* populations (Cousins et al., 2016). Fire had a negative effect on coning in Population B in that it burnt developing cones which may have explained the number of malformed seeds found in the sample although this would need further investigating. The

timing of fire is an important consideration in how it affects fecundity, cone development and subsequent seedling recruitment.

The spatial pattern in the *E. latifrons* Population B displays a similar clustered pattern to many cycads worldwide. Clustering of plants was especially evident among the seedlings. Juveniles were less clustered with greater observed mean distances from the adult stages suggesting some thinning of plants with an increase in stage class. This is also observed in other cycad species such as *Macrozamia miquelii* (F. Muell.) A. DC. (Hall and Walter, 2013). Some seedlings germinated on an overhang above the female plant discounting the possibility that they were dispersed by gravity. Seed dispersal by birds, rodents or hyraxes may explain limited dispersal of some of the seed and subsequent germination of seedlings in suitable sites further away from the female (Schneider et al., 2002).

### 13. Current and future threats

There is still a real poaching threat to *E. latifrons* populations that remain in the wild. Population A is relatively secure as it exists on private land and is constantly monitored with restricted access to the public. This population is currently not reproducing naturally; its survival appears to be solely dependent on the landowner's interest in artificially pollinating female cones and augmenting the wild population with artificially propagated seedlings. The relative anonymity of Population B has resulted in it being less disturbed than more exposed and better-known populations. Threats to this population would include urban encroachment and infrastructure development (such as the expansion of wind farms) and possibly altered fire regimes due to climate change but there is still much uncertainty around this.

There is growing evidence that loss of biodiversity may be accelerated by a changing climate (McCarthy et al., 2001, Bálint et al., 2011, Laidlaw and Forster, 2012, Jantz et al., 2015, Wiens, 2016). This is particularly evident in regions such as the Greater Cape Floristic Region (GCFR) where climate change is likely to effect a change in fire regime resulting from a warming climate and increased drought prevalence (Altwegg et al., 2014, Wilson et al., 2015). The GCFR is a large region characterised by east–west divisions in rainfall patterns, fire climate zones and temperatures as well as regional climatic gradients (Kraaij and van Wilgen, 2014). The western extreme of the GCFR is undoubtedly becoming hotter and drier whereas the east of South Africa is predicted to become wetter (Altwegg et al., 2014). It is uncertain whether the eastern extreme of the GCFR (including the *E. latifrons* distribution range) will fall into this area predicted to receive more rainfall (Altwegg et al., 2014). Studies have found that climate strongly affects vegetation recovery time after fire and that there is significant variation in post-fire recovery rates across the GCFR (Wilson et al., 2015). How this will affect fire regimes in the eastern GCFR and the response of sprouting species such as *E. latifrons* is currently unknown. Evidence does suggest that resprouting species, through a combination of resistance and resilience, are more tolerant to a change in fire-frequencies compared to fire-killed serotinous species found in fire-prone environments (Lamont et al., 2011, Enright et al., 2014). Repeated short fire frequencies (4–6 years) are suggested to favour the resprouting life-history in fynbos vegetation (Van Wilgen, 2013, Enright et al., 2014). Resprouters tend to have an advantage over non-sprouting species with increasing fire frequency but this may also depend on the time taken for a resprouter to become fire

tolerant (Lamont et al., 2011). Unlike *O. grandis*, where seedlings did not appear to be fire tolerant, *E. latifrons* seedlings were able to sprout following a fire thereby increasing the chances of survival in the very young stages. While there is still uncertainty whether sprouting ability can be considered a trade-off against fecundity, timing of a fire may affect seed viability or seedling recruitment if the fire occurs before the seed has germinated and established. Plants scorched in fire while in cone did result in nonviable seeds, reducing the chances of seedling recruitment in coning years (Swart, unpublished data). The effect of this may prove substantial due to the sporadic and limited coning intervals seen in *E. latifrons* and possibly other cycad species in similar environments. Given this potential for limited sexual recruitment, it has been suggested that resprouters tend to preserve their genetic diversity even in small populations due to their long generation time (Bond and Midgley, 2001). Preliminary investigations into the genetic structure and diversity of known *E. latifrons* populations revealed no evidence of population differentiation (Da Silva et al., 2012). Population B was not included in the study and further investigation is needed to determine whether it forms part of a single panmictic population reported by da Silva et al. (2012).

## 14. Conclusion and future research

The study of a previously undocumented population of *E. latifrons* has raised interesting new questions regarding why there are such differences in recruitment ability between two populations of the same species. Further investigation is required to determine reasons for these differences. Some hypotheses include:

1. Population B is larger and more intact than Population A. Population B may therefore sustain plant–animal mutualisms such as pollination. Although, there is evidence that Population A was previously able to naturally sustain itself according to survey reports of 1991.
2. Land management including the exclusion of fire/low fire frequencies, past and existing disturbances, control of seed predators/herbivory may have reduced natural levels of seed production in Population A.

New insights into the biology of *E. latifrons* revealed in this study may be used to update the non-detriment finding for *E. latifrons* in terms of the Convention of International Trade in Endangered Species of Wild Flora and Fauna (CITES, 1973) and possibly identify generalisations for making findings that apply across a group or species within the *Encephalartos* genus.

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