The conservation, ecology, and distribution of the Critically Endangered *Encephalartos latifrons* Lehm.

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY (SCIENCE)

of

RHODES UNIVERSITY

by

CARIN SWART

Department of Botany

March 2019

ABSTRACT

Cycads have attracted global attention both as horticulturally interesting and often valuable plants; but also as some of the most threatened organisms on the planet. In this thesis I investigate the conservation management, biology, reproductive ecology and distribution of *Encephalartos latifrons* populations in the wild and draw out conclusions on how best to conserve global cycad biodiversity. I also employ computer-modelling techniques in some of the chapters of this thesis to demonstrate how to improve conservation outcomes for *E. latifrons* and endangered species in general, where information on the distribution, biology and habitat requirements of such species are inherently limited, often precluding robust conservation decision-making.

In Chapter 1 of this thesis I introduce the concept of extinction debt and elucidate the importance of *in situ* cycad conservation. I explain how the concept of extinction debt relates to single species, as well as give details on the mechanisms causing extinction debt in cycad populations. I introduce the six extinction trajectory threshold model and how this relates to extinction debt in cycads. I discuss the vulnerability of cycads to extinction and give an overview of biodiversity policy in South Africa. I expand on how national and global policies contribute to cycad conservation and present various global initiatives that support threatened species conservation. I conclude Chapter 1 by explaining how computer-based models can assist conservation decision-making for rare, threatened, and endangered species in the face of uncertainty.

Chapter 2 of this thesis illustrates how a modelling approach, using limited available historical and present day locality information, is a feasible method to determine areas of suitable habitat for *E. latifrons* and other critically endangered cycad species where locality information is inherently uncommon. Results from this chapter show that conservation planning through structured decision-making may be improved by the use of computer models, even when locality data are limited. These results may be incorporated into biodiversity conservation plans or used to assist conservation-decision makers when undertaking recovery efforts for *E. latifrons* and may provide guidance to conservation planners and policy makers when undertaking conservation plans to improve cycad biodiversity both nationally and globally.

There was limited information available in the biology and ecological requirements of *E. latifrons*. This information is important when making policy decisions such as the publication of non-detriment findings and compiling biodiversity management plans for this and other cycad species. Chapter 3 investigates the life-history, population structure, fire response and survival of an *in situ E. latifrons* population. A demographic census was undertaken between 2013 and 2017 on a previously undiscovered population. Population characteristics of the "new" population were compared to the demographics of a well-known and intensively managed population. Results of this chapter show that at least one *in situ E. latifrons* population is stable and increasing under current environmental conditions. Importantly, the population is naturally recruiting seedlings without the need for artificial pollination. Demographic information described in this chapter is a necessary precursor to undertaking a Population Viability Assessment for the species. This will assist conservation decision-makers when determining the best conservation management strategy for *E. latifrons*. It may also be useful to apply generalisatons to other cycad species (with similar life-histories and habitat requirements) where there is limited information available on the species biological and ecological requirements, restricting robust policy conservation decision-making.

It was important for this study to determine the extent and variety of cone fauna within existing *E. latifrons* wild populations. Previous anecdotal evidence suggested that *E. latifrons* is functionally extinct as a species, but evidence to the contrary was found when a healthy, self-sustaining wild population was discovered to be naturally recruiting. It was important to establish the existence and diversity of male cone faunal species (an important breeding site for weevil pollinators) within wild populations. Chapter 4 set out to determine if potential pollinators exist in the wild and if so, how diverse are they and in what numbers. This is the first comprehensive analysis of cone fauna present in wild *E. latifrons* populations. Equally important was the need to determine if wild populations are capable of producing viable seeds under conditions conducive to natural pollination. Results of this chapter show that there is a relatively high diversity of insect fauna in the male cones of some wild *E. latifrons* populations. Furthermore, some wild populations are capable of producing viable seeds through natural pollination; even though they may not be naturally recruiting seedlings into the population. A staggered germination pattern displayed by one of the wild *E. latifrons*

populations was studied, suggesting the evolution of an adaptive trait given the stochastic environment (climatically and disturbances such as fire) within which *E. latifrons* populations may be found.

Species recovery (restoration and/or population augmentation) may be the only conservation solution remaining to save endangered species such as *E. latifrons* from extinction in the wild. Chapter 5 involves the return of 25 seedlings germinated as part of a seed viability experiment (see Chapter 4) back into a wild population from where they originated. The primary threat to seedling survival at the site was livestock activity (grazing/trampling). The population was subsequently fenced off to mitigate this threat and seedlings planted both inside and outside a fenced area to establish if there was a difference in seedling survival between the unprotected and protected sites. A high percentage (92%) of seedlings planted perished in total. None of the seedlings planted outside the fenced area survived over the monitoring period, while only two seedlings planted within the fenced area survived. Survival of the seedlings inside the fenced area was only after placing individual cages on the seedlings to prevent further losses. The primary causes of death for all seedlings included uprooting, and defoliation with some of the seedlings missing completely. This chapter found that the lack of natural seedling recruitment at the site was as a result of livestock activity. Grazing by livestock poses a significant threat to natural recruitment in some *E. latifrons* populations. Alternative restoration methods are suggested and protection of seedlings while undertaking a restoration/augmentation programme is emphasised.

Developing conservation management plans for rare and/or endangered species is often met with high levels of uncertainty, particularly if there is limited information available on the biology and ecological requirements for the species concerned. Population viability analysis (PVA) is often suggested as a tool to determine conservation management scenarios that may enhance wild population persistence. The standard PVA approach is however problematic as it is a time-consuming process requiring the collection of demographic data over long time periods. In addition, the PVA approach does not take in to account non-biological factors which may impede the effective implementation of conservation plans. Chapter 6 of this thesis makes use of a Multi-Criteria Decision Making (MCDM) approach called the Analytical Hierarchy Process (AHP) to decide on the best conservation management strategy for an *E. latifrons*

population. Sensitivity analysis was completed to test the robustness of the decision and to identify which criteria influenced the original results. In this study, the development of the decision tree and criteria judgements, were made solely by the researcher. It is emphasised that the decision outcome may be biased if not conducted as part of a multi-stakeholder workshop using the same approach. Nevertheless, it is recommended that a Population Viability Risk Management (PVRM) assessment be undertaken for *E. latifrons* using an MCDM approach such as AHP as a prestudy, before the revision of the Biodiversity Management Plan (BMP) for *E. latifrons*. This method is particularly useful when non-biological criteria are to be incorporated into the decision-making process. It is also a viable and holistic alternative to the standard PVA approach when developing conservation management plans for rare and endangered species.

In Chapter 7 I review the concept of extinction debt in cycads using *E. latifrons* as an example. I assimilate historical information to understand mechanisms that may have impacted on *E. latifrons* populations in the past. This was done to understand the scale of extinction time lags on *E. latifrons* and to relate this to its present position on the exitinction trajectory. I recommend aligning South African policies and biodiversity assessments with international initiatives and draw out general conclusions for the conservation of global cycad biodiversity. I conclude by recommending further research for *E. latifrons*.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

LIST OF APPENDICES

PREFACE

This thesis is presented as a series of papers to be submitted for publication. Chapter 2 was submitted to the Biodiversity and Conservation Journal where it was accepted for publication in February 2018. This paper was co-authored by J. Donaldson and N. Barker. In this case, I carried out the research and analysis, wrote the paper and conceived the research questions. The co-authors are my co-supervisors who assisted in conceptualising the research, securing funding and commenting on the final draft of the paper. For the remaining chapters, I have indicated to which journals they will be submitted for publication where I remain the lead author. As the thesis is made up of papers intended for independent publications, there may be some repetition in the introduction of each chapter.

ACKNOWLEDGEMENTS

I am grateful to my supervisor Prof. Susanne Vetter (Rhodes University) and my co-supervisors, Prof. Nigel Barker (University of Pretoria) and Prof. John Donaldson (South African National Biodiversity Institute) for their support and advice throughout my research. My supervisors at DEDEA, Mr. Quintus Hahndiek and Thembinkosi Tyali are also thanked for allowing me extra time during work hours to work on this thesis. Further acknowledgments are listed under each chapter heading below.

Chapter 1

Biodiversity Hotspot GIS data was obtained from Conservation International and the Critical Ecosystem Partnership Fund (www.cepf.net/our-work/biodiversity-hotspots accessed on the 30/04/2018).

Chapter 2

I am grateful to Roger Rowswell for assistance in the field, as well as the landowners who kindly shared their local knowledge. Thanks to Quintus Hahndiek, Ricky Hannan, Gerrie Ferreira and Thembinkosi Tyali (Eastern Cape Department of Economic Development and Environmental Affairs) for supplying information on historical permitting. I also thank Susanne Vetter (Rhodes University) and Tony Palmer (Agricultural Research Council) for offering advice and support throughout the research. I would like to thank three anonymous reviewers who helped improve our manuscript. Special thanks to Rose Prevec (Albany Museum) for her insightful comments on early drafts of the manuscript. Cynthia Kulongowski is thanked for

editing a final version of the manuscript. Financial support for this study was provided by the South African National Biodiversity Institute (SANBI). Rhodes Geography Department is acknowledged for the use of their ArcGIS license.

Chapter 3

This chapter would not have been possible without the field support and motivation from Roger Rowswell. Land owners are also thanked for access to their property. William Snow is acknowledged for access and permission to use his demographic data collected in 2010 as part of his BSc Honours Project.

Chapter 4

Permits to undertake research activities for this chapter was issued by the Department of Economic Development and Environmental Affairs (DEDEA), Eastern Cape Province. Noluthando Bam is thanked for her efforts in this regard. Ruaan Strauss (Rhodes University) is greatly appreciated for offering to sterilise heaps of soil handed to him in batches. Steven, Tristan and Julian Boy are thanked for watering seedlings when I was unable to, and for spotting germination events with keen interest and excitement. Phakamani Xaba (SANBI) is thanked for his horticultural advice and expertise. I am also grateful to Theresa Williams for help with cleaning and preparing seeds.

Chapter 5

Roger Rowswell is again thanked for his assistance in the field and design of the seedling cages. Special thanks to the *E. latifrons* landowner for allowing a portion of his farm to be fenced off for conservation of the population on his property and for providing labour to put up the fence. The landowner in this case deserves a conservation award for the effort and dedication he showed regarding the conservation of *E. latifrons* on his property.

Chapter 6

Chapter 1 and Chapter 6 would not have been possible without the availability of open-source software such as PrieST, MaxEnt, QGIS, R and Excel/ArcGIS Plugins. Thanks to all those kind, hardworking computer software specialists who make their software available on the free open-source market. Thanks also to the Cycad Society of South Africa for a complementary digital copy of backdated *Encephalartos* journal articles.

LIST OF ABBREVIATIONS AND ACRONYMS

AHP	Analytical Hierarchy Process
ANN	Average Nearest Neighbour
AUC	Area Under the Curve
AZE	Alliance for Zero Extinction
BAM	Biotic-Abiotic-Mobility
BGIS	Biodiversity Geographic Information Systems
BMP-S	Biodiversity Management Plan for Species
CBA	Critical Biodiversity Area
CBD	Convention on Biological Diversity
CSG-ESRP	Cycad Conservation Group – Ex Situ Recovery Programme
CBSG	Conservation Planning Specialist Group
CFR	Cape Floristic Region
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
COP	Conference of the Parties
CR	Critically Endangered
DEA	Department of Environmental Affairs
DEDEA	Department of Economic Development, Environmental Affairs and Tourism
ECBCP	Eastern Cape Biodiversity Conservation Plan
ELF	Encephalartos Latifrons Forum
EN	Endangered
ESRI	Environmental Systems Research Institute
FDI	Fire Danger Index
GCFR	Greater Cape Floristic Region
GIS	Geographical Information Systems
GSPC	Global Strategy for Plant Conservation
IBA	Important Bird Areas
IPA	Important Plant Area
IUCN	International Union for Conservation of Nature
KBA	Key Biodiversity Area
LPT	Lowest Presence Threshold

MAP	Mean Annual Precipitation
MCDM	Multi-Criteria Decision Making
M-P-A	Maputaland-Pondoland-Albany
MTG	Mean Time to Germination
NBSAP	National Biodiversity Strategy and Action Plan
NDF	Non Deteriment Finding
NEMBA	National Environmental Management: Biodiversity Act
NIV	Natural Intact Vegetation
NPAES	National Protected Area Expansion Strategy
NSAPMC	National Strategy and Action Plan for the Management of Cycads
OLI	Operational Land Imager
PHVA	Population Habitat Viability Assessment
PVRM	Population Viability Risk Management
SANBI	South African National Biodiversity Institute
SANBSAP	South African National Biodiversity Strategy and Action Plan
SASPC	South African Strategy for Plant Conservation
SDM	Species Distribution Modelling
SQF	Suurberg Quartzite Vegetation
SSC	Species Survival Commission
SWOT	Strengths, Weakness, Opportunities, Threats
TC	Tasselled Cap
TRAFFIC	Wildlife Trade Monitoring Network
UNEP	United Nations Environment Programme

CHAPTER 1
Introduction

Extinction threats and the importance of conservation in the wild

Global biodiversity is under threat. The major culprits identified are changes in land use, overexploitation (Pereira et al. 2012; Sala et al. 2000) and exotic plant invasions (Downey and Richardson 2016). This is followed by climate change as an emerging major threat (Pereira et al. 2012). Mediterranean climate regions, such as the Greater Cape Floristic Region (GCFR) in south-western South Africa, are likely to experience proportionately greater future changes to biodiversity compared to most other regions (Cox and Underwood 2011; Sala et al. 2000) yet they are poorly represented within formally protected areas (Cox and Underwood 2011). It has been proposed that small conservation efforts can make a difference to global biodiversity conservation. Significant global biodiversity gains can be realised through managing unprotected natural and semi-natural lands for threatened species persistence (Pereira et al. 2012). These lands, outside of protected areas, may ultimately become important refugia for threatened and endemic species in the face of future and current global threats (Keppel et al. 2015; Pereira et al. 2012).

Biogeographical regions with high levels of endemism containing areas that are largely irreplaceable but at the same time highly threatened with destruction are known as biodiversity hotspots (Mittermeier et al. 2011). There are currently 36 recognised hotspots globally (www.cepf.net accessed 16/08/2018) occupying 2.3 % of the earth's surface with each hotspot holding at least 1 500 endemic plant species (over 150 000 endemic plant species in the hotspots combined) maintaining 77% of all endemic plant species (Mittermeier et al. 2011). Threats to biodiversity hotspots are similar, but more concentrated, compared to global threats to biodiversity (Jantz et al. 2015; Sloan et al. 2014). All hotspot areas have each lost 70% or more of its original habitat and for some hotspots, the percentage of vegetation lost is as much as 95% (Mittermeier et al. 2011; www.cepf.net). Globally, around 40% of all cycad species are within biodiversity hotspot areas (Nadarajan et al. 2018). This highlights the need to concentrate global

conservation efforts within the hotspots; although some criticism has been directed at this concentrated focus on hotspot biodiversity conservation (Marchese 2015).

Cycads are considered one of the most endangered organisms globally, and are by far, the most endangered group of gymnosperms on the planet (Fragnière et al. 2015; Hoffmann et al. 2010). With 63.2% of cycad species threatened, threat levels remain high throughout most areas of global cycad distribution (Fragnière et al. 2015). Southern Africa, particularly the eastern regions, are considered a hotspot of cycad diversity (Yessoufou et al. 2017) with a high concentration of threatened species (Cousins and Witkowski 2017). Most cycad species are naturally rare and geographically restricted (Nackley et al. 2018) increasing their vulnerability to current threats such as loss of habitat, illegal and selective removal of individuals for the horticultural trade, changes in disturbance regimes such as fire, and species invasions (Cousins and Witkowski 2017; Mankga and Yessoufou, 2017; Marler 2013; Marler and Ferreras, 2017; Negron-Ortiz and Gorchov, 2000; Okubamichael et al. 2016; Wu et al. 2010). Their threatened status, rarity and horticultural appeal make cycads an ideal flagship group for *ex situ* conservation and commercialisation for conservation (Griffith et al. 2015; Winter and Botha 1994). While *ex situ* conservation is important and has many advantages (Donaldson 2009), it should never be the preferred choice over *in situ* conservation. Conservation of species in the wild is considered more effective and efficient than *ex situ* conservation as threatened species are more likely to persist if they are able to function on their own *in situ*, rather than depend on human intervention for their survival (Stokes 2018). Wild species contribute to sustaining ecosystems to which they belong, thus playing an important role in maintaining ecosystem health. For cycads, this would include providing an important breeding site for weevil pollinators (Terry et al. 2012), a food source for a variety of animals (Ballardie and Whelan, 1986; Giddy, 1974; Pérez-Farrera et al. 2006) as well an important source of traditional food, medicine and handicrafts for indigenous communities in many countries (Coates et al. 2015; Cousins and Witkowski, 2017; Russell-Smith et al. 1997; Williams et al. 2014; Zander et al. 2014). Much emphasis has been placed on the economic and horticultural value of cycads. By comparison, little importance is placed on how communities may identify with cycads in their natural environment where *ex situ* conservation will always fall short in capturing the cultural value of wild cycads to indigenous communities and the link between biodiversity and cultural diversity (Bamigboye et al. 2017; Bonta and Bamigboye 2018; Hill et al. 2011).

Extinction debt and single species

A species is considered extinct when no individuals have been recorded after exhaustive surveys throughout the species native range where the species could have been expected to occur, leaving no reasonable doubt that the last individual has died (IUCN 2014). For this thesis, the definition is refined to include the last individual *in situ* and in *ex situ* collections as opposed to extinct in the wild. There are numerous *ex situ* cycad collections that may play an important role in restoring extinct populations or those that are on the brink of collapse (IUCN/SSC Cycad Specialist Group: ex situ conservation and recovery programme – www.cycadgroup.org accessed 16/08/2018). Botanical gardens play a particularly important role in maintaining gene banks for some of the most threatened cycad taxa (Donaldson 2003) provided recommended protocols are followed such as using the species biology to inform the collection strategy (Griffith et al. 2015).

Tilman et al. (1994) coined the term 'extinction debt' to describe the delayed effect of habitat and environmental destruction on species extinctions i.e. the future ecological cost of current environmental disturbances. An environmental disturbance may cause the loss of habitats and/or individuals in a population, but not necessarily cause the immediate extinction of the species (Kuussaari et al. 2009). Relaxation time is defined as the lag time from the disturbance or extinction causing event to the completion of the extinction process (Cronk 2016). Life-history traits are considered a strong predictor of the probability a species will experience extinction debt after a disturbance and the relaxation time to extinction (Cronk 2016). Intrinsic factors at the species level increasing the lag time and vulnerability of species to extinction debt include species with long-generation times and low turnover rates, species that are habitat specialists and presence of a seed bank (Cronk 2016; Halley et al. 2017; Kuussaari et al. 2009).

Mechanisms causing extinction debt are best understood at the level at which extinctions occur i.e. the species level (Hylander and Ehrlén, 2013). Downey and Richardson (2016) have suggested a six-threshold conceptual framework to explain how species go through different phases in the extinction trajectory from the time of disturbance to eventual extinction. Their conceptual model was developed to explain how plant invasions may alter the extinction trajectory of certain native species with a

seedbank. The conceptual model was adjusted for this thesis to explain how long-lived species without a seedbank, such as cycads, may traverse through the six thresholds towards extinction. Figure 1.1 illustrates this concept where species may display different convexities of the survivorship curves (models I, II or III) between extinction thresholds (Deevey 1947; Demetrius 1979) depending on the environmental disturbances and threats acting on the species.

In general, stable and healthy cycad populations fit the conventional description of an S-selected life history typically conforming to a Deevey type III (model III) survivorship curve where the highest mortality rate is experienced in the smallest stage class with high adult survival and reproductive potential (Borsboom et al. 2015; Castillo-Lara et al. 2018; Deevey 1947; Grime 1977; Octavio-Aguilar et al. 2017; Pérez Farrera and Vovides 2004; Yáñez-Espinosa and Sosa-Sosa 2007). The convexity of the survivorship curve is however highly sensitive to environmental disturbance (Demetrius, 1979) where some populations may deviate from the type III model if recruitment and/or mortality rates are negatively impacted upon. For example, Pulido et al. (2015) found that although the general survivorship curve for populations of the endangered Mexican cycad, *Ceratozamia fuscoviridis* displayed a model type III curve, some populations displayed significantly different shape of the survivorship curve from type III to model type I. A change in the convexity of the curve was attributed to the absence of larger plants in the population possibly due to the targeted extraction of larger individuals (Pulido et al. 2015). Similar deviation from the type III model to a type I model was seen in *Zamia inermis* populations which are dominated by adults due to extremely low levels of recruitment (Octavio-Aguilar et al. 2017).

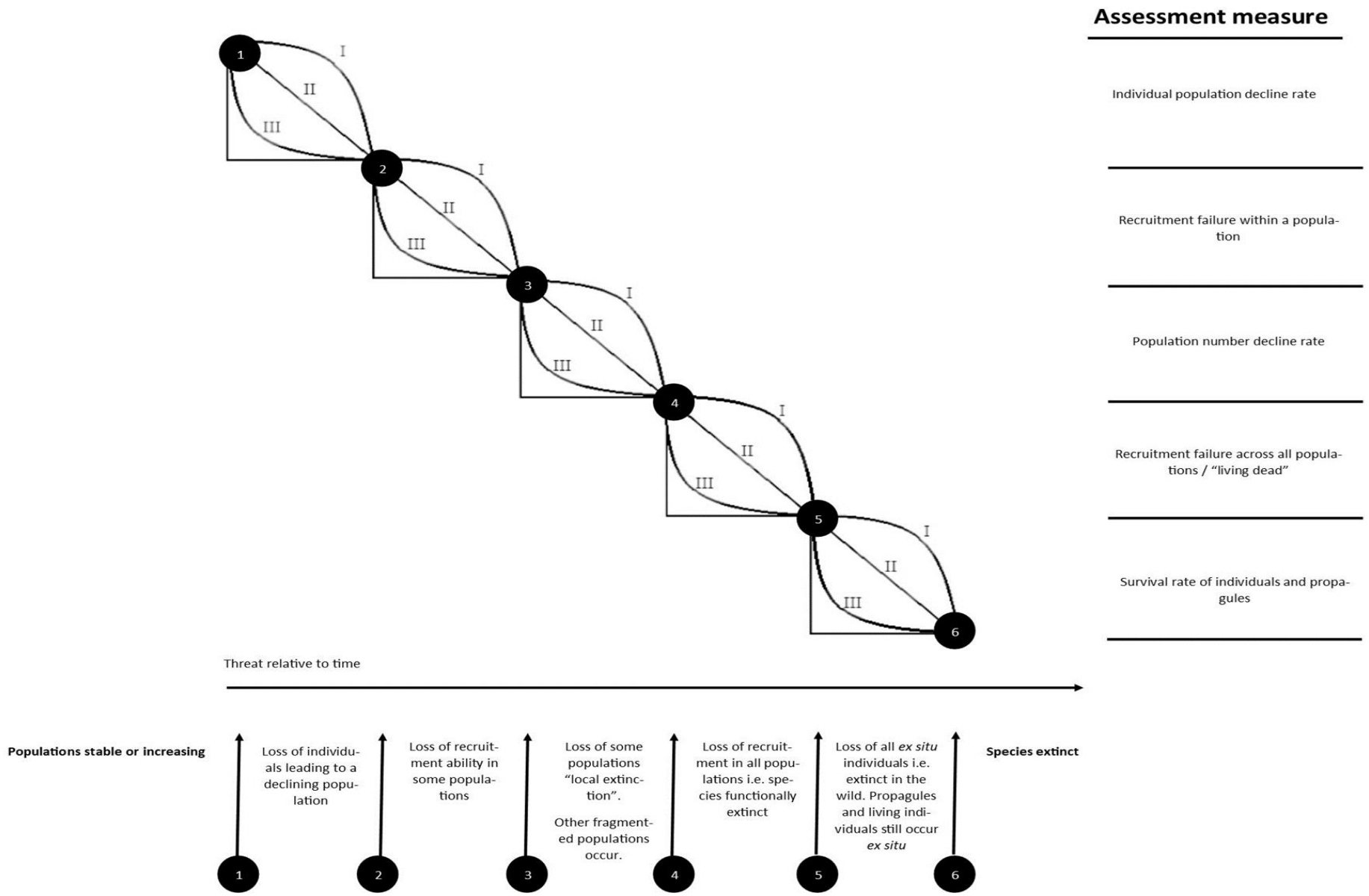


Figure 1.1 The six extinction trajectory threshold adapted from Downey and Richardson (2016) to illustrate the trajectory a long-lived perennial tree species may experience as it becomes threatened with extinction

The extinction trajectory is punctuated by six-thresholds as proposed by Downey & Richardson (2016). The species may first experience a loss of individuals within intact populations, resulting in a reduction of local population size, moving the species along the extinction trajectory from threshold 1 to 2. The species is likely to breach the second threshold as some populations lose the ability to recruit naturally. This may be due to a number of reasons such as skewed sex ratios (in dioecious plants) as a result of the loss of individuals, local loss of mutualisms such as specialist pollinators, loss of environmental conditions under which germination and seedling recruitment occurs and other pressures that come with environmental disruption of populations and the habitats to which they belong (Cabrera-Toledo et al. 2008; Dhar et al. 2008; Donaldson 2003; Marler and Lawrence 2012; Menz et al. 2011; Potts et al. 2010; Ravele and Makhado 2009; Wilcock and Neiland 2002). Should the disturbance continue before equilibrium is reached, the species is likely to breach the third threshold on the extinction trajectory where some populations may disappear completely with the species becoming locally extinct (Aerts et al. 2006; Albrecht and McCue 2010; Cibrián-Jaramillo et al. 2010; Keppel 2002; Kuussaari et al. 2009; Volis 2016). Other populations may remain fragmented within the natural distribution range either as non-recruiting remnant populations or still able to retain some recruiting ability. An example of a cycad species likely to move from threshold 3 to the next level is the Mexican cycad, *Zamia inermis*. Only a single known natural population of *Z. inermis* remains. Owing to extremely low levels of natural recruitment as a result of the extinction of its natural pollinator there is a high probability that populations will lose the ability to naturally recruit in the near future (Octavio-Aguilar et al. 2017). The fourth threshold is breached when all remaining populations lose the ability to self-sustain through natural recruitment. Examples of cycad species at this stage in the extinction trajectory include the Cuban cycad, *Microcycas calocoma* (Vovides et al. 1997) and *Encephalartos middelburgensis* in South Africa (Xaba 2014). This is not unique to dioecious cycads but other gymnosperms have reached this threshold including *Pinus sylvestris* (Castro et al. 1999) and *Taxus baccata* (García et al. 2000 see also conclusion in Chapter 7). Once the species reaches this threshold it is considered functionally extinct. The species breaches the fifth extinction threshold when all individuals are lost from the wild, including adults which existed as non-reproducing members of the population. The species is finally considered extinct (threshold 6) when all individuals with known provenance in *ex situ* collections no longer remain.

Vulnerability of cycads to extinction

Prior to the Anthropocene (Smith and Zeder 2013), it has been proposed that prehistoric mechanisms acted on a once widespread and dominant group of plants to reduce the success of cycads and render most species geographically restricted and rare. Nackley et al. (2018) suggest that a declining ambient CO_2 level in the Cenozoic Era reduced the success of cycads, particularly the more ancient group of cycads such as the Encephalarteae sub-group (Condamine et al. 2015). Given their phylogenetic conservatism, cycads were not able to effectively adapt to a decline in CO_2 levels from the Mesozoic era when atmospheric CO_2 levels greatly exceeded today's (Nackley et al. 2018). Current ambient CO_2 conditions have left them CO_2 'starved' restricting their fecundity (e.g. the production of carbon rich massive cones) and plant growth rates (Nackley et al. 2018). Since the Anthropocene, threats that have contributed to the vulnerability of cycad to extinction, particularly species that are already rare and restricted, include: ecosystem loss i.e. habitat conversion, forest and bush clearing for agriculture, (Donaldson 2003; Mankga and Yessoufou 2017; Marler and Ferreras 2017; Vovides and Iglesias 1994), selective removal of individuals of certain species (Cousins and Witkowski 2017; Donaldson 2003; Okubamichael et al. 2016; Raimondo and Donaldson 2003; Vovides and Iglesias 1994), change in disturbance regime such as fire (Griffiths et al. 2005; Keppel 2002; Marler and Ferreras 2017; Negron-Ortiz and Gorchov 2000), changes to ecosystem connectivity i.e. increased fragmentation of ecosystem patches (Cibrián-Jaramillo et al. 2010; López-Gallego 2008), species invasions (Marler 2013; Wu et al. 2010), and evolutionary changes (Lopez-Gallego and O'Neil 2010). These threats, their consequences and examples of how they relate to extinction debt are discussed in more detail in the next section of this chapter.

Donaldson (2003) gives many examples where cycad species are threatened by habitat conversion through bush clearing for urban expansion, resort development, agriculture, dam construction and afforestation for plantations. After a disturbance such as habitat conversion and resultant ecosystem loss, extinction debt and delayed extinctions are largely dependent on the life history or species attributes (Krauss et al. 2010; Kuussaari et al. 2009). Habitat destruction may result in the loss of individuals within populations, where remnant fragmented populations containing individuals with long generation times remain on the peripheries, thereby delaying extinction. An example is witnessed in populations of the Critically Endangered *Cycas wadei* of the

Culion Island in the Philippines. Habitat destruction for the planting of Para Rubber Tree Plantations within *C. wadei* natural distribution range is resulting in remnant isolated populations in fragmented patches (Marler and Ferreras 2017). Another example are the remnant populations of *Cycas seemannii* surrounded by pine and sugarcane plantations (Keppel 2002). These fragmented plant populations are more vulnerable to pollination-limitation (Menz et al. 2011) thereby reducing seed set and recruitment, especially in plants with specialist pollination mutualisms such as cycads (Terry et al. 2009). Habitat destruction may also result in the culmination of other threats, such as targeted illegal collection of adult plants. Donaldson (2003) noted that when the surrounding vegetation is removed, plants are likely to become visible and more accessible to poachers. Selective removal of individuals for the horticultural market or of parts of the plant such as bark harvesting for the indigenous medicinal trade is considered a major threat to cycad populations, and is particularly acute in Africa (Bamigboye et al. 2017; Cousins and Witkowski 2017; Donaldson 2008; Okubamichael et al. 2016; Williams et al. 2014).

A further compounding threat includes evolutionary changes to cycad populations brought about by habitat disturbance. An example of this is seen in *Zamia fairchildiana* populations in Costa Rica and Panama, where populations in degraded habitats exhibited life history changes (i.e. earlier reproduction, faster growth in males due to increased light availability) and exhibit a weaker spatial genetic structure compared to populations in un-degraded forests (Lopez-Gallego and O'Neil 2010). Similar evolutionary changes were seen in populations of *Cycas seemannii* that displayed lower levels of genetic variation due to habitat fragmentation compared to less disturbed populations (Keppel 2002). However, some endangered cycad species with highly restricted distributions and critically low population sizes show surprising resilience to disturbances by maintaining high levels of genetic diversity within adult populations such as *Dioon caputoi* and *Encephalartos latifrons* (Cabrera-Toledo et al. 2008; Da Silva et al. 2012). One possible explanation for this high genetic diversity of adult plants is that samples taken from adult individuals established in past environmental and demographic conditions enabling high levels of gene flow may be different to the conditions the plants are experiencing today (Cabrera-Toledo et al. 2008; Da Silva et al. 2012). The seedling stages in both studies displayed loss of genetic integrity. Whether this high genetic diversity in the adult population represents another

example of extinction debt in critically small populations of endangered cycads remains to be seen.

Cycads are common in fire-prone habitats throughout the world (Griffiths et al. 2005; Lamont and Downes 2011; Preece et al. 2007; Tang 1990), tolerating fire by sprouting (Clarke et al. 2013). Although cycad populations are usually well adapted to natural disturbances such as fire, changes in fire regime due to changing land management practices (Hill 2003) combined with increased exotic plant invasions (Liddle 2004) are mechanisms that may move vulnerable cycad populations along the extinction trajectory. Fires can provide benefits to cycad populations such as increased stem growth (Griffiths et al. 2005) and stimulation of cone production (Pérez-Farrera et al. 2006). The negative effects of fire are usually caused by changes to the historical fire regime that may affect long-term population dynamics by influencing seedling recruitment and survival (Griffiths et al. 2005; Hill 2003) or by directly damaging foliage, reproductive structures and increasing adult plant mortality (Keppel 2002; Marler and Ferreras 2017). An example of the negative impacts of a change in fire frequency is the case of *Cycas wadei*, where fire frequency has started to exceed the time needed for cycad populations to recover from disturbance. A decreased frequency of disturbances from fire, on the other hand, can contribute to increasing fuel loads, resulting in fires with greater intensities that are likely to increase damage to individual plants directly (Marler and Ferreras 2017). The timing, season, and frequency of fire as well as the intensity of the disturbance would therefore be important mechanisms acting on cycad population dynamics and the shape of the survivorship curve between extinction thresholds on the trajectory.

There is limited information in the published literature on the direct effect of exotic vegetation on cycad populations. In South Africa, one study using data from matched photographs found that exotic vegetation was responsible for very few instances of population decline (Donaldson and de Wet Bosenberg 1999) but the impact of exotic vegetation on global cycad populations needs further exploration, including impacts on seedling germination and recruitment and possible reduced coning due to shading (Donaldson 2003). Liddle (2004) found that *Cycas armstrongii* populations in areas invaded by exotic grasses in Australia experienced significantly higher adult mortalities compared to non-invaded areas due to increased fire intensities in the grassy woodland habitat.

Threats of exotic invasive species to cycad populations are not limited to exotic plants. Evidence is emerging on how exotic insect pests may play a role in reducing cycad population resilience to natural disturbances. An example of this is seen in the *Cycas micronesica* populations in Guam. Usually resilient to natural weather events such as tropical cyclones, *C. micronesica* populations are currently threatened by the invasion of the armoured scale insect *Aulacaspis yasumatsu* that spread to natural forest habitats in Guam in 2005 (Marler 2013). The extent of stem damage to individuals of *C. micronesica* caused by the scale insect is not apparent until years after the infestation, where the aggressive feeding behaviour compromises the mechanical integrity of the stem to such an extent that the next tropical cyclone is likely to cause the extirpation of *C. micronesica* on Guam (Marler 2013). Similar threats to native cycad populations of *Cycas taitungensis* in Taiwan have resulted from the dual attack by *A. yasumatsu* and *Chilades pandava* -a native tropical butterfly that has become extra-limital occurring in previously unoccupied regions through range expansion (Wu et al. 2010). This is a classic example of delayed extinction where unhealthy populations persist for years before rapidly declining (Wu et al. 2010).

Biodiversity policy in South Africa and threatened species

South Africa is a country rich in biodiversity and is home to 6% of the world's plant species (Driver et al. 2012). Biodiversity in South Africa however is also under severe threat with one in eight of its plant species threatened with extinction (Driver et al. 2012). South Africa has a strong policy and legislative framework for the conservation of biological diversity (Government of South Africa 2015). Strategies and action plans to conserve plant biodiversity in South Africa such as the National Biodiversity and Action Plan 2015 – 2025 (SANBSAP v2 2015) and the South African Strategy for Plant Conservation (Raimondo 2015) are aligned with global strategies and targets such as the Global Strategy for Plant Conservation (GSPC) (Convention on Biological Diversity 2011a) and Aichi Targets (Convention on Biological Diversity 2011b).

International initiatives such as the sixth Conference of the Parties to the Convention on Biological Diversity (COP-6) promoting biodiversity conservation at the highest level have fallen behind in reaching their intended targets (Funk et al. 2017). New targets were developed in the form of the Aichi Targets during COP-10 (Convention on Biological Diversity 2011b). Aichi Target 12 deals directly with

threatened species aiming to prevent the extinction of known threatened species (particularly those most in decline) by 2020 by improving their conservation status. Linked to this target is Strategic Objective 1.2 of the South Africa's 2nd National Biodiversity Strategy and Action Plan 2015 – 2025 to sustainably manage species of special concern with the target to conserve 60% of threatened plant species *in situ* in the country (Government of South Africa 2015). Species of special concern mentioned in the nationally strategy include threatened South African cycad species. Fine-scale conservation action is required to effectively conserve habitats that contain cycad populations as they are known for their clumped distributions often confined to highly specialised habitats such as inselbergs or outcrops (Cousins and Witkowski 2017). Targeted site conservation initiatives such as Key Biodiversity Areas (KBAs) are an important approach to fill the conservation gap for species not represented in formally protected areas (Eken et al. 2004). KBA sites contribute to global persistence of biodiversity by representing the most important sites for biodiversity conservation on a global scale complimenting established and/or expanding formal protected areas. KBAs are identified nationally using a set of globally standardised criteria and thresholds (IUCN 2016). KBAs are considered an umbrella designation including initiatives such as Important Bird Areas, Important Plant Areas and Alliance for Zero Extinction sites (IUCN 2016) all contributing to meeting Aichi Targets, specifically Target 11 and 12 for species of special concern.

South Africa is also a Party-member of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), an international agreement between governments with the aim is to ensure that international trade in specimens of wild fauna and flora does not threaten their survival. The illegal trade in wild plants and animals is not only a threat to Africa's biodiversity, but pose a substantial economic and security risk to the African continent (UNEP 2016). In South Africa, there is a growing concern regarding the high incidence of illegal activities related to biodiversity (Government of South Africa 2015) for example the highly publicised and emotive 'war' on rhino-poaching (Büscher 2016; Duffy 2014). The illegal trade and harvesting of cycads in South Africa have received less of an emotive response but is considered to be one of the main causes of decline of South African *Encephalartos* populations as well as cycad populations across the African continent (Cousins and Witkowski 2017).

In order to assess the risk of international trade and export to CITES-listed species, non-detriment findings (NDFs) are published as science-based risk

assessments for individual species in terms of the applicable national legislation. To date, 26 NDFs have been gazetted in South Africa, 12 of which are for Critically Endangered Appendix I CITES-listed *Encephalartos* species. All 12 *Encephalartos* species are considered at high risk to international trade which is considered detrimental to the survival of the species (DEA 2016). Up-to-date quantitative data on the abundance and trends in national populations and a thorough understanding of the species biology is not a requirement to undertake an NDF (Smith et al. 2011). Of the 12 NDFs gazetted for *Encephalartos* species in South Africa, three were based on anecdotal evidence, four on good local knowledge and five on quantitative data (outdated and/or recent) concerning population dynamics, species abundance and national population trends (DEA 2016). Smith et al (2011) suggests that this uncertainty in the information available on the biology and population trends of the species may affect the quality and confidence of NDF decisions. One way to overcome this uncertainty is to identify generalisations for making NDFs that apply across a group of taxa (Smith et al. 2011). Other research directions for CITES-listed species suggested by Smith et al. (2011) include: researching the levels of risk involved in making NDFs under high levels of uncertainty, research broader impacts of harvesting on populations and researching the population biology of CITES-listed species.

Sites containing CITES-listed CR and EN species, particularly cycads, are likely to satisfy KBA criteria and thresholds in that they are often confined to a single or a few scattered sites. In order to qualify under criterion A1 of the KBA IUCN guidelines, a site must contain a significant (as per defined threshold) population size of a globally threatened (as per IUCN Red-list) species (IUCN 2016). Cycads listed as CR or EN are likely to satisfy the A1 as well as B1 criteria where sites hold a significant (as per defined threshold) proportion of the global population size of a geographically restricted species contributing to the global persistence of biodiversity at the species level (IUCN 2016). KBA sites can also be identified through quantitative analysis of irreplaceability (i.e. the contribution of individual sites to species persistence) under criterion E of the KBA IUCN guidelines. A sub-set of KBAs include Alliance for Zero Extinction (AZE) sites (http://www.zeroextinction.org). These sites are the highest priority sub-set of KBAs based on a species' extreme vulnerability and irreplaceability. AZE sites are focussed on species threatened by immediate extinction where more than 95% of the species population is restricted to a single site (Funk et al. 2017). AZE sites can be distinguished from another relevant KBA sub-set, Important Plant Areas (IPA)

(Eken et al. 2004), in that an IPA is a site must contain exceptional botanical richness (a group of rare, threatened and/or endemic plant species) and/or vegetation of high botanic value (Marignani and Blasi 2012). An IPA is similar to an AZE site in that it is a site based approach but is dissimilar in that it does not focus on a single species vulnerability and/or irreplaceability such is an AZE site dedicated to safeguarding the entire population of a CR or EN species (Brooks et al. 2016). Identification of an AZE site does not by default imply that the site is legally protected or recognised by national government, but it does give the site some recognition according to the agreement between the secretariat of the CBD and the AZE alliance where nations should account for their progress in protecting AZE sites and species in their National Biodiversity Strategies and Action Plans (NBSAPs). To date, only Brazil, Columbia and Mexico have included AZE sites in their NBSAPs (Lamoreux et al. 2015). Diniz et al (2017) identified 234 trigger species located in 140 AZE sites in Brazil. Mexico has the highest number of AZE sites with 151 trigger species (referring to a species that qualifies a site for AZE designation) and 68 sites. In contrast, South Africa has 11 sites (http://zeroextinction.org/ accessed 23-08-2018), 6 of which are cycad trigger species. South African has recently embarked on identifying more cycad trigger species with three more cycad trigger species proposed as AZE trigger species (https://globally-threatened-bird-forums.birdlife.org/2017/07/cycads-2017-aze-update-consultation/ accessed 23/08/2018). All AZE sites in South Africa are however still awaiting confirmation as KBA sites according to the Alliance for Zero extinction official site accessed on the 23/08/2018. The listing of CR and EN cycads as AZE trigger species and subsequent application as KBA sites is however not aligned with the revised SANBSAP. Even though the SA plant Conservation strategy mentions goal of 60% threatened species conserved *in situ*, the SANBSAP lacks a focus on in situ conservation (Government of South Africa, 2015). Identifying AZE sites for CR and EN cycad species will not only improve in situ conservation contributing to national and international biodiversity targets but also formalise cycad conservation and align to global standards.

Conservation-decision making in the face of uncertainty and the role of computer-based models

No matter how much information is available for a threatened species, there will always be an element of uncertainty when it comes to making conservation decisions for conservation action (Guisan et al. 2013), and this uncertainty can take different forms. Sources of uncertainty include: stochasticity of the environment and demographic processes, limited information on the ecology and biology of a species (and how it will react to change), and observational uncertainty i.e. the unknown number and distribution of populations and individuals within a defined area (Rout et al. 2009). Lack of information on the biology, distribution and ecology of endangered species is common due to their scarcity and elusive nature (Gregory and Long, 2009). Conservation decisions involving threatened and/or endangered species therefore often have to be made under conditions of severe uncertainty (Canessa 2015; Canessa et al. 2015; McDonald-Madden et al. 2010; Moore et al. 2011; Regan et al. 2005; Rout et al. 2009).

Computer based models, such as species distribution modelling (SDM) and Multi-Criteria Decision Making (MCDM) models can support conservation decision-makers when uncertainty is high and data for the species are limited. Coarse models using sparse data can be valuable decision-making tools when uncertainty is incorporated and accounted for in the model system (Burgman and Yemshanov 2013; Marechaux et al. 2017). Models add value to the conservation decision-making process by collating the available information in a systematic, unbiased and balanced way, as well as allowing decision-makers to explore alternative scenarios and possible consequences of management decisions (Addison et al. 2013). Models should be seen as decision-making tools to assist decision-makers rather than as a replacement to override the autonomy of decision-makers (Addison et al. 2013). Models also allow for adaptive management where knowledge, as it becomes available, can be incorporated into model systems to adjust conservation actions accordingly (Yousefpour et al. 2012). Expert knowledge is still vital when making any conservation decision for threatened species (Martin et al. 2012) here the decision-process should be participatory, including a multitude of stakeholders from diverse backgrounds to avoid bias (Ishizaka and Labib, 2011). This ultimately results in improved conservation management decisions

(Addison et al. 2013). It is imperative that there is a strong relationship and understanding between scientists/modellers and policy-makers/conservation decision-makers in order to bridge the gap between scientific knowledge and the implementation of conservation actions (Keith et al. 2011). Bridging the science-policy gap is not only achieved through rigorous scientific methodology rather, of equal import, is clear communication and framing knowledge in a policy relevant way (Rose et al. 2018).

Thesis aims and structure

The study area for this thesis is confined to the eastern extreme of the Fynbos Biome (Rebelo et al. 2006). The area also falls within the Maputaland-Pondoland-Albany hotspot, considered an exceptionally diverse area where six of South Africa's eight major vegetation types converge. The meeting point of these two important biodiversity hotpots: the Cape Floristic Region (CFR) hotspot and the Maputaland-Pondoland-Albany (M-P-A) hotspot (Mittermeier et al. 2011) is the focus of this thesis (Figure 1.2). This area is sometimes referred to as the south-eastern Greater Cape Floristic Region (GCFR) (Bergh et al. 2014).

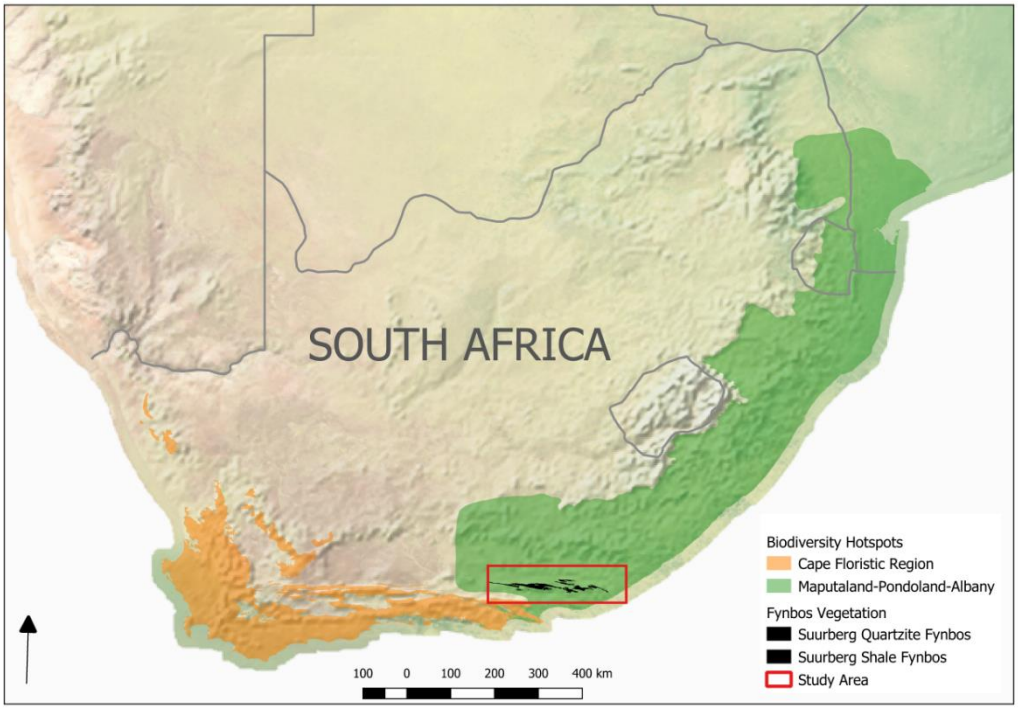


Figure 1.2 Map showing the two biodiversity hotspots relevant to this study: Cape Floristic Region (CFR) and the Maputaland-Pondoland-Albany (M-P-A) hotspots. The red rectangle shows the part of the CFR that extends into the M-P-A, considered the Greater Floristic Region representing the study area

Future land-use changes are projected to reduce natural vegetative cover by 99 – 100% in both the CFR and M-P-A hotspots by the year 2100 (Jantz et al. 2015). To put this in perspective, at present, the remaining Natural Intact Vegetation (NIV) of the CFR currently stands at 32.9% while the figure is much higher for the M-P-A hotspot with 6.4% remaining NIV (Sloan et al. 2014). This could have dire consequences for South African cycad species as the geographical distributions of cycad taxa in South Africa are almost exclusively within the M-P-A hotspot specifically considered a regional centre of cycad diversity (Cousins and Witkowski 2017).

The focus of this thesis is the conservation of *E. latifrons* in the wild. It is the first detailed study of the natural distribution, biology, reproductive ecology, restoration and conservation of existing *in situ E. latifrons* populations. It is hoped that this study will provide valuable insight and information to assist conservation decision-makers in solving conservation problems related to this and other endangered cycad species.

In order to revise the past, adapt current, and inform future conservation decision for *E. latifrons*, it was important that information on the biology, reproductive ecology, restoration, and distribution of the species is available. A detailed scientific study of *E. latifrons* was identified as important in the Population Habitat Viability Assessment (PHVA) undertaken for the species (Daly et al. 2006). South Africa's national legislation also makes provision for a Biodiversity Management Plan for Species (BMP-S) aimed at ensuring the long-term survival in nature of the species to which the plan relates (NEMBA Act 10/2004). The BMP-S provides the platform for an implementing organisation/responsible entity to monitor and report on the progress of implementing the BMP-S. The BMP-S for *E. latifrons*, developed in 2011, recommends that research should focus on undertaking a restoration study using the propagules made available to conservation through artificial propagation by a private land owner under the provision of the BMP-S (DEA 2011). This was not possible for this PhD research project due to certain logistical and political constraints; primarily due to conflicting opinions regarding the location of a suitable restoration site and whether private property or state land should be used for this purpose.

As the research needed to continue in spite of these constraints, it was decided the first aim was to identify areas of suitable habitat for *E. latifrons* to guide future restoration and/or translocation efforts. This was to ensure that decisions made regarding the location of restoration/translocation sites is based on scientific research rather than subjective opinion. In Chapter 2, I use the MaxEnt modelling approach to

determine areas of suitable habitat for *E. latifrons* using a limited number of locality records for input into the model (gleaned from historical permitting information, herbarium records and current locality points). This is the first published study where the distribution of an endangered cycad was modelled, in order to assist with making conservation decisions and to reflect back on past conservation approaches.

Chapter 3 investigates the general life history, population structure, response to fire and survival of a wild *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. A demographic census was undertaken over 5 years between 2013 and 2017 on a previously undiscovered population. Population characteristics of the 'new' population were compared to earlier studies undertaken in 2010 of a well-known and intensively managed population. Information on the life history of *E. latifrons*, particularly its response to fire, can be used to inform conservation strategies, particularly relating to fire regime and land management practices.

One of the critical questions that needed further investigating was to determine if some *E. latifrons* populations are able to produce viable seed under conditions of natural pollination. Chapter 4 includes a preliminary investigation into the reproductive ecology of *E. latifrons*. Anecdotal evidence suggests that *E. latifrons* populations are not capable of natural regeneration in the wild (Daly et. al 2006; da Silva 2012) thereby rendering them functionally extinct. One proposed reason for this was the extinction of natural species-specific pollinators in wild populations (DEDEA 2011). It was therefore important to establish the status and species composition of cone fauna within wild populations as an initial investigation of potential pollinators, or the lack thereof in wild populations. This included sampling insect fauna in male cones and sampling wild seed to test viability under conditions of natural and artificial pollination. This research needs to be developed further to determine the effectiveness of weevil pollination in wild *E. latifrons* populations under natural conditions.

In Chapter 5, I undertook as small scale restoration project on private property where the *E. latifrons* population is made up of two individuals, an adult male and female plant. It was not expected that wild seed collected from a wild population to test seed viability would result in some of the seed germinating. When seeds were found to germinate, this presented an opportunity to test whether restoration was possible on a small scale by augmenting the wild population from which the seeds originated. A

limited number of seedlings were available for this study (as is often the case for restoration efforts involving critically endangered plants). Nevertheless, important lessons were learnt from this experiment which may assist future restoration efforts for *E. latifrons* and other threatened cycad species.

In Chapter 6 I suggest a possible method for the revision of the PHVA which may in turn inform the revision of the BMP-S for E. latifrons. I provide a motivation why a traditional PVA is not feasible with only 5 years of census data collected as part of this study. I also suggest an alternative approach to the standard PVA method by incorporating logistic and socio-economic factors into an Analytical Hierarchy Process approach, as part of the decision-making process to determine the best conservation management strategy for an *E. latifrons* population. The importance of the life history characteristics of *E. latifrons* were assessed against extinction risk susceptibility and population viability.

In Chapter 7 I synthesise my findings and suggest further research needed for the effective conservation of *E. latifrons* populations in the Eastern Cape Province of South Africa. I also undertake an assessment of the last known viable population of *E. latifrons* against the AZE criteria and make recommendations concerning the future conservation of this site and how it may be included as a Key Biodiversity Area according to the IUCN guidelines and feed back into national conservation planning initiatives. I apply the extinction trajectory model to *E. latifrons* and make recommendations regarding how to prevent its further decline along the extinction trajectory. I draw out general conclusions applicable to conserving critically endangered species in Africa and elsewhere in the world.

References

Addison PFE, Rumpff L, Bau SS, Carey JM, Chee YE, Jarrad FC, McBride MF, Burgman MA (2013) Practical solutions for making models indispensable in conservation decision-making. Divers. Distrib. 19: 490–502

Aerts R, Maes W, November E, Negussie A, Hermy M, Muys B (2006) Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. For. Ecol. Manage. 230: 23–31

Albrecht MA, McCue KA (2010) Changes in demographic processes over long time scales reveal the challenge of restoring an endangered plant. Restor. Ecol. 18: 235–243

Ballardie RT, Whelan RJ (1986) Masting, seed dispersal and seed predation in the cycad *Macrozamia communis*. Oecologia 70: 100–105

Bamigboye SO, Tshisikhawe PM, Taylor PJ (2017) Detecting threat to *Encephalartos transvenosus* (Limpopo cycad) in Limpopo Province in South Africa through the indigenous knowledge. Indian Journal of Traditional Knowledge 16(2): 251-255

Bergh NG, Verboom GA, Rouget M, Cowling RM (2014) Vegetation types of the Greater Cape Floristic Region. In: Allsop N (ed) Fynbos: Ecology, evolution and conservation of a megadiverse region. Oxford University Press, pp 1–25

Bonta MA, Bamigboye SO (2018) Use of cycads as ritual and recreational narcotics, in: 44th Annual Congress of the South African Association of Botanists. South African Association of Botanists, University of Pretoria, Hatfield Campus, pp. 276–330

Borsboom AC, Wang J, Forster PI (2015) Determining maturity and population structure in *Macrozamia parcifolia* (Zamiaceae), a threatened Australian cycad. Aust. J. Bot. 63: 392–402

Brooks TM, Akçakaya HR, Burgess ND, Butchart SHM, Hilton-Taylor C, Hoffmann M, Juffe-Nignoli D, Kingston N, MacSharry B, Parr M, Perianin L, Regan EC, Rodrigues ASL, Rondinini C, Shennan-Farpon Y, Young BE (2016) Analysing biodiversity and conservation knowledge products to support regional environmental assessments. Sci. Data 3: 160007

Burgman MA, Yemshanov D (2013) Risks, decisions and biological conservation. Divers. Distrib. 19: 485–489

Büscher B (2016) 'Rhino poaching is out of control!' Violence, race and the politics of hysteria in online conservation. Environ. Plan. A 48: 979–998

Cabrera-Toledo D, González-Astorga J, Vovides AP (2008) Heterozygote excess in ancient populations of the critically endangered *Dioon caputoi* (Zamiaceae, Cycadales) from central Mexico. Bot. J. Linn. Soc. 158: 436–447

Canessa S (2015) Decision analysis for threatened species management across the captive-wild spectrum. PhD thesis. School of BioSciences. The University of Melbourne

Canessa S, Guillera-Arroita G, Lahoz-Monfort JJ, Southwell DM, Armstrong DP, Chades I, Lacy RC, Converse SJ (2015) When do we need more data? A primer on calculating the value of information for applied ecologists. Methods Ecol. Evol. 6: 1219–1228

Castillo-Lara P, Octavio-Aguilar P, De-Nova JA (2018) *Ceratozamia zaragozae* Medellín-Leal (Zamiaceae), an endangered Mexican cycad: new information on population structure and spatial distribution. Brittonia 70: 155–165

Castro J, Gomez JM, Garcia D, Zamora R, Hodar JA (1999) Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecol. 145: 115–123

Cibrián-Jaramillo A, Daly AC, Brenner E, Desalle R, Marler TE (2010) When North and South don't mix: genetic connectivity of a recently endangered oceanic cycad, *Cycas micronesica*, in Guam using EST-microsatellites. Mol. Ecol. 19: 2364–2379

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ and Knox KJE (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol. 197:19–35

Coates RI, Aguirre A, Campos-Villanueva Á (2015) Plant use by artisans within the Los Tuxtlas Biosphere Reserve, southern Mexico. Hum. Ecol. 43: 621–631

Condamine F L, Nagalingum NS, Marshall CR and Morlon H (2015) Origin and diversification of living cycads: a cautionary tale on the impact of the branching process prior in Bayesian molecular dating. BMC Evol. Biol. 15: 65

Convention on Biological Diversity (2011a) Global strategy for plant conservation (2011 - 2020). In: Conf. Parties to CBD, by Decis. X/17. https://www.cbd.int/gspc/default.shtml Accessed 16 Aug 2018

Convention on Biological Diversity (2011b) Conference of the Parties Decision X/2: Strategic Plan for biodiversity 2011-2020. https://www.cbd.int/decision/cop/?id=12268 Accessed 16 Aug 2018

Cousins SR, Witkowski ETF (2017) African Cycad Ecology, Ethnobotany and Conservation: A Synthesis. Bot. Rev. 83: 152–194

Cox RL, Underwood EC (2011) The importance of conserving biodiversity outside of protected areas in Mediterranean ecosystems. PLoS One 6: 1–6

Cronk Q (2016) Plant extinctions take time. Science 353: 446–448

Da Silva J, Donaldson JS, Reeves G, Hedderson TA (2012) Population genetics and conservation of critically small cycad populations: a case study of the Albany Cycad, *Encephalartos latifrons* (Lehmann). Biol. J. Linn. Soc. 105: 293–308

Daly, B., Donaldson, J.S., Friedmann, Y., Hahndiek, Q., King, N. Newton, D. and Southwood, A. (editors) (2006) Population and habitat viability assessment for the Albany cycad (Encephalartos latifrons). Conservation Breeding Specialist Group (SSC /IUCN) / CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg

DEA (2016) Non-detriment findings. National Environmental Management: Biodiversity Act 10 of 2004. South African Government Gazette No. 40021(575)

Deevey ES (1947) Life Tables for Natural Populations of Animals. Q. Rev. Biol. 22: 283–314

Demetrius L (1979) Relations between demographic parameters. Demography 16: 329–338

Dhar A, Ruprecht H, Vacik H (2008) Population viability risk management (PVRM) for *in situ* management of endangered tree species — a case study on a *Taxus baccata* L. population. For. Ecol. Manage. 255: 2835–2845

Diniz MF, Gonçalves TV & Brito D (2017) Last of the green: identifying priority sites to prevent plant extinctions in Brazil. Oryx 51(1): 131-136

Donaldson J (2008) South African *Encephalartos* Species: NDF Workshop Case Study 4 (WG3)

Donaldson J (2003) Cycads: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK

Donaldson J, de Wet Bosenberg J (1999) Changes in the abundance of South African cycads during the 20th century: preliminary data from the study of matched photographs, in: Chen CJ (Ed.), Proceedings of the 4th International Conference on Cycad Biology. Academic Publishers, Beijing, Panzhihua, China

Donaldson JS (2009) Botanic gardens science for conservation and global change. Trends Plant Sci. 14: 608–613

Downey PO, Richardson DM (2016) Alien plant invasions and native plant extinctions: a six-threshold framework. AoB Plants 8: 1–21

Driver A, Sink KJ, Nel JN, Holness S, Van Niekerk L, Daniels F, Jonas Z, Majiedt PA, Harris L, Maze K, (2012) National Biodiversity Assessment 2011: an assessment of South Africa's biodiversity and ecosystems. Synthesis Report. South African National Biodiversity Institute and Department of Environmental Affairs, Pretoria

Duffy R (2014) Waging a war to save biodiversity: the rise of militarized conservation. Int. Aff. 90: 819–834

Eken G, Bennun L, Brooks TM, Darwall W, Fishpool DC, Foster M, Knox D, Langhammer P, Matiku P, Radford E, Salaman P, Sechrest WES, Smith ML, Tordoff A (2004) Key Biodiversity Areas as site conservation targets. Bioscience 54: 1110–1118

Fragnière Y, Bétrisey S, Cardinaux L, Stoffel M, Kozlowski G (2015) Fighting their last stand? A global analysis of the distribution and conservation status of gymnosperms. J. Biogeogr. 42: 809–820

Funk SM, Conde D, Lamoreux J, Fa JE (2017) Meeting the Aichi targets: pushing for zero extinction conservation. Ambio 46: 443–455

García D, Zamora R, Hódar JA, Gómez JM, Castro J (2000) Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. Biol. Conserv. 95: 31–38

Giddy C (1974) Cycads of South Africa. First Edit. ed. Purnell and Sons Pty Ltd, Cape Town

Government of South Africa (2015) National Biodiversity Strategy and Action Plan 2015 – 2025. Department of Environmental Affairs, Pretoria

Gregory R, Long G (2009) Using structured decision making to help implement a precautionary approach to endangered species management. Risk Anal. 29: 518–532

Griffith MP, Calonje M, Meerow AW, Tut F, Kramer AT, Hird A, Magellan TM, Husby CE (2015) Can a botanic garden cycad collection capture the genetic diversity in a wild population? Int. J. Plant Sci. 176: 1–10

Griffiths AD, Schult HJ, Gorman J (2005) Wild harvest of *Cycas arnhemica* (Cycadaceae): impact on survival, recruitment and growth in Arnhem Land, northern Australia. Aust. J. Bot. 53: 771–779

Grime JP. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, Mcdonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. Ecol. Lett. 16: 1424–1435

Halley JM, Monokrousos N, Mazaris AD, Vokou D (2017) Extinction debt in plant communities: where are we now? J. Veg. Sci. 28: 459–461

Hill KD (2003) Regional overview: Australia, in: Donaldson, J. (Ed.), Cycads: Status, Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK, Gland, Switzerland: IUCN Species Survival Commission, pp. 20–24

Hill R, Cullen-Unsworth L, Talbot L, McIntyre-Tamwoy S (2011) Empowering Indigenous peoples' biocultural diversity through World Heritage cultural landscapes: a case study from the Australian humid tropical forests. Int. J. Herit. Stud. 17: 571–591

Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks, TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Katariya V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vie J-C, Aguiar JM, Allen DJ, Allen GR and Amori G (2010) The impact of conservation on the status of the world's vertebrates. Sci New Ser 330:1503–1509

Hylander K, Ehrlén J (2013) The mechanisms causing extinction debts. Trends Ecol. Evol. 28: 341–346

Ishizaka A, Labib A (2011) Review of the main developments in the analytic hierarchy process. Expert Syst. Appl. 38: 14336–14345

IUCN (2014) Guidelines for using the IUCN Red list Catergories and Criteria version 11, Prepared by the Standards and Petitions Subcommitte. Downloable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf

IUCN (2016) A global standard for the identification of Key Biodiversity Areas: version 1.0. Gland, Switzerland: IUCN

Jantz SM, Barker B, Brooks TM, Chini LP, Huang Q, Moore RM, Noel J, Hurtt GC (2015) Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. Conserv. Biol. 29: 1122–1131

Keith DA, Martin TG, McDonald-Madden E, Walters C (2011) Uncertainty and adaptive management for biodiversity conservation. Biol. Conserv. 144: 1175–1178

Keppel G (2002) Low genetic variation in a Pacific cycad: conservation concerns for *Cycas seemannii* (Cycadaceae). Oryx 36: 41–49

Keppel G, Mokany K, Wardell-Johnson GW, Phillips BL, Welbergen JA, Reside AE (2015) The capacity of refugia for conservation planning under climate change. Front. Ecol. Environ. 13: 106–112

Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, Lindborg R, Öckinger E, Pärtel M, Pino J, Pöyry J, Raatikainen KM, Sang A, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol. Lett. 13: 597–605

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. 24: 564–571

Lamont BB, Downes KS (2011) Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. Plant Ecol. 212: 2111–2125

Lamoreux JF, Mcknight MW, Hernandez RC (2015) Amphibian Alliance for Zero Extinction Sites in Chiapas and Oaxaca. IUCN, Gland, Switzerland: IUCN

Liddle DT (2004) The ecology of *Cycas armstrongii* and management of fire in Australia's tropical savannas. PhD thesis. Charles Darwin University, Australia, Darwin

López-Gallego C (2008) Demographic variation in cycad populations inhabiting contrasting forest fragments. Biodiv. Conserv. 17: 1213-125

López-Gallego C, O'Neil P (2010) Life-history variation following habitat degradation associated with differing fine-scale spatial genetic structure in a rainforest cycad. Popul. Ecol. 52: 191–201

Mankga LT, Yessoufou K (2017) Factors driving the global decline of cycad diversity. AoB Plants 9: plx022

Marchese C (2015) Biodiversity hotspots: a shortcut for a more complicated concept. Glob. Ecol. Conserv. 3: 297–309

Marechaux I, Rodrigues ASL, Charpentier A (2017) The value of coarse species range maps to inform local biodiversity conservation in a global context. Ecography 40: 1166–1176

Marignani M, Blasi C (2012) Looking for important plant areas: selection based on criteria, complementarity, or both? Biodivers. Conserv. 21: 1853–1864

Marler TE (2013) Increased threat of island endemic tree's extirpation via invasion-induced decline of intrinsic resistance to recurring tropical cyclones. Commun. Integr. Biol. 6: e22361

Marler TE, Ferreras U (2017) Current status, threats and conservation needs of the endemic *Cycas wadei*. J Biodivers Endanger Species 5: 1–8

Marler TE, Lawrence JH (2012) Demography of *Cycas micronesica* on Guam following introduction of the armoured scale *Aulacaspis yasumatsui*. Journal of Tropical Ecology 28(3): 233-242

Martin TG, Burgmann MA, Fidler F, Kuhnert PM, Low-Choy S, McBride M, Mengersen K (2012) Eliciting expert knowledge in conservation science. Conserv. Biol. 26: 29–38

McDonald-Madden E, Probert WJM, Hauser CE, Runge MC, Possingham HP, Jones ME, Moore JL, Rout TM, Vesk PA, Wintle BA (2010) Active adaptive conservation of threatened species in the face of uncertainty. Ecol. Appl. 20: 1476–1489

Menz MHM, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends Plant Sci. 16: 4–12

Nackley L, Midgley GF, de Wet Bosenberg J and Donaldson JS (2018) A cycad's non-saturating response to carbon dioxide enrichment indicates Cenozoic carbon limitation in pre-historic plants. Austral Ecology 43: 447-455

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Global biodiversity conservation: the critical role of hotspots, in: Zachos FE, Habel JC (Eds.) Biodiversity Hotspots. Springer-Verlag, Berlin, Heidelberg, pp. 3–22

Moore CT, Fonnesbeck CJ, Shea K, Lah KJ, McKenzie PM, Ball LC, Runge MC, Alexander HM (2011) An adaptive decision framework for the conservation of a threatened plant. J. Fish Wildl. Manag. 2: 247–261

Nadarajan J, Benson EE, Xaba P, Harding K, Lindstrom A, Donaldson J, Seal CE, Kamoga D, Agoo EMG, Li N, King E, Pritchard HW (2018) Comparative biology of cycad pollen, seed and tissue - a plant conservation perspective. Bot. Rev. https://doi.org/10.1007/s12229-018-9203-z

Negron-Ortiz V, Gorchov DL (2000) Effects of fire season and post fire herbivory on the cycad *Zamia pumila* (Zamiaceae) in Slash Pine Savanna, Everglades National Park, Florida. Int. J. Plant Sci. 161: 659–669

Octavio-Aguilar P, Rivera-Fernández A, Iglesias-Andreu LG, Vovides AP, de Cáceres-González FFN (2017) Extinction risk of *Zamia inermis*: a demographic study in its single natural population Biodivers. Conserv. 26: 787–800

Okubamichael DY, Jack S, De Wet Bösenberg J, Hoffman T, Donaldson JS (2016) Repeat photography confirms alarming decline in South African cycads. Biodivers. Conserv. 25: 2153–2170

Pereira HM, Navarro LM, Martins IS (2012) Global biodiversity change: the bad, the good, and the unknown. Annu. Rev. Environ. Resour. 37: 25–50

Pérez-Farrera MA and Vovides AP (2004) Spatial distribution, population structure and fecundity of *Ceratozamia matudai* Lundell (Zamiaceae) in El Triunfo Biosphere Reserve, Chiapas, Mexico. Botanical Review 70 (2): 299-311

Pérez-Farrera MA, Vovides AP, Octavio-Aguilar P, González-Astorga J, Cruz-Rodríguez JD LA, Hernández -Jonapá R, Villalobos-Méndez SM (2006) Demography of the cycad *Ceratozamia mirandae* (Zamiaceae) under disturbed and undisturbed conditions in a biosphere reserve of Mexico. Plant Ecol. 187: 97–108

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25: 345–353

Preece LD, Duguid AW, Albrecht DE (2007) Environmental determinants of a restricted cycad in central Australia, *Macrozamia macdonnellii*. Aust. J. Bot. 55: 601–607

Pulido MT, Vargas-Zenteno M, Vite A, Vovides PA (2015) Range extension of the endangered Mexican cycad *Ceratozamia fuscoviridis* Moore (teosintle): implications for conservation. Trop. Conserv. Sci. 8: 778–795

Raimondo D (ed) (2015) South African strategy for plant conservation. South African National Biodiversity Institute and the Botanical Society of South Africa, Pretoria

Raimondo DC, Donaldson JS (2003) Responses of cycads with different life histories to the impact of plant collecting: simulation models to determine important life history stages and population recovery times. Biol. Conserv. 111: 345–358

Ravele AM, Makhado RA (2009) Exploitation of *Encephalartos transvenosus* outside and inside Mphaphuli Cycads Nature Reserve, Limpopo Province, South Africa. Afr. J. Ecol. 48: 105–110

Regan HM, Ben-Haim Y, Langford B, Wilson WG, Lundberg P, Andelman SJ, Burgman MA (2005) Robust decision-making under severe uncertainty for conservation management. Ecol. Appl. 15: 1471–1477

Rout TM, Hauser CE, Possingham HP (2009) Optimal adaptive management for the translocation of threatened species. Ecol. Appl. 19: 515–526

Rose DC, PNM Brotherton, Owens S and Pryke T (2018) Honest advocacy for nature: presenting a persuasive narrative for conservation. Biodivers Conserv. 27: 1703 - 1723

Russell-Smith J, Lucas D, Gapindi M, Gunbunuka B, Kapirigi N, Namingum G, Lucas K, Giuliani P, Chaloupka G (1997) Aboriginal resource utilization and fire management practice in Western Arnhem Land, monsoonal northern Australia: notes for prehistory, lessons for the future. Hum. Ecol. 25: 159–195

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NLR, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774

Sloan S, Jenkins CN, Joppa LN, Gaveau DLA, Laurance WF (2014) Remaining natural vegetation in the global biodiversity hotspots. Biol. Conserv. 177: 12–24

Smith BD, Zeder MA (2013) The onset of the Anthropocene. Anthropocene 4: 8–13

Smith MJ, Benitez-Diaz H, Clemente-Munoz MA, Donaldson J, Hutton JM, McGough HN, Medellin RA, Morgan DHW, O'Criodain C, Oldfield TEE, Schippmann U, Williams RJ (2011) Assessing the impacts of international trade on CITES-listed species: current practices and opportunities for scientific research. Biol. Conserv. 144: 82–91

Stokes DL (2018) Why conserving species in the wild still matters. Biodivers. Conserv. 27: 1539–1544

Tang W (1990) Reproduction in the cycad *Zamia pumila* in a fire-climax habitat: an eight-year study. Bull Torrey Bot Club 117: 368–374

Terry I, Roe M, Tang W, Marler TE (2009) Cone insects and putative pollen vectors of the endangered cycad. Micronesica 41: 83–99

Terry I, Tang W, Blake A, Donaldson JS, Singh R, Vovides AP, Jaramillo A (2012) An overview of cycad pollination studies. Mem. N. Y. Bot. Gard. 106: 352–394

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371: 65 - 66

UNEP (2016) Global environment outlook: GEO-6 regional assessment for Africa. Nairobi, Kenya

Volis S (2016) Conservation meets restoration – rescuing threatened plant species by restoring their environments using threatened plant species. Isreal J. Plant Sci. 63: 262–275

Vovides AP, Iglesias CG (1994) An integrated conservation strategy for the cycad *Dioon edule* Lindl. Biodiversity and Conservation 3: 137–141

Vovides AP, Ogata N, Sosa V, Peña-García E (1997) Pollination of endangered Cuban cycad *Microcycas calocoma* (Miq.) A. DC. Bot. J. Linn. Soc. 125: 201–210

Wilcock C, Neiland R (2002) Pollination failure in plants: why it happens and when it matters. Trends Plant Sci. 7: 270–277

Williams VL, Cousins SR, Witkowski ETF (2014) From fragments to figures: estimating the number of *Encephalartos* stems in a muthi market. South African J. Bot. 93: 242–246

Winter J, Botha D (1994) The release of endangered plants into the horticultural trade: conservation or exploitation? Biodivers. Conserv. 3: 142–147

Wu LW, Yen SH, Lees DC, Hsu YF (2010) Elucidating genetic signatures of native and introduced populations of the Cycad Blue, *Chilades pandava* to Taiwan: a threat both to Sago Palm and to native Cycas populations worldwide. Biol. Invasions 12: 2649–2669

Xaba P (2014) Pollination and germination as limiting factors in the propagation of threatened cycads, Encephalartos (Zamiaceae). MSc thesis. University of the Western Cape, South Africa, pp 1 – 138

Yáñez-Espinosa L and Sosa-Sosa F (2007) Population structure of *Dioon purpusii* Rose in Oaxaca, Mexico. Neotropical Biology and Conservation 2:46–54

Yessoufou K, Daru BH, Tafirei R, Elansary HO, Rampedi I (2017) Integrating biogeography, threat and evolutionary data to explore extinction crisis in the taxonomic group of cycads. Ecol. Evol. 7: 2735–2746

Yousefpour R, Bredahl Jacobsen J, Thorsen BJ, Meilby H, Hanewinkel M, Oehler K (2012) A review of decision-making approaches to handle uncertainty and risk in adaptive forest management under climate change. Ann. For. Sci. 69: 1–15

Zander KK, Austin BJ, Garnett ST (2014) Indigenous peoples' interest in wildlife-based enterprises in the Northern Territory, Australia. Hum. Ecol. 42: 115–126

CHAPTER 2

Predicting the distribution of *Encephalartos latifrons*, a critically endangered cycad in South Africa

[This chapter was published in Biodiversity and Conservation Journal in the February 2018 online edition. Full text is available at the following link: http://rdcu.be/Hf8V]

Abstract

This study evaluates how a modelling approach to determine areas of suitable habitat for the Critically Endangered Albany cycad *Encephalartos latifrons* can assist in systematic conservation planning for this and other rare and threatened cycads. A map distinguishing suitable from unsuitable habitat for *E. latifrons* was produced and important environmental predictors (climate, geology, topography and vegetation) influencing the suitable habitat were estimated. The maximum entropy (MaxEnt) modelling technique was chosen for this study as it has consistently performed well compared with alternative modelling methods and is also an appropriate model choice when the sample size is small and locality records are relatively few. Predicted habitat suitability showed that some locations chosen for translocation and restoration of *E. latifrons* specimens are not suitable. This revealed that modelling suitable habitat can guide relocation and regeneration of *E. latifrons* and perhaps other threatened cycads with restricted distributions and few locality records. The species distribution model constructed for *E. latifrons* is the first reported habitat model for a Critically Endangered cycad in South Africa. The results may be incorporated into conservation planning and structured decision-making about translocations and restoration programmes involving vulnerable cycads, which are among the most threatened organisms globally.

Keywords: conservation planning, environmental predictors, hotspot, Maximum Entropy model, suitable habitat

Introduction

Threats to global biodiversity are increasing at an alarming rate, with cycads notably one of the most threatened groups (Hoffmann et al. 2010; IUCN 2010). Harvesting of wild plants is the primary threat to native cycad species in Africa (TRAFFIC 2003). In South Africa, conservation authorities have begun implementing biodiversity management plans for endangered cycad species (DEA 2015; DEA 2011) in addition to promulgating stricter legislation prohibiting the harvesting of wild plants (NEMBA Act 10 of 2004: Threatened and/or Protected Species Regulations). The country has also adopted the National Strategy and Action Plan for the Management of Cycads (DEA 2014), highlighting the need to identify and map critical cycad habitat.

The establishment of formal protected areas is a direct way to conserve species at risk. A few reserves in South Africa have been created to directly conserve cycad populations, such as the Mphaphuli and Modjadji Cycads Nature Reserves in Limpopo Province, and the Cycad Provincial Nature Reserve in Grahamstown, Eastern Cape Province (Donaldson 1995; Ravele and Makhado 2010). At least 25 African species are directly or indirectly included in one or more of the protected areas in Africa (Donaldson 2003); however, it is of concern that 13 Critically Endangered, 4 Endangered and 8 Vulnerable species on the African continent, as assessed by the IUCN, do not occur in any protected area (Donaldson 2003). In South Africa, 72 protected areas encompass 24 cycad species—approximately 65% of all South African species (Osborne 1995a). Although reserves protect cycad populations from habitat destruction, not all reserves adequately reduce illegal harvesting, while most lack sufficient security to do so (Donaldson 2003). In keeping with Aichi target 11, which aims to "prevent the extinction of all known threatened species and improve and sustain their conservation status" (Convention on Biological Diversity 2011), the South African Government identified shortcomings in the network of formal protected areas in regard to conserving species representative of South African biodiversity, as well as in maintaining key ecological processes. This led to the development of the National Protected Area Expansion Strategy (NPAES) (South African Government 2010). However, threatened ecosystems rather than individual threatened species were used to identify the priority areas, and it is uncertain whether/how many South African cycad species or populations are included in these areas.

Knowledge of suitable habitat for *Encephalartos latifrons* can guide conservation authorities in where to place confiscated plants (Osborne 1995b), choose restoration sites (Donaldson 2003), and identify areas in need of protection (Berliner and Desmet 2007). Confiscated plants include *E. latifrons* specimens seized by law enforcement authorities when illegal harvesting has occurred (Vice 1995). Restoration sites are areas to be identified for the placement of artificially propagated plants (originating from wild parental stock) made possible by the gazetted Biodiversity Management Plan (BMP-S) for the species (DEA 2011). Species distribution modelling (SDM) is useful for determining suitable habitat for rare and endangered species (Kumar and Stohlgren 2009; Gogol-Prokurat 2011; Chunco et al. 2013). Nonetheless, predicting suitable habitat for a rare species with a narrow geographic range has unique challenges when the distribution is patchy and the sample size is small (Williams et al. 2009). Especially in the case of *E. latifrons*, obtaining sufficient data points is a difficult task owing to the species' rarity, with reportedly less than 100 wild plants existing at only three localities (Daly et al. 2006).

The Maximum Entropy (MaxEnt) model was chosen for this study as it has performed well compared with alternative modelling methods, such as GARP, DOMAIN and ENFA (Elith et al. 2006), and it is an appropriate model choice with small sample sizes or few locality records (Pearson et al. 2007; Wisz et al. 2008; Gogol-Prokurat 2011; Jackson and Robertson 2011; Razgour et al. 2011; Chunco et al. 2013; Marcer et al. 2013; Fois et al. 2015).

The primary aim of this study was to produce a map distinguishing suitable from unsuitable habitat for *E. latifrons*, as needed for systematic conservation planning and decision making. A second aim was to estimate the relative contribution of the environmental variables used in the model, to determine if any stood out as important predictors of *E. latifrons* suitable habitat. A third aim was to determine how predictions from the model may have influenced past decisions relating to the conservation of *E. latifrons* by the construction of a decision-making scheme.

Materials and methods

Study area and species

The study area lies in the eastern-most extreme of the Cape Floristic Region referred to as the Greater Cape Floristic Region (GCFR) (Bergh et al. 2014) within the Albany Centre of Endemism, South Africa (van Wyk and Smith 2001). The area has a predominantly bi-modal rainfall pattern, with peaks in spring (September–November) and autumn (March–April). Populations of *Encephalartos latifrons* are associated with the Mediterranean-climate Fynbos Biome, specifically the Suurberg Quartzite Fynbos (SQF) (Rebelo et al. 2006). SQF is characterised by sandy, infertile soils, and can be distinguished from other types of fynbos as occurring on finer-textured soils, with relatively higher nutrient levels, where summer droughts are less pronounced (Cowling 1983; Campbell 1986). The study area (Figure 2.1) was divided into two fire-climate zones, as adapted from Kraaij et al. (2014). In the western inland region, around Grahamstown, the fire frequency is typically every 4–6 years; in the coastal region, around the village of Bathurst, fires are typical at most every 15 years (Kraaij et al. 2014; unpublished records obtained from landowners). The SQF vegetation becomes patchy and fragmented in the coastal areas and surrounded by Kowie Thicket and Albany Thicket vegetation (Lubke et al. 1986; Hoare et al. 2006). This inland/coastal delineation roughly corresponds to the ecoregions described by Kleynhans et al. (2005) and the climate-gradient zones of Thuiller et al. (2004) within the GCFR.

Model development

Selection of the study area

The chosen area applied to the model represents the two ecoregions within which *E. latifrons* populations are found, namely the Southern Fold Mountains and the South-Eastern Coastal Belt ecoregions (as delineated by Kleynhans et al. [2005]), derived from data on terrain and vegetation with altitude, rainfall, runoff variability, air temperature, geology and soil. Ecoregion GIS data were obtained from the South African Department of Water and Sanitation (http://www.dwa.gov.za/iwqs/gis_data/ecoregions/get-ecoregions.aspx. Accessed 30/03/2015). The study area represents the geographical range considered accessible to this species, which is an important consideration in the modelling process (Fourcade et

al. 2014). The biotic–abiotic–mobility (BAM) model proposed by Soberón and Peterson (2005) was used to describe the model for *E. latifrons*, where A = M ≠ B. Mobility (M) is the area accessible to the species, given its dispersal ability, and is derived from the two ecoregions (representing an area of relative homogeneity) where *E. latifrons* populations currently exist. The fundamental niche (A) would therefore be represented by the area M (Soberón and Peterson 2005). The limiting region B in the theoretical model represents the poorly understood biotic factors potentially affecting the distribution of the species but not included in the analysis.

Model resolution

The MaxEnt model was run at a resolution of a 30 arc-second (approximately 1 x 1 km) grid (the grid resolution for which the data layers, particularly the climate layers, were available). It was considered a broad-scale model as opposed to a finer local-scale model run at 30 x 30 m grids, as in some other studies of rare-species distribution (e.g. Gogol-Prokurat 2011). MaxEnt requires the cell size and spatial extent of each layer to be precisely the same (Phillips 2010); therefore, the data have to be resampled and upscaled to the coarsest grid in the dataset. Consequently, the resolution depicts a regional overview of *E. latifrons* distribution rather than a concentrated finer-scale local distribution.

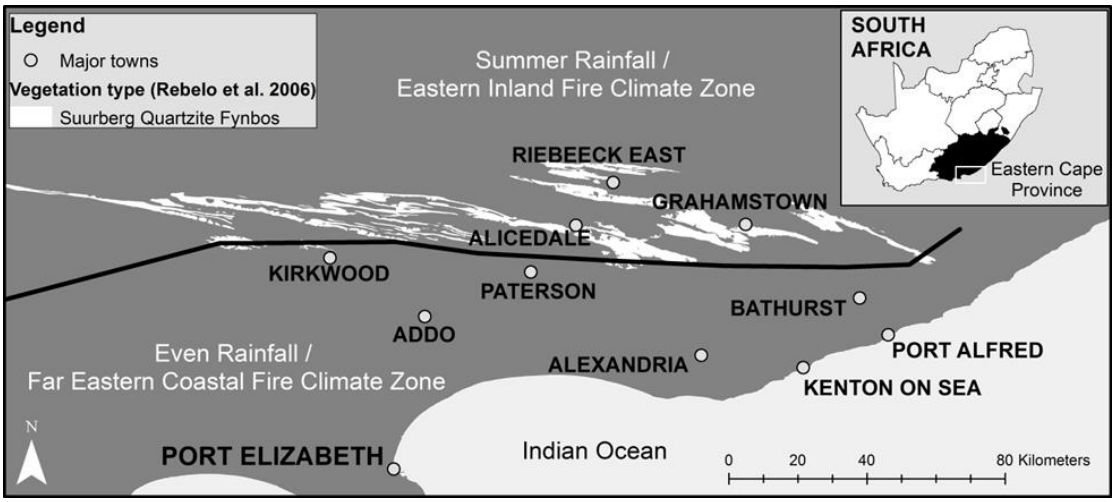


Figure 2.1 Map of the study area showing Suurberg Quartzite Fynbos, a vegetation group of the Fynbos Biome associated with the distribution of the Albany cycad *Encephalartos latifrons*. The solid black line denotes separation of the study area into two rainfall regions (adapted from Rebelo et al. [2006]) and different fire-climate zones (adapted from Kraaij et al. [2014])

Occurrence data

The estimate of the fundamental niche (as described by the BAM model for *E. latifrons*) depends on how it is represented by the locality points chosen for the model (Soberón and Peterson 2005). For this study, locality points included current and historical populations of *E. latifrons* across the species' distribution, thus considered to be representative of A. An underestimation of A would be expected if the model was based only on the distribution of existing populations, where positive interactors may be missing (e.g. pollinators) or where negative interactors occur extensively (e.g. theft of wild plants). Records of insect pollination and self-recruitment in *E. latifrons* populations date back to as recently as 1991 (Basson 1991). Moreover, recently discovered populations of the cycad were found to be naturally recruiting, indicating that at least some populations cannot be considered functionally extinct (unpublished data). Negative factors, such as illegal harvesting or limited pollination, are therefore accounted for in the model via inclusion of the historical locality points. All known existing *E. latifrons* populations and individuals were verified in the field and then digitized onto a 1:10 000 recent (2013) geo-referenced aerial photograph using ArcGIS 10.2 (ESRI 2012). Historical locality points detailed in the permit records held by the DEDEA, and herbarium records at the Albany Museum were also employed as valuable information (Swart 2017). Verification of locality points derived from the permit and herbarium records was done by interviewing landowners who were able to confirm exact positions of plants where they once existed in situ but no longer remain today. All historical records were verified in this way and then digitized on 1:10 000 aerial photographs and recorded in a GIS. All occurrence points were digitized at an accuracy of 2–5 meters. In total, 18 occurrence points were verified and digitized; the occurrence points are not reported here due to the sensitivity of the information (cf. Yeld 2014).

Three areas where populations of *E. latifrons* were known to have occurred were not included in the model and were used to test the model results: 1) Beggars Bush Nature Reserve, since unpublished permit records held at the DEDEA, as well as interviews with the managers who were in charge of the reserve at the time, indicated that this reserve once held a large population of *E. latifrons*. Because cycad theft was a major problem at the reserve, a decision was taken to remove all the wild plants in the reserve and place them at a nearby Forest Station, from where they subsequently disappeared. 2) A private farm in the Howieson's Poort area, where the presence of a

wild *E. latifrons* plant was determined according to herbarium records. 3) A private farm near Fraser's Camp, where an unpublished 1981 survey report (written by nature conservation authorities) mentions three large clumps of *E. latifrons* (>20 plants), where males and females occurred in close proximity. The report also states that *E. latifrons* at the site were reproducing in a natural way since seedlings were evident. The plants were eventually stolen from the property (according to records detailing the court case), but subsequently found and confiscated. In all three cases, it was not possible to determine the exact location of the plants. These could not be included as locality points but were useful for testing the results of the model.

Environmental data

Four categories of environmental predictors were chosen for input into the model, based on relevance to *E. latifrons* distribution: climate, geology, vegetation, and topography (Table 2.1). Climate data were obtained from the WorldClim database, at a spatial resolution of 1 km2 (Hijmans et al. 2005; http://worldclim.org/). To test autocorrelations of the climate data (a potential source of bias) the SDMtoolbox function was used in ArcGIS 10.2 (ESRI 2012; Brown 2014); climate predictors were considered highly correlated if Pearson's coefficient was ≥0.8. The 1:250 000 geological layer was obtained from the Council for Geoscience, South Africa. Geology was used as a substitute for soil data which were not readily available for the study area. Populations of *E. latifrons* are predominantly associated with rock outcrops of the Witteberg Group, where the soil is typically shallow, sandy and acidic as a result of the slow weathering of sandstones and quartzites (Shone and Booth 2005; DEA 2011). Three vegetation indices as well as an albedo index (a measure of the Earth's surface reflectance, included as a predictor of rock outcrops) were extracted from remotely sensed data for input into the model. Remotely sensed data in the form of satellite imagery have been successful in predicting suitable habitats of rare and endangered species (Raxworthy et al. 2003; Lahoz-Monfort et al. 2010; Gogol-Prokurat 2011) and are appropriate for measuring the habitat characteristics of such species (Bradley et al. 2012). Albedo values vary based on land cover, where vegetation associated with rock outcrops has a higher value as compared with thicket and forest areas (Roy et al. 2014). Landsat Operational Land Imager (OLI) data (path 170, row 83; path 171, row 83), acquired for spring 2013 and 2014, was used to calculate albedo (total reflectance) and the three vegetation indices: tasselled cap (TC) brightness, TC wetness, and TC

greenness. Tasselled-cap transformation converts original Landsat bands into three biologically meaningful indicators of vegetation (Kauth and Thomas 1976). Prior to transforming Landsat images into the indices mentioned, top-of-atmosphere reflectance (i.e. image correction for the fluctuating scattering and absorbing effects of atmospheric gases) was calculated from the raw calibrated digital numbers of the image. Topographical variables included elevation above sea level (m) and slope (degrees), calculated with ArcGIS Spatial Analyst tools (ESRI 2012). Hillshade (a predictor of shaded relief) and aspect (a predictor of slope direction) were excluded because model performance improved with their exclusion.

Model calibration

The model was calibrated to eliminate spatial clusters possibly leading to over-fitting towards environmental biases (e.g. *E. latifrons* occurrence data where certain areas were sampled more intensively) by running the spatially rarefy occurrence data tool in SDMtoolbox (Brown 2014). To determine what distances to rarefy the occurrence points, the climatic and topographic heterogeneity of the study area was explored. Topographic features displayed higher levels of heterogeneity than climate data within the study area. The occurrence points were rarefied at different distances based on an input topographic heterogeneity raster using the altitude predictor; three heterogeneity classes were used, at a maximum of 25 km and a minimum of 5 km. After filtering for sampling bias, 12 occurrence points were available for input into the model. The Gaussian kernel density of sampling localities tool was used to create a bias file in order to differentiate areas of potentially unsuitable habitat from areas where the habitat may be suitable yet uncolonised for the selection of background points. The spatial distance used to quantify the region of spatial bias was 0.3 decimal degrees.

Table 2.1 Categories of environmental data included in the MaxEnt model for identifying suitable habitat for *Encephalartos latifrons*. All layers were projected to the Transverse Mercator WGS84 datum coordinate system. WorldClim bioclimatic variables are coded as follows: BIO1 - annual mean temperature (°C * 10), BIO3 - isothermality (mean diurnal temperature range (BIO2)/ temperature annual range (BIO7)) (unit less ratio * 100), BIO12 - annual precipitation (mm), BIO5 - maximum temperature in the warmest month (°C * 10), BIO6 - maximum temperature in the coldest month (°C * 10)

Category	Predictor	Grain	Source
Climate	BIO1	1 km	WorldClim database
	BIO3	1 km	(www.worldclim.org)
	BIO12	1 km	
	BIO5	1 km	
	BIO6	1 km	
Topography	Elevation (m above sea level)	1 000 m	Generated in ArcGIS
	Slope (degrees)	1 km	
Geology	Substrate	1:250 000 geological layer	Council for Geoscience, South Africa
Landsat indices of vegetation	Albedo	30 m	Landsat 8 imagery (www.earthexplorer.usgs.gov, accessed 05/03/2015)
	TC brightness	30 m	
	TC wetness	30 m	
	TC greenness	30 m	

Model validation

The MaxEnt program reports area under the curve (AUC) scores by default, summarising predictive performance under a range of thresholds (Phillips 2010). However, AUC scores should not be used as the only test when determining model performance when there are a limited number of occurrence points (Pearson et al. 2007); nevertheless, the AUC scores are reported here for comparative purposes. In addition, the jackknife technique as described in Pearson et al. (2007) was used to test the predictive accuracy of the model due to the small number of locality points. Model robustness and significance were calculated with the value of the 'minimum training

presence area' and the success rate (converse to the minimum training presence test omission) using pValueCompute software and the methods of Pearson et al. (2007).

Model parameters

The following settings were used in the MaxEnt program when running the model: regularisation multiplier = 1; number of background points used = 10 000; replicates = 12; replicated run type = cross-validation; threshold rule applied = minimum training presence; in addition, spatial jackknifing was performed and the auto features used.

Conservation gap-analysis

Once the model was run and areas of suitable habitat for *E. latifrons* were identified, conservation gaps for this species were identified by comparing areas of suitable habitat within the current formal protected areas (promulgated under the National Environmental Management: Protected Areas Act 57 of 2003), the future protected area expansion identified in the NPAES, and the Critical Biodiversity Areas (CBAs) identified in the Eastern Cape Biodiversity Conservation Plan (ECBCP) (Berliner and Desmet 2007). CBAs are categorised according to their level of biodiversity; this study selected CBA1 areas, which are identified as natural landscapes to be managed for no loss of biodiversity (Berliner et al. 2007). Thus, the three conservation data layers considered were: formal protected areas, future protected area expansion, and CBA1 areas. All data were downloaded from the portal of the South African National Biodiversity Institute (SANBI) BiodiversityGIS (BGIS) (http://bgis.sanbi.org, accessed 17/07/2015). The data layer from the SDM output raster file (standard output format from MaxEnt) was converted to a vector file in ArcGIS 10.2 (ESRI 2012) and overlaid with the conservation data layers. The SDM vector (shapefile) for *E. latifrons* was intersected and clipped according to the boundaries of the conservation layers, using Geoprocessing Wizard in ArcGIS 10.2 (ESRI 2012). The predicted areas (in hectares) of suitable habitat within the conservation layers were subjectively categorised according to values denoting suitability for *E. latifrons*, with 0–0.49 signifying highly unsuitable, 0.5–0.69 marginally suitable, 0.7–0.79 moderately suitable (an acceptable threshold for conservation planning: Graham et al. 2008), and 0.8–0.94 highly suitable or critical habitat.

Conservation decisions

To assess the past conservation decisions involving *E. latifrons* plants made by conservation authorities (see Introduction), a decision-making scheme (see Guisan et al. 2013) was constructed based on the SDM results. The first step was problem identification: two conservation problems faced by conservation authorities involved the placement of *E. latifrons* plants (i.e. confiscated plants and the placement of seedlings for restoration) and a common set of objectives (explained in Table 2.2: the objectives apply to both problems, resulting in the same decision-making process). The plants (translocated and seedlings) originated from the same population. Once the objectives were defined, the translocation and restoration sites (formal protected areas) were compared with areas of suitable habitat identified by the SDM. The next three steps in the decision-making process (namely, defining possible actions, identifying the consequences of those actions, and a trade-off analysis) were followed according to Guisan et al. (2013).

Table 2.2 The first steps of structured decision analysis (Guisan et al. 2013) for the conservation problems faced by South African authorities in regard to placement of *Encephalartos latifrons* wild plants: problem identification and defining objectives

Problem identification	1. Where to place confiscated plants stolen from the wild in 1993 (Vice 1995)	2. Identification of a restoration site for seedlings (Donaldson, 2003)
Defining objectives	Identify a suitable site to place confiscated plants based on the following factors (adapted from Osborne 1995b): a. survival prospects of the specimens (i.e. suitability of habitat); b. formal protected area; c. proximity to original population; d. security from theft; e. possible genetic contamination of wild populations; f. potential germplasm value; g. value for education, research, and display purposes. (Author has added points b and c; points f and g are not applicable in the present context.)	

Results

The MaxEnt model predicted areas of suitable habitat with a high success rate. The proportion of records correctly predicted were 91.66% successful ($p < 0.0001$) at the 'lowest presence threshold' (LPT) calibrated with 12 occurrence records. The mean AUC score for the model was 0.961 (±0.048). The majority of occurrence points fell within the higher range of suitability values, at 0.70–0.86, except for two locality points that fell within areas of lesser suitability, at 0.54–0.59, considered to be marginally suitable habitat within the South-Eastern Coastal Belt ecoregion. The two core areas of suitable habitat predicted by the model within the Southern Fold Mountains ecoregion (Figure 2.2) are: 1) east of Grahamstown, in the Kap River Mountains and slightly north towards Coombs Valley; 2) southwest of Grahamstown, in an extension of the Highlands Range towards Howieson's Poort. The three test localities (i.e. those not included in the model) fell within the range of highly suitable habitat, with values of 0.8–0.9 for Beggar's Bush Nature Reserve, 0.7–0.8 for the farm near Howieson's Poort, and 0.6–0.7 for the farm near Fraser's Camp. The actual translocation site chosen for the confiscated plants (Waters Meeting Nature Reserve) was projected as highly unsuitable, as was most of the restoration site chosen for the seedlings (Roundhill Nature Reserve), except for an adjacent site, still within the latter reserve, with a suitability value of 0.5 (marginally suitable).

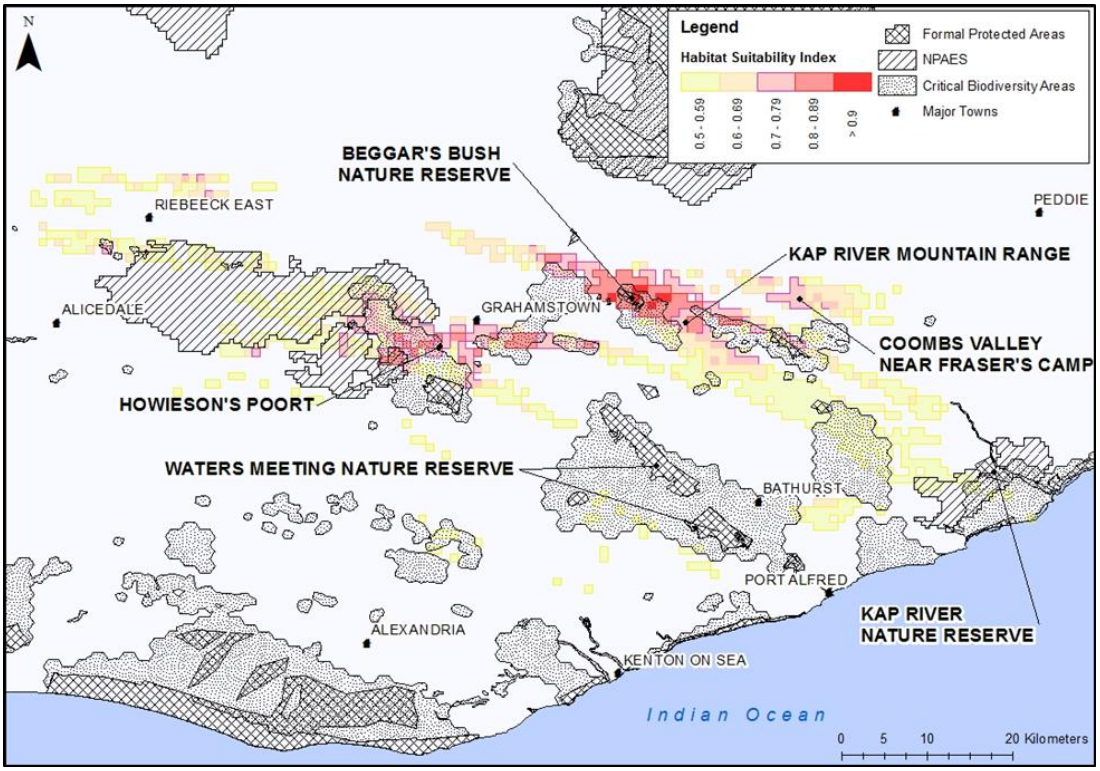


Figure 2.2 Habitat suitability index map for the Albany cycad *Encephalartos latifrons*, including formal protected areas, areas forming part of the NPAES, and critical biodiversity areas (i.e. CBA1 areas, as defined in Berliner et al. [2007]), Eastern Cape, South Africa

Environmental predictors

The geological group represented by the Witpoort Formation (Witteberg Group, Lake Mentz Subgroup, Paleozoic Cape Supergroup, and Cape Fold Belt) and associated SQF was the most important predictor of suitable habitat for *E. latifrons*, according to the MaxEnt model's internal jackknife test of variable importance, at 73.3% contribution. Annual precipitation (BIO12) was the second most important predictor, at 24.1%. Logistic probability increased as annual precipitation increases, peaking in areas receiving 698–837 mm of rainfall, thus restricting suitable habitat locales to the wetter western regions of the study area. Slope, maximum temperature of the warmest month (BIO5), and isothermality (BIO3) contributed very little and were not important predicators of suitable habitat, at 2.2, 0.2, and 0.1%, respectively. All the remaining predictors, including the vegetation indices, annual mean temperature (BIO1), minimum temperature of the coldest month (BIO6), and albedo, did not contribute as predictors of suitable habitat, with 0% contribution.

Protected and conservation areas

The model results show that an area of 5 882 hectares (0.51% of the study area) represents highly suitable habitat for *E. latifrons* (Table 2.3). Of this area, only 276 hectares of highly suitable habitat are contained within one formal state protected area (Beggar's Bush Nature Reserve). In terms of the National Protected Area Expansion Strategy, a further 220 hectares (0.17% of the NPAES within the study area) of highly suitable habitat is contained in the Howieson's Poort area and along the Highlands Road outside Grahamstown. There are large conservation gaps, however, with most of the suitable habitat in the hills south of Grahamstown and in the Kap River Mountains not included in this prioritised area. The CBAs within the study area contain a larger portion of highly suitable habitat (1.18%) over a wider extent (2 446 hectares), and also include more of the Highlands area extending towards Howieson's Poort and the hills south of Grahamstown. Some sections of the Kap River Mountains and the area around Beggar's Bush are also included as CBA1. The areas for *E. latifrons* protection previously listed by Osborne (1995a) were identified as highly unsuitable or unsuitable habitat in the Waters Meeting Nature Reserve and the Kowie Local Nature Reserve. Finally, no existing in situ populations of *E. latifrons* exist within a formal protected area, except for plants that were artificially placed there through restoration and/or translocation.

Table 2.3 Areas (in hectares) of predicted habitat suitability within the study area (see Fig. 2) in relation to three conservation layers: the current network of formal protected areas, the network of the National Protected Area Expansion Strategy (NPAES), and critical biodiversity areas (i.e. CBAs of category CBA1)

Suitability values	Habitat suitability categories (subjectively defined)	Suitable habitat within the study area (hectares)	Proportion of suitable habitat within the study area (%)	Proportion of suitable habitat within the current network of state protected areas (%)	Proportion of suitable habitat identified in the NPAES (%)	Proportion of suitable habitat within CBA1 (%)
0–0.39	Highly unsuitable	1 036 261	91.30	99.46	86.53	89.80
0.4–0.49	Unsuitable	35 608	3.14	0.13	5.98	3.15
0.5–0.69	Marginally suitable	46 935	4.13	0.21	6.6	4.13
0.7–0.79	Moderately suitable	10 472	0.92	0.03	0.7	1.74
0.8–0.94	Highly suitable (critical)	5 881	0.51	0.17	0.18	1.18

Discussion

Environmental predictors

The model results indicate that the distribution of *Encephalartos latifrons* is restricted predominantly by rainfall and geology. The Witpoort Formation and associated SQF is limited to the eastern parts of the GCFR, where rainfall is aseasonal or bimodal (peaks in spring and autumn), as compared with the winter-rainfall regions of the western parts of the Fynbos Biome. Modern-day cycads were originally thought to be climate relicts whose range contracted to refuge habitats during past climate-change events (Treutlin et al. 2005) – specifically a shift from the warm 'equable' late Miocene climate to a cooler climate with more seasonal precipitation, characteristic of the present day. More recent studies suggest that cycads have diversified since the Miocene (Nagalingum et al. 2011; Salas Leiva et al. 2013; Yessoufou et al. 2014) and have successfully occupied more xeric habitats along with other species adapted to greater aridity such as C4 grasses and succulents (Fragniere et al. 2015; Gutiérrez-Ortega et al. 2017). Nevertheless, some cycads remain restricted to more mesic habitats (Gutiérrez-Ortega et al. 2017) and this is likely the case for *E. latifrons* which appears restricted to the upper range of the mean annual precipitation for SQF vegetation, at 220–820 mm (Rebelo et al. 2006). Comparable responses to climatic variables were seen in the distributions of 88 species of *Leucadendron* proteas within the GCFR (Thuiller at al. 2004). Gradients of aridity were recognised as a strong factor affecting *Leucadendron* species distributions, followed by the seasonality of water availability, heat, and cold stress (Thuiller et al. 2004). Thuiller et al. (2004) further suggested that stress-tolerant *Leucadendron* species are usually slow-growing and range-restricted, often occurring at the edge of environmental gradients, befitting the life-history characteristics and distribution of *E. latifrons*.

Populations of *E. latifrons* appear to be restricted to quarzitic rock outcrops owing to their slow life history (less interspecific competition), dual fire avoidance/tolerance, and stress-tolerance strategies (first author's unpublished data). Accordingly, an albedo index was included in the model. It is not certain why albedo was not an important predictor for *E. latifrons* habitat in the broad-scale model, but this factor should be included in a finer-scale model for analysing local population distribution. Indices of habitat rockiness and fire-frequency were poor predictors in the case of other cycad species growing in arid-zone vegetation types in Australia (Preece

et al. 2007). Though fire is an important environmental disturbance, its frequency was not included in the model here yet should be considered in local-scale modelling, depending data availability. SQF (also known as Grassy Fynbos) is prone to frequent fires, which includes the two core *E. latifrons* suitable habitat areas identified by the model. A high fire-frequency in the core *E. latifrons* area (Eastern Inland Fire Zone) is in contrast to the fire frequency nearer the coast (South-Eastern Coastal Zone), where marginally suitable habitat was identified. The cycads in this coastal region may be outlier populations, based on interpretation of the model results predicting areas of marginally suitable habitat for *E. latifrons*. Finer-scale modelling may reveal smaller patches of suitable habitat in the coastal area with the inclusion of data for soils, fire history, and other factors not included in the broad-scale model.

Conservation decisions

Translocation site

Based on the results of the SDM, the symbol (+) indicates that the objective was met by the reserve, and the symbol (–) means it was not met (Table 2.4). The 1993 decision to translocate confiscated plants to the Waters Meeting Nature Reserve was assigned the symbol (–) for objective (a) in Table 4. The reserve's vegetation type and the characteristics of the underlying geology resulted in a habitat suitability score of 0 (highly unsuitable) in the SDM. Vegetation in this 4 247-ha reserve consists of Kowie Thicket and Albany Coastal Belt vegetation (Hoare et al. 2006; Stickler and Shackleton 2014) overlying the Weltevrede Formation (oldest formation of the Witteberg Group). Stickler and Shackleton (2014) mention that two *Encephalartos* species are found on the reserve, *E. altensteinii* and *E. latifrons*, but fail to mention that *E. latifrons* was artificially translocated there (Daly et al. 2006). The results indicate that the geological and vegetation features of this reserve mark it as unsuitable for *E. latifrons*. The primary difference between the Witpoort Formation (an important predictor for *E. latifrons* distribution) and the Weltevrede Formation (the main geological group underlying the Waters Meeting Nature Reserve) is the proportion of quartzite to shales: the Witpoort Formation has a far greater proportion of quartz arenites (>85%), in contrast to the Weltevrede Formation where shales occur as the greater proportion (Booth 2002). The quartz arenites of the Witpoort Formation form the weathered rocky outcrops to which species like *E. latifrons* and other Fynbos paleoendemics (such as the Near Threatened

tree *Oldenburgia grandis*) are currently restricted (Meadows and Dewey 1986). Waters Meeting Nature Reserve is a formal protected area (+) but is approximately 20 kilometres from the origin population of the translocated plants (–), which is relatively far given the species' highly restricted distribution. Moreover, no historical records suggest that *E. latifrons* has ever occurred within the reserve's area. Security from theft is low (+) since access to the reserve is restricted and closely controlled. Lastly, the possible genetic contamination of wild plants at the translocation site is high (–) as it falls within the natural distribution range of *E. altensteinni* (Stickler and Shackleton 2014).

Table 2.4 Table showing whether or not the defined conservation objective was met, based on the results of the species distribution model (SDM), for two conservation decisions made by South African authorities in regard to the placement of *Encephalartos latifrons* wild plants in 1993 (cf. Table 2.2)

	Recommendation informed by the SDM	
Objectives	*Translocation site for mature plants*	*Restoration site for wild seedlings*
	Waters Meeting Nature Reserve	Roundhill Nature Reserve
a. Survival prospect of the specimens (i.e. suitability of habitat)	–	–
b. Formal protected area	+	+
c. Proximity to the original population	–	+
d. Security from plant thefts	+	–
e. Possible genetic contamination of wild population	–	+

Restoration site

The decision to choose the Roundhill Nature Reserve as a restoration site for wild cycad seedlings was assigned the symbol (–) for objective (a) in Table 4. The reserve is situated in the middle of a Witpoort Formation quartzite ridge (forming the Kap River Mountains) that extends in a continuous band towards the coast. However, the reserve is overlaid by the remains of a limestone deposit belonging to the Bathurst Formation

(Algoa Group), resulting in a habitat-suitability score of 0 in the SDM. The *E. latifrons* seedlings were planted on this limestone deposit (or koppie) (Donaldson 2003) and none have survived. The site is approximately 13 km from the original population (+), which is relatively close to the remaining wild population. The Roundhill Nature Reserve is a formal protected area (+), security there is inadequate (–). In addition, there is no historical record of *E. latifrons* or any other *Encephalartos* species on the reserve, thus the possibility of genetic contamination would be low (–) had the plants survived.

Following the definition of conservation objectives, Guisan et al. (2013) recommend defining the possible actions to be taken. Three possible actions for the surviving translocated plants at the Waters Meeting Nature Reserve are: 1) Keep the plants where they are, although in what is predicted to be unsuitable habitat. 2) Re-translocate the plants to a more suitable site, as predicted by the model and potentially reaffirmed by a finer-scale SDM and/or expert opinion. 3) Re-translocate the plants back to the wild population from where they originated. Any future restoration projects should include choosing a suitable conservation site based on SDM predictions and expert opinion; actions may also include shifting policy decisions to encompass stewardship programs on both private and state land.

Next, the consequences of the conservation actions taken must be examined. There is a direct consequence to having the translocated plants at the Waters Meeting Nature Reserve remain in what is considered unsuitable habitat for *E. latifrons*. The plants will remain isolated with no connectivity to extant populations and are unlikely to survive beyond the lifespan of the existing cluster; thus, a self-sustaining cycad population there is unlikely. If the decision is made to move the plants to an area considered as more suitable habitat, it is possible that some of the mature plants will not survive translocation. Anecdotal evidence suggested mean mortality rates among translocated *Encephalartos* species as high as 67% (Vice 1995). The original survival rate for the confiscated *E. latifrons* used as an example in this study was 21% after 18 months of monitoring (Vice 1995). Moving the plants back to the original population also creates the risk of introducing pathogens/pests into the source population (Maunder 1992). Restoring seedlings into areas considered unsuitable habitat exacerbates the risk of extinction for the species if the restoration fails. There are also risks from inaction when available plants are not used for restoration because information on suitable habitat is lacking.

Finally, a trade-off analysis builds on the identified consequences of the actions (Guisan et al 2013). In the present case, the translocated plants at the Waters Meeting Nature Reserve do not contribute to the overall conservation of the species as they are likely to remain a functionally extinct population. The trade-off involves the risk of removing them from the site to a more suitable site, in terms of habitat and connectivity to the original population, which may also provide an opportunity to achieve restoration of the pollinators and eventually a self-sustaining population of cycads. Overall, the risks from inaction and/or the restoration of seedlings to areas of unsuitable habitat are a trade-off against the time needed to plan and research appropriate areas for the introduction of *E. latifrons*.

A population and habitat viability assessment for *E. latifrons* (Daly et al. 2006) recommended the Kap River Nature Reserve as a translocation/restoration site for plants sourced from outlier *E. latifrons* groups closer to the coast. While the SDM results did not reveal the reserve to be suitable for *E. latifrons*, this may be more a function of model scaling rather than the occurrence of suitable habitat, based on information in the literature and historical records for the reserve. Towards the coast, areas of SQF increasingly become smaller, patchier, and more isolated from the larger areas inland (Lubke et al. 1986); local-scale modelling would be needed to tease out the suitable areas. Finer-scale modelling, including data on soils, the 1:10 000 geological layer, vegetation and an albedo index, may further refine the model to determine if the Kap River Nature Reserve contains any areas of suitable habitat. A floral survey of the reserve identified small patches of undisturbed Cape Fynbos (now classified as SQF) on the steep south-facing slopes of Witteberg quartzite (Cloete and Lubke 1999). The reserve contains three other species of *Encephalartos*: *E. altensteinii*, *E. caffer* and *E. trispinosus,* thus the threat of genetic contamination in other populations may exist. Permit records at the DEDEA indicated populations of *E. latifrons* on properties adjacent to the reserve, in the Kap River Conservancy (a cluster of privately owned farms aiming to conserve local biodiversity). The exact locality points could not be confirmed, but herbarium records point to the existence of a natural *E. latifrons* x *E. altensteinii* hybrid at Wylmington farm (a property now incorporated into the reserve), suggesting that there was once a *E. latifrons* populations in close proximity. Whether the geology and vegetation of the reserve, and that of the abutting conservancy, amounts to patches of suitable habitat for *E. latifrons* needs to be confirmed with finer-scale modelling. Therefore, the area may provide suitable habitat for cycad translocation and

restoration projects provided that conservation authorities are willing to shift policy decisions currently restricting the placement of *E. latifrons* exclusively on formally protected land. Biodiversity stewardship projects already make provision for this arrangement, yet require further formalisation between private landowners and conservation managers.

Conservation planning

Areas of suitable habitat for *E. latifrons* are poorly protected in the current network of formal state protected areas, as shown in the broad-scale model. The total area identified as suitable habitat may be slightly increased with finer-scale modelling, perhaps with smaller patches of SQF identified nearer the coast or on reserves, such as the Kap River Nature Reserve. Even so, it is proposed that formal protected areas will play a small role for *E. latifrons* conservation in the future, based on the areas of suitable habitat encompassed in the NPAES. No *E. latifrons* populations occur in formal protected areas (as currently known) except for those translocated there (Daly et al. 2006). The SQF is classified as Least Threatened throughout its range, with only 1% of the areas transformed (Rebelo et al. 2006) and approximately 32% of the vegetation type conserved (the conservation target is 23%). Margules and Pressey (2000) advise that areas containing rare and/or threatened species should be allocated protection status irrespective of their contribution to conservation targets, and they refer to these as 'commitment areas.' Another solution to the gaps in formal protected areas as regards rare species like *E. latifrons* (with many other rare and endangered species particularly prevalent in the Cape region: Cowling et al. [2003]) is the establishment of micro-reserves. Micro-reserves have played an important role in protecting rare and endangered flora in eastern Spain (Laguna et al. 2004), for example, and provision for the formation of these reserves (as 'special nature reserves') is accommodated within South African conservation legislation. The formal protected areas previously identified as '*E. latifrons* reserve' by Osborne (1995a) included the Waters Meeting Nature Reserve (incorporating the Bathurst State Forest), yet the present investigation found it is not representative of suitable habitat for *E. latifrons* based on the modelling results. The one formal protected area that stood out as containing critical habitat for *E. latifrons* is Beggar's Bush Nature Reserve—a conclusion supported by both the SDM results and historical records. The network of areas identified by the NPAES includes a slightly greater amount of suitable habitat for *E. latifrons*, although an essential

conservation gap remains around Grahamstown and the Kap River Mountain Range. Among all the conservation layers considered in this study, the CBA1 areas provide the largest area of suitable habitat for *E. latifrons*; unfortunately, these are not legally binding areas of conservation but their identification serves only as a guideline for conservation planning.

Future research

This study aimed to distinguish suitable from unsuitable habitat for *E. latifrons*, across the species' restricted distribution, using broad-scale modelling. Further refinement of this SDM is needed, particularly to discern where areas of suitable habitat become patchy towards the coast. This can be done with the use of finer-scale (30 m) climate, geology, soils, fire, albedo and vegetation indices. The greatest restriction to the modelling process was lack of climate data at a finer scale as well as detailed fire records. Nevertheless, the model output was able to identify core areas of *E. latifrons* habitat as well as important environmental predictors (e.g. rainfall and geology) influencing the species' distribution. Importantly, *E. latifrons* conservation must involve structured decision-making that also incorporates expert opinion and site visits (Fois et al. 2015) as well as the results of fine- or broad-scale species distribution modelling.

Climate-change modelling would be an important component of future population-distribution modelling for this species. The Fynbos Biome is predicted to contract within the distribution area of *E. latifrons* under a changing climate regime (Guo et al. 2017), and changing climate patterns are predicted to alter fire regimes across the Fynbos Biome (Altwegg et al. 2014). It is uncertain how well long-lived sprouting species like *E. latifrons* might withstand these changes, but integrated modelling of habitat suitability and demographics has improved our ability to predict shifts in distribution and the risks of extinction under the impact of climate change for many vulnerable plant species (Fordham et al. 2012).

Finally, making decisions that are in the best interest of rare threatened species are often limited by lack of scientific information, especially for extremely small populations (Meek et al. 2015). Combining historical data, expert knowledge and new technologies to aid conservation decision-making may be applied to other range restricted, endangered cycad species. Examples include *Ceratozamia zaragozae* (Castillo-Lara et al. 2017) and *Zamia inermis* (Iglesias-Andreu et al. 2017) among

others. Testing past conservation decisions is also necessary for adaptive conservation management of the worlds most threatened organisms (Marler and Lindström 2017).

References

Altwegg R, West A, Gillson L, Midgley GF (2014) Impacts of climate change in the Greater Cape Floristic Region. In: Allsop N, Colville JF, Verboom GA (eds) Fynbos: ecology, evolution and conservation of a megadiverse region. Oxford University Press, pp 299–320

Basson M (1991) Eerste verslag wat die bron en status van die *Encephalartos* spesies in die Trappe's Valley area in die Oos-Kaap aandui met spesiale verwysing na die *Encephalartos latifrons*. Cape Nature Conservation Survey Report, South Africa

Bergh NG, Verboom GA, Rouget M, Cowling RM (2014) Vegetation types of the Greater Cape Floristic Region. In: Allsop N (ed) Fynbos: Ecology, evolution and conservation of a megadiverse region. Oxford University Press, pp 1–25

Berliner D, Desmet P (2007) Eastern Cape Biodiversity Conservation Plan: technical report. Pretoria, South Africa

Berliner D, Desmet P, Hayes R (2007) Eastern Cape Biodiversity Conservation Plan Handbook. Department of Water Affairs and Forestry Project No 2005 – 012, King Williams Town

Booth PWK (2002) Thrust faults and fold vergence in the Palaeozoic Middle and Upper Witteberg Group, Cape Supergroup (Cape Fold Belt), Steytlerville: an interpretation of their relationship. South African J Geol 105:25–38

Bradley BA, Olsson AD, Wang O, Dickson BG, Pelech L, Sesnie SE, Zachmann LJ (2012) Species detection vs. habitat suitability: Are we biasing habitat suitability models with remotely sensed data? Ecol Modell 244:57–64

Brown JL (2014) SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol 5:694–700

Campbell BM (1986) Montane plant communities of Fynbos Biome. Vegetatio 66:3–16

Castillo-Lara P, Octavio-Aguilar P and Arturo De-Nova J (2017) *Ceratozamia zaragozae* Medellín-Leal (Zamiaceae), an endangered Mexican cycad: New information on population structure and spatial distribution. Brittonia 1-11

Chunco AJ, Phimmachak S, Sivongxay N, Stuart BL (2013) Predicting environmental suitability for a rare and threatened species (Lao Newt, *Laotriton laoensis*) using validated species distribution models. PLoS ONE 8:1–13

Cloete EC, Lubke RA (1999) Flora of the Kap River Reserve, Eastern Cape, South Africa. Bothalia 29:139–149

Convention on Biological Diversity (2011) Conference of the Parties Decision X/2: Strategic Plan for Biodiversity 2011-2020. https://www.cbd.int/decision/cop/?id=12268. Accessed 27 Oct 2017

Cowling RM (1983) Phytochorology and vegetation history in the south-eastern Cape, South Africa. J Biogeogr 10:393–419

Cowling RM, Pressey RL, Rouget M, Lombard AT (2003) A conservation plan for a global biodiversity hotspot - the Cape Floristic Region, South Africa. Biol Conserv 112:191–216

Daly, B., Donaldson, J.S., Friedmann, Y., Hahndiek, Q., King, N. Newton, D. and Southwood, A. (editors) (2006) Population and habitat viability assessment for the Albany cycad (*Encephalartos*

latifrons). Conservation Breeding Specialist Group (SSC /IUCN) / CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg

DEA (2011) Biodiversity Management Plan for Albany cycad, *Encephalartos latifrons*. National Environmental Management: Biodiversity Act (10/2004): South African Government Gazette No. 34388

DEA (2015) Biodiversity Management Plan for 11 Critically Endangered and 4 Endangered *Encephalartos* species. Government of South Africa, South Africa

DEA (2014) National Strategy and Action Plan for the Management of Cycads. Pretoria, South Africa

Donaldson JS (ed) (1995) Cycad Conservation in South Africa: Issues, Priorities and Actions. 1–27 Cycad Society of South Africa, South Africa

Donaldson JS (ed) (2003) Cycads. Status survey and conservation action plan. IUCN/SSC Cycad Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Townsend Peterson A, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS and Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data Ecography 29:129–151

ESRI (2012) ArcGIS: Environmental Systems Research Institute, Redlands California.

Fois M, Fenu G, Lombraña AC, Cogonia D, Bacchetta G (2015) A practical method to speed up the discovery of unknown populations using species distribution models. J Nat Conserv 24:42–48

Fordham DA, Resit Akçakaya H, Araújo MB, Elith J, Keith DA, Pearson R, Auld TD, Mellin C, Morgan JW, Regan TJ, Tozer M, Watts, MJ, White M, Wintle, BA, Yates, C and Brook BW (2012) Plant extinction risk under climate change: Are forecast range shifts alone a good indicator of species vulnerability to global warming? Glob Chang Biol 18:1357–1371

Fourcade Y, Engler JO, Rodder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE 9:1–14

Fragniere Y, Bétrisey S, Cardinaux L, Stoffel M and Kozlowski, G (2015) Fighting their last stand? A global analysis of the distribution and conservation status of gymnosperms. Journal of Biogeography 42(5): 809–820

Gogol-Prokurat M (2011) Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. Ecol Appl 21:33–47

Graham CH, Elith J, Hijmans RJ, Guisan A, Townsend Peterson A, Loiselle BA and Nceas T (2008) The influence of spatial errors in species data used in distribution models. J Appl Ecol 45:239–247

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan T, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin, TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435

Gutiérrez-Ortega JS, Yamamoto T, Vovides AP, Pérez-Farrera MA, Martínez JF, Molina-Freaner F, Yasuyuki Watano Y and Kajita T (2017) Aridification as a driver of biodiversity: a case study for the cycad genus *Dioon* (Zamiaceae). Annals of Botany 00:1 - 15

Guo D, Desmet PG, Powrie LW (2017) Impact of the future changing climate on the southern Africa biomes, and the importance of geology. J Geosci Environ Prot 5:1–9

Hijmans RJ, Cameron SE, Parra JL, Jones PG and Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hoare D, Mucina L, Rutherford MC, Vlok JH, Euston-Brown D, Palmer AR, Powrie LW, Lechmere-Oertel RG, Proches SM, Dold AP and Ward RA (2006) Albany Thicket Biome. In: Mucina L, Rutherford MC (eds) The vegetation of South Africa, Lesotho and Swaziland, 1st edition. South African National Biodiversity Institute (Strelitzia 19), Pretoria, South Africa, pp 541–567

Hoffmann M, Hilton-taylor C, Angulo A, Böhm M, Brooks, TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Katariya V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vie J-C, Aguiar JM, Allen DJ, Allen GR and Amori G (2010) The impact of conservation on the status of the world's vertebrates. Sci New Ser 330:1503–1509

Iglesias-Andreu LG, Octavio-Aguilar P, Vovides A, Meerow A, Núñez de Cáceres-González FF and Galván-Hernández DM (2017) Extinction risk of *Zamia inermis* (Zamiaceae): a genetic approach for the conservation of its single natural population. International Journal of Plant Sciences 178: 715–723

IUCN (2010) IUCN Red List of Threatened Species. In: IUCN Glob. Species Program. Red List Unit. http://www.iucnredlist.org. Accessed 24 Oct 2017

Jackson CR, Robertson MP (2011) Predicting the potential distribution of an endangered cryptic subterranean mammal from few occurrence records. J Nat Conserv 19:87–94

Kauth RJ, Thomas GS (1976) The tasselled cap: a graphic description of the spectral-temporal development of agricultural crops as seen by Landsat. LARS Symposia. Paper 159

Kleynhans CJ, Thirion C, Moolman J (2005) A level 1 river ecoregional classification system for South Africa, Lesotho and Swaziland. Pretoria, South Africa

Kraaij T, Wilgen BW Van, Van Wilgen BW (2014) Drivers, ecology, and management of fire in fynbos. In: Allsop N, Colville JF, Verboom GA (eds) Fynbos: ecology, evolution, and conservation of a megadiverse region. Oxford University Press, pp 47–72

Kumar S, Stohlgren TJ (2009) Maxent modeling for predicting suitable habitat for threatened and endangered tree *Canacomyrica monticola* in New Caledonia. J Ecol Nat Environ 1:94–98

Laguna E, Deltoro VI, Pèrez-Botella J, Perez-Rovira P, Serra LI, Olivares A, Fabregat C (2004) The role of small reserves in plant conservation in a region of high diversity in eastern Spain. Biol Conserv 119:421–426

Lahoz-Monfort JJ, Guillera-Arroita G, Milner-Gulland EJ, Young RP and Nicholson E (2010) Satellite imagery as a single source of predictor variables for habitat suitability modelling: How Landsat can inform the conservation of a critically endangered lemur. J Appl Ecol 47:1094–1102

Lubke RA, Everard DA, Jackson S (1986) The biomes of the Eastern Cape with emphasis on their conservation. Bothalia 16:251–261

Marcer A, Saez L, Molowny-Horas R, Pons X, Pino J (2013) Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. Biol Conserv 166:221–230

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:242

Marler TE and Lindstrom AJ (2017) First do no harm. Communicative and Integrative Biology, 10:5-6, e1393593

Maunder M (1992) Plant reintroduction: an overview. Biodivers Conserv 1:51–61

Meadows ME, Dewey FE (1986) The relationship between soils and vegetation, Beggar's Bush Forest Reserve, Grahamstown. South African Geogr J 68:144–153

Meeka MH, Wells C, Tomalty KM, Ashander J, Cole EM, Gille DA, Putmand BJ, Rose JP, Savoca MS, Yamane L, Hull JM, Rogers DL, Rosenblum EB, Shogren JF, Swaisgood RR and May B (2015) Fear of failure in conservation: The problem and potential solutions to aid conservation of extremely small populations. Biological Conservation 184: 209–217

Nagalingum NS, Marshall CR, Quental, TB, Rai HS, Little DP and Mathews S (2011) Recent synchronous radiation of a living fossil. Science 334: 796 - 799

Osborne R (1995a) An overview of cycad conservation in South Africa. In: Donaldson JS (ed) Cycad conservation in South Africa: issues, priorities and actions. Cycad Society of South Africa, Stellenbosch, South Africa. pp 1–7

Osborne R (1995b) Confiscated plants: where can they best be used in the interest of conservation? In: Donaldson JS (ed) Cycad conservation in South Africa: issues, priorities and actions. Cycad Society of South Africa, Stellenbosch, South Africa. pp 26–27

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117

Phillips S (2010) A brief tutorial on Maxent. Lessons Conserv 107–135

Preece LD, Duguid AW, Albrecht DE (2007) Environmental determinants of a restricted cycad in central Australia, *Macrozamia macdonnellii*. Aust J Bot 55:601–607

Ravele AM, Makhado RA (2010) Exploitation of *Encephalartos transvenosus* outside and inside Mphaphuli Cycads Nature Reserve, Limpopo Province, South Africa. Afr J Ecol 48:105–110

Raxworthy CJ, Martinez-Meyer E, Horning N, Nussbaum RA, Schneider GE, Ortega-Huerta MA and Townsend Peterson A (2003) Predicting distributions of known and unknown reptile species in Madagascar. Nature 426:837–841

Razgour O, Hanmer J, Jones G (2011) Using multi-scale modelling to predict habitat suitability for species of conservation concern: the grey long-eared bat as a case study. Biol Conserv 144:2922–2930

Rebelo AG, Boucher C, Helme N, Mucina L and Rutherford MC (2006) Fynbos Biome. In: Mucina L, Rutherford MC (eds) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute., Pretoria, South Africa, pp 53–219

Roy DP, Wulder MA, Loveland TR, Woodcock CE, Allen RG, Anderson MC, Helder D, Irons JR, Johnson DM, Kennedy R, Scambos TA, Schaaf CB, Schott JR, Sheng Y, Vermote EF, Belward AS, Bindschadler R, Cohen WB, Gao F, Hipple JD, Hostert P, Huntington J, Justice CO, Kilic A, Kovalskyy V, Lee ZP, Lymburner L, Masek JG, McCorkel J, Shuai Y, Trezza R, Vogelmann J, Wynne RH, Zhu Z (2014) Landsat-8: science and product vision for terrestrial global change research. Remote Sens Environ 145:154–172

Salas-Leiva DE, Meerow AW, Calonje M, Griffith MP, Francisco-Ortega J, Nakamura K, Stevenson DW, Lewis CE and Namoff S (2013) Phylogeny of the cycads based on multiple single-copy nuclear

genes: congruence of concatenated parsimony, likelihood and species tree inference methods. Annals of Botany 112(7): 1263 - 1278

Shone RW, Booth PWK (2005) The Cape Basin, South Africa: a review. J African Earth Sci 43:196–210

Soberón J, Townsend Peterson A (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Informatics 2:1–10

South African Government (2010) National Protected Area Expansion Strategy for South Africa 2008: priorities for expanding the protected area network for ecological sustainability and climate-change adaptation. Government of South Africa, Pretoria, South Africa

Stickler MM, Shackleton CM (2014) Local wood demand, land cover change and the state of Albany thicket on an urban commonage in the Eastern Cape, South Africa. Environ Manage 55:411–422

Swart C (2017) The globetrotting Albany cycad. Veld Flora 103:79–80

Thuiller W, Lavorel S, Midgley G, Lavergne S and Rebelo T (2004) Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. Ecology 84:1688–1699

TRAFFIC (2003) Review of significant trade cycads. PC14 Doc. 9.2.2 Annex 1. pp 3 - 44

Treutlein J, Vorster P, Wink M (2005) Molecular relationships in *Encephalartos* (Zamiaceae, Cycadales) based on nucleotide sequences of nuclear ITS 1and2, Rbcl, and genomic ISSR fingerprinting. Plant Biol 7:79–90

van Wyk, Smith GF (2001) Regions of floristic endemism in southern Africa: a review with emphasis on succulents. Umdaus Press, South Africa

Vice A (1995) *Encephalartos altensteinii*: a massive rape and recovery. Encephalartos 1:15–19

Williams JN, Seo C, Thorne J, Nelson JK, Erwin S, O'Brien JM and Schwartz MW (2009) Using species distribution models to predict new occurrences for rare plants. Divers Distrib 15:565–576

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A and NCEAS Predicting Species Distributions Working Group (2008) Effects of sample size on the performance of species distribution models. Divers Distrib 14:763–773

Yeld J (2014) Thieves make off with cycads worth about R500 000. In: Cape Argus https://www.pressreader.com/south-africa/cape-argus/20140807/282510066712732. Accessed 15 Sep 2017

Yessoufou K, Bamigboye SO, Daru BH and van der Bank M (2014) Evidence of constant diversification punctuated by a mass extinction in the African cycads. Ecology and Evolution 4: 50 - 58

CHAPTER 3

Population structure and survival of the critically endangered *Encephalartos latifrons*

[Target journal: South African Journal of Botany]

Abstract

This study investigates the population structure and life history traits of the Critically Endangered cycad, *Encephalartos latifrons*. Populations of *E. latifrons* are considered functionally extinct and not capable of natural recruitment in the wild. Previous research and survey reports have suggested that this is true for all *E. latifrons* populations since evidence of natural recruitment has not been witnessed in almost 30 years. The discovery of a previously undocumented population of *E. latifrons* has however made it possible to build on previous research into the life history and regeneration capabilities of this captivating species. A demographic census was undertaken over 5 years between 2013 and 2017 on the previously undiscovered population. Population characteristics of the 'new' population were compared to earlier studies in 2010 of a well-known and intensively managed population. Results of this study show that at least one remaining population of *E. latifrons* is stable and increasing under current environmental conditions through natural recruitment. The discovery of a "new" *E. latifrons* population has however uncovered many more questions and further research is needed. Information on the life history of *E. latifrons*, particularly its response to fire, can be used to inform conservation management decisions in an age where the impact of climate change is predicted to have a major influence in Mediterranean-climate regions.

Keywords: life-history, fire, Fynbos, resprouter, demography, endangered

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 hotpots 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, amongst 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 (Malaisse 1995; Wilson 2002; Donaldson 2003; Octavio-Aguilar et al. 2009; Ogwal 2017). Rare species with small world populations are at a greater risk to extinction from a number of threats such as changes to the environment, disruption of mutualisms, and genetic threats to name a few (Oostermeijer 2003; Matthies et al. 2004).

Cycads are generally long-lived woody perennials, have slow life histories and are dioecious but vary in aspects such as growth form, fecundity, longevity, pollination biology, drought tolerance and fire response. 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, although they tend to mast seed in response to environmental cues (e.g. *E. cycadifolius*). 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. *E. villosus*). Many cycad species display clumped distributions often as a result of poor seed dispersal (Watkinson and Powell 1997; Pérez Farrera and Vovides 2004; Pérez-Farrera et al. 2006; Octavio-aguilar et al. 2008; Álvarez-Yépiz et al. 2011, 2014; Hall and Walter 2013). It has been suggested that some fleshy-fruit producing plants such as

cycads, relied on now extinct Pleistocene megafauna to disperse large seed loads over long distances, possibly in herds (Guimarães et al. 2008; Malhi et al. 2016). In Australia, extinct flightless birds such as *Genyornis* may have been responsible for dispersing large seeds in this way, similar to the dispersal mechanisms displayed by present day species such as emus and cassowaries. The result was the formation of new cycad groves rather than the dispersal of individual seeds (Hall and Walter 2013). In South Africa, the closest possible flightless bird disperser may have been the ostrich. Ostrich bones, dating back to over 12 000 years, have been found in the Nelson Bay Cave on the southern coast (Klein 1972), suggesting that their distribution extended much farther south than it does today. This is probably due to the then open grassland habitat in the region at the time during the late Pleistocene (Steele 2007). Poor dispersal possibly owing to the extinction of megafaunal dispersers and/or range contraction of present day dispersers 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 (Álvarez-Yépiz et al. 2011, 2014). This advantage is however 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; Lamont and Downes 2011). Species growing in these environments survive fire by sprouting, a tolerance trait considered responsible for driving persistence at the plant level (Clarke et al. 2013). Resprouting is seen as correlated to persistence, where it is considered a trade-off against growth and reproduction (Bond and Midgley 2001; Vesk and Westoby 2004). Lamont et al. (2011) however suggest that there is little evidence supporting the fact that carbohydrates stored to support resprouting after a fire is at the expense of fecundity among resprouting species in fire-prone environments. 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). Knowledge of the effects of fire regime (frequency, season and intensity) on cycad populations in Mediterranean-climate ecosystems is lacking in the published literature, including how climate change and future fire regimes may influence cycad populations in the long-term.

Fires and fynbos

Mediterranean climate regions such as the Greater Cape Floristic Region (GCFR) typically burn on a 5 – 50-year cycle averaging 15 – 25 years (Rebelo et al. 2006). However, 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 hot, dry 'berg' winds occurring mostly in winter (May – August) (Cowling and Richardson 1995; Kraaij and Wilgen 2014) but are generally less seasonal than in the west (Van Wilgen 2013). Fires at a higher frequency (4 – 6 years) tend to favour the resprouting life history with lower recruitment after fires in older vegetation (Rebelo et al. 2006). Topography can also have an influence on fire intensity where rocky habitats result in cooler fires allowing for increased canopy survival (Clarke 2002; Rebelo et al. 2006). These rocky habitats may act as fire refugia for tree species persisting in fire prone environments (Adie et al. 2017). Typical fynbos fire avoider fynbos species include *Heeria argentia*, *Maytenus oleiodes*, *Podocarpus elongatus* and *Aloe mitriforma* (Kraaij et al. 2014).

Conservation of *Encephalartos latifrons* in South Africa

Historically, 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 by harvesting wild plants as well as habitat destruction over the years (Daly et al. 2006). The formal conservation of *E. latifrons* started when government authorities realised that pressure on wild cycad populations was reaching a critical level in the early 1970's mostly due to the harvesting of wild plants. This was evident from letters written to the then Director of Nature Conservation in 1973 (Swart 2017). This, in part, prompted the promulgation of conservation legislation in the Cape Province, where *E. caffer*, *E. latifrons* and *E. woodii* were declared endangered (Nature and Environmental Conservation Ordinance No. 19 of 1974). Under this legislation, any activity involving endangered cycad species was prohibited. It was 17 years later in 1991, that the conservation authorities undertook an extensive survey of all *E. latifrons* populations in the Eastern Cape Province of South Africa with the realisation that there was an urgent need to record all known *E. latifrons* populations so that they could be monitored and conserved. Records show that a large population of *E. latifrons* disappeared from the Beggars Bush state reserve between

1988 and 1990 as a result of theft and urgent action was needed to prevent the extirpation of further populations. The survey report mentions a total of 63 adult *E. latifrons* individuals found in five populations in the natural distribution area (Basson 1991). Three of the 'populations' had a single plant at each locality, while the remaining two populations had between 26 and 30 adult plants. At the time of the survey, the sex ratio for all 63 plants found across the *E. latifrons* distribution range was 4 males to 1 female. Four natural seedlings were found in one population whereas all other populations had no seedlings. It was not long after this survey that plants were illegally harvested from one of the populations (the only population where natural seedlings had been recorded as part of the 1991 survey). Fortunately, the consignment of stolen plants was confiscated and the *E. latifrons* plants translocated to a protected area approximately 15 kilometres from the original site.

It was much later in 2004 that legislation came into effect imposing harsher fines and potential imprisonment concerning illegal activities involving cycads and other threatened and/or protected species (NEMBA Act 10/2004: Threatened and/or Protected Species Regulations). This new legislation made provision for the development of Biodiversity Management Plans for species (BMP-S) listed as Critically Endangered. Once in place, the BMP allows for the trade in seedlings propagated from wild parent stock to commence and authorises the artificial management of wild plants on private farms as an incentive to conserve the few remaining plants in the wild. This was based on the premise that *E. latifrons* is functionally extinct and not capable of natural recruitment in the wild, partly due to failed natural pollination (Giddy 1974; Daly et al. 2006). The development of the BMP-S was based on a Population and Habitat Viability Assessment multi-stakeholder workshop for *E. latifrons* held in 2006 with 21 participants representing landowners, government conservation authorities, cycad collectors, conservation NGO's and researchers and according on all the information available for the species at the time.

A key concept addressed in this chapter is that not all *E. latifrons* populations are functionally extinct and that some are capable of natural regeneration in the wild. I explore if there is a difference in how populations are structured in heavily managed and unmanaged populations. I also examine how fire affects growth, mortality and fecundity as well as the spatial structure of the life-history stages within the populations studied.

Materials and methods

Climate of study area

The climate of the study area reflects bimodal to aseasonal rainfall with a spring (September and November) and autumn (March and April) peak. The mean annual precipitation (MAP) for Suurberg Quartzite Fynbos ranges from 220 – 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 minimum number (5) of frost days (Rebelo et al. 2006).

Study species

Encephalartos latifrons (Zamiaceae) is an endemic cycad found in 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 with most populations highly fragmented (Department of Environmental Affairs 2011). It is an arborescent species able to reach heights of up to 3 meters. It is one of the slowest growing species 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* and *Loxostylis alata.* 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 confused with *E. arenarius*, having numerous triangular pungent lobes curving strongly downwards and inwards. Like all cycads, *E. latifrons* is dioecious with male and female cones developing on separate plants. The female plant produces one cone per stem whereas the male plant can have up to five cones on a single stem (this study). 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; this study). Seeds are large consisting of a woody kernel surrounded by a bright red fleshy sarcostesta. Pollen shedding takes place during the winter months between June and August. The female cone disintegrates spontaneously during the summer months of December/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 fertilization (Giddy 1974). Cycads therefore experience a form of Non Deep Morphophysiological dormancy associated with a poorly developed embryo at the time of seed shed (Xaba 2014).

Study sites

There are only three remaining *E. latifrons* populations currently known to exist (where there are more than two individual plants). This chapter focuses on two of these populations located at either extreme of the species distribution. Excluded in this population count are individual plants that remain scattered where once larger populations existed. The third population was not included in this study as access to the site was not granted by the landowner at the time when the study was undertaken. Individuals in the third population excluded from this study remain relatively scattered with only one female and no natural regeneration recorded from any survey.

The study populations are referred to as Population A and Population B (Table 3.1). Population A was included in the PHVA study as well as in the 1991 survey. Population B is undocumented and recently discovered and has not been included in any 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 Coastal Sour Grassveld (Lubke et al. 1986), Kowie Thicket and Albany Coastal Belt vegetation types (Hoare et al. 2006). The fire climate of this site is considered as the far eastern coastal zone (Kraaij et al. 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 et al. 2014). Population A exists in clusters across two properties divided by a game fence. The 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). Population B displays all *E. latifrons* morphological characteristics as described under the heading “Study Species”. The population is also found within the

natural distribution range of *E. latifrons* (Giddy 1974; Grobbelaar 2004). There are however slight morphological anomalies between this and other populations such as Population A and other more inland populations closer to Grahamstown. It is possible that this population may contain introgressed genotypes from a species such as *Encephalartos longifolius* or that it is a different "variety" from the other well-known populations. Variety in this case refers to the plasticity of various morphological features some cycad species dislay in populations at various geographical localities (Walters and Osborne, 2004). It is often an "informal" reference to a population displaying unique morphological characteristcs at a certain location, compared to other populations of the same species. For example, *E. latifrons* individuals originating from the Trappes Valley area are referred to as the Trappes Valley variety or form whereas wild individuals originating from the Greenhills area are referred to as the Greenhills variety due to certain morphological differences individuals tend to display. It is unknown whether these varieties are genetically distinct populations and this would need to be confirmed through genetic studies populaitons across the species distribution range. Population B does not fall within what is known to be the natural distribution range of *E. longifolius* (Giddy 1974; Grobbelaar 2004) but similarities in habitat requirements between *E. longifolius* and *E. latifrons* do exist. Both *E. latifrons* and *E. longifolius* are found within the Fynbos Biome persisting in fire-prone ecosystems associated with rocky outcrops in the Eastern Cape Province of South Africa. There may be an overlap between the species distribution of *E. latifrons* and *E. longifolius* but this will only be confirmed by further research through modelling the distributions of both species and undertaking genetic studies.

Population A and B both occur within the 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 3.1 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*
Altitude (masl)	115 - 176	115 - 176	660 - 725	620 - 630	625 - 635	515-520	480-485	480-495
Aspect	SW	S	N	E	N	E	SW	NE
Disturbance level	High	High	Low	Low	Low	Medium	Low	Medium
Disturbance type	Intensive management	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
History	Population intensively managed for many years. Male and female plants uprooted and planted closer together in 1980.	The only site where natural seedlings were discovered in 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.
Land use	Livestock and crop farm	Game Reserve	Informally protected area with light recreational use					
Fire Frequency	> 15 years		1 – 3 years					
Fire climate zone (Kraaij et al., 2014)	Far Eastern Coastal Zone		Eastern Inland Zone					
Mean Annual Precipitation (Puttick et al. 2011; R. Rowswell pers. comm)	720 mm		767 mm					

Demographic census

A 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 demographic analysis of Population A at site 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. A census of Population B was undertaken from 2013 to 2017 where all plants found were tagged, stem height and circumference measured, number of stems counted, coning events 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 plants 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/growth/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 and where possible, any growth in stem height between the first census in 2013 and the last census in 2017. The youngest leaves were tagged at each census making it possible to measure growth between the first and last leaf flush over the study period for plants with a measureable stem. 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. In similar cases where growth and/or age were difficult to determine in some cycad species, plants were dissected and cone domes counted (Vovides 1990). This was not an option for this study due to the rarity and endangered status of the species. Seedlings in Population B were without a measurable stem. Seedling height was therefore recorded as the size of the plant from the ground to the tip of the largest 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.

Determining stage classes

For studies on long-lived woody tree species, the use of morphological characteristics that describe stage rather than age is the preffered 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 thesis 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 divided into two categories, se1 and se2 and without a measurable stem. Se1 plants included the shortest individuals with leaf lengths of 5 to 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 (Plate 3.1). Se 1 seedlings were plants in the youngest stage class having germinated within the last 2 years with between 1 to 4 leaves on each plant. These are the smaller leaves before “true” leaves develop (Giddy 1974).

Plate 3.1 Seedling from the se1 stage with two young leaves differing in shape and margins from the older stages

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 plants 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 to 4 suckers 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 therefore tended to have more stems and a greater potential to bear cones and reproduce. A two sample Kolomogorov-Smirnov test was used to test whether the structure of Population A and B differed significantly. Data was analysed using the Real Statistics Resource Pack software (version 4.14) Zaiontz (2017).

Data analysis

A static life table was constructed for Population B based on female numbers according to Krebs (1978). Population A was excluded from the life table analysis as 10 females in the population was considered a low sample size to expect realistic results, particularly since it does not represent the original population (with the removal of 15 adult plants and/or stems 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. For plants in Population B where the sex of an individual was unknown, the sex ratio of known 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 (this was possible to calculate as seedlings in close proximity to the female are likely to be her offspring). The finite rate of mortality (q_x) was calculated as $(n_x-n_x+1)/n_x$ and killing power (k_x) as $\log10nx-\log10nx^{+1}$ 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 $\Sigma e^{-rx} l_x m_x = 1$ 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. Individuals surviving (0) or dying (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 meter in length and or height were calculated 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 the 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).

Results

Differences in the distribution of Population A and B did not differ significantly D (N=6;6) = 0.67, p = 0.07 despite Population A having no seedlings (Figure 3.1).

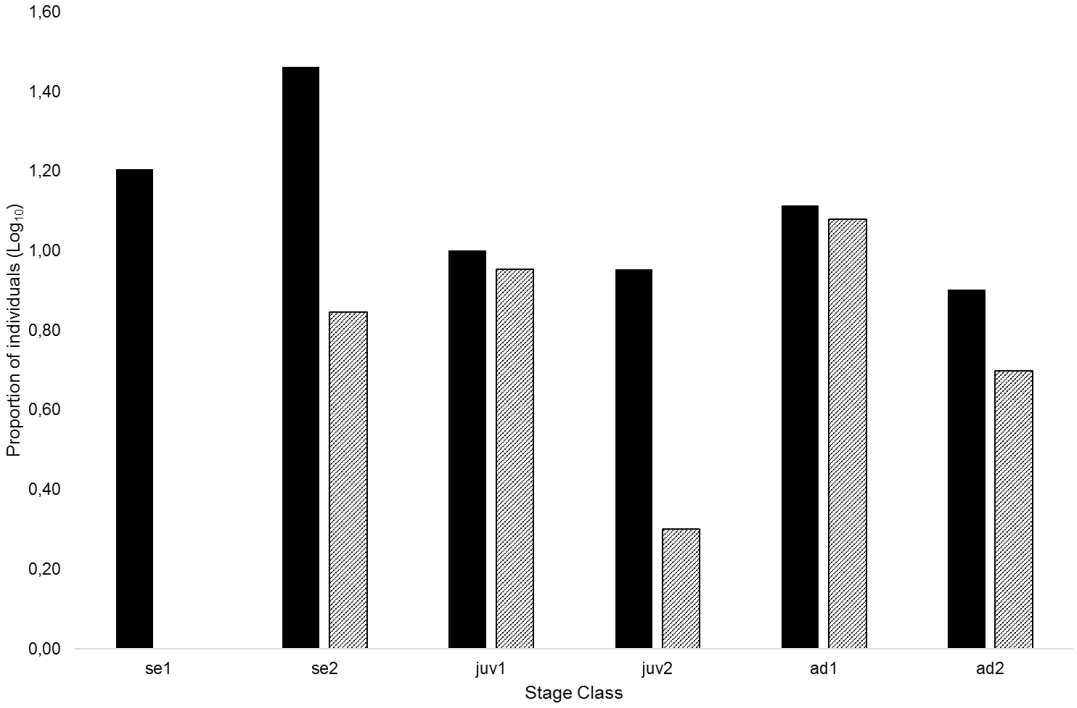


Figure 3.1 Structures of Population A (grey bars) and B (black bars) based on the proportion of individuals according to the stage classes se1 and se2 (seedlings), juv1 and juv2 (juveniles) and ad1 and ad2 (adults)

Population B has a healthy number of seedlings making up 55% of the population. At the time of the census in 2010, Population C did not have any plants in the smaller seedling (se1) stage class. 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 (Figure 3.2). Larger plants tend to have a multi-stemmed growth form. Cumulative stem height (i.e. the sum of individual stem height for each plant) was therefore used to construct the survivorship curve to refect the difference between the smaller single-stemmed plants and the larger multi-stemmed individuals.

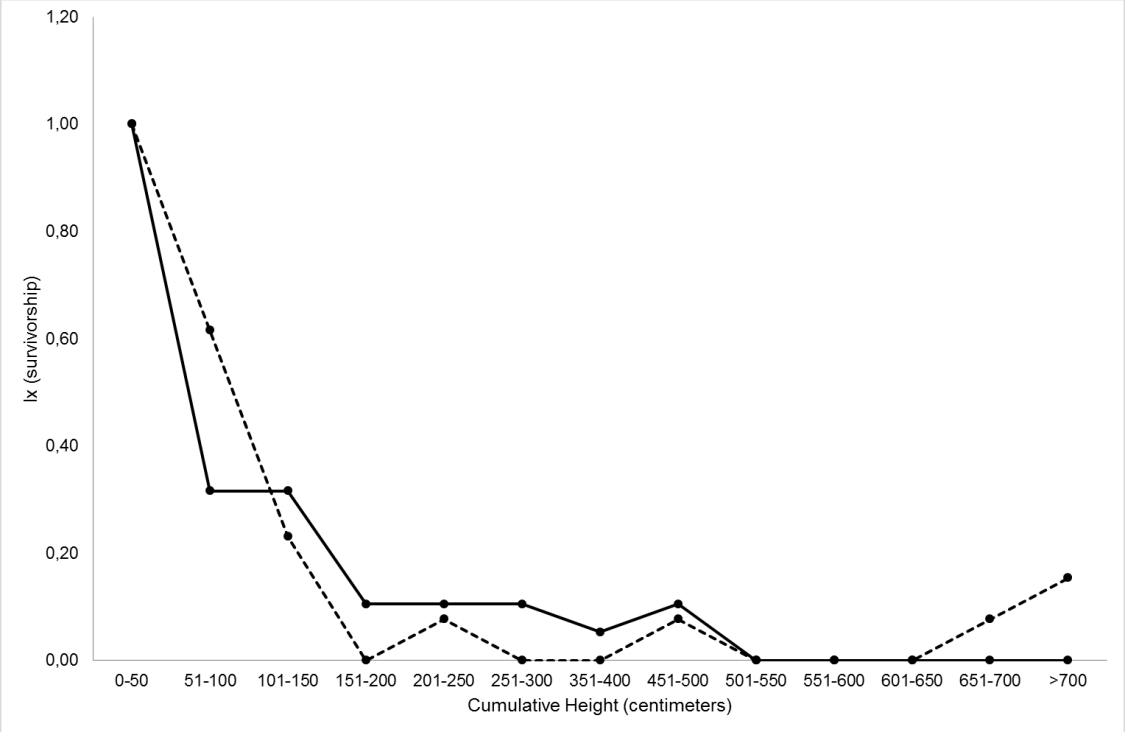


Figure 3.2 Survivorship curve for *Encephalartos latifrons* representing the cumulative height of individuals for each height class in Population A (dashed line) and Population B (solid line). The cumulative height of individuals (i.e. the sum of all stem heights) was categorised into height classes represented on the x-axis

Despite the challenges estimating a pattern of growth in *E. latifrons*, growth measurements from a few individuals made it possible to estimate growth over the study period. Mean juvenile (juv1) stem height increased by 0.63 (N = 2; SE = 0.38) cm yr^{-1}. Mean growth rate for adult plants in the a1 category was 1.50 (N = 5; SE = 0.14) cm yr^{-1} while for plants in the a2 category 1.75 (N = 2; SE = 0.83) cm yr^{-1}. Few individuals produced a flush of new leaves in the absence of fire. Growth in the absence of fire was almost impossible to determine, as the majority of plants were subjected to fire over the study period.

A female based life table for Population B is shown in Table 3.2. The highest rate of death (q_x) occurs in the early stage of the plants 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). This is in general agreement with the survivorship curve. The net reproductive rate (or replacement rate) per generation (R_0) indicates that the population is increasing on average by 2 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 3.2 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 (λ) 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
λ	1.47

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 ($Z = 14.98$; $p < 0.0005$). Figure 3.4 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).

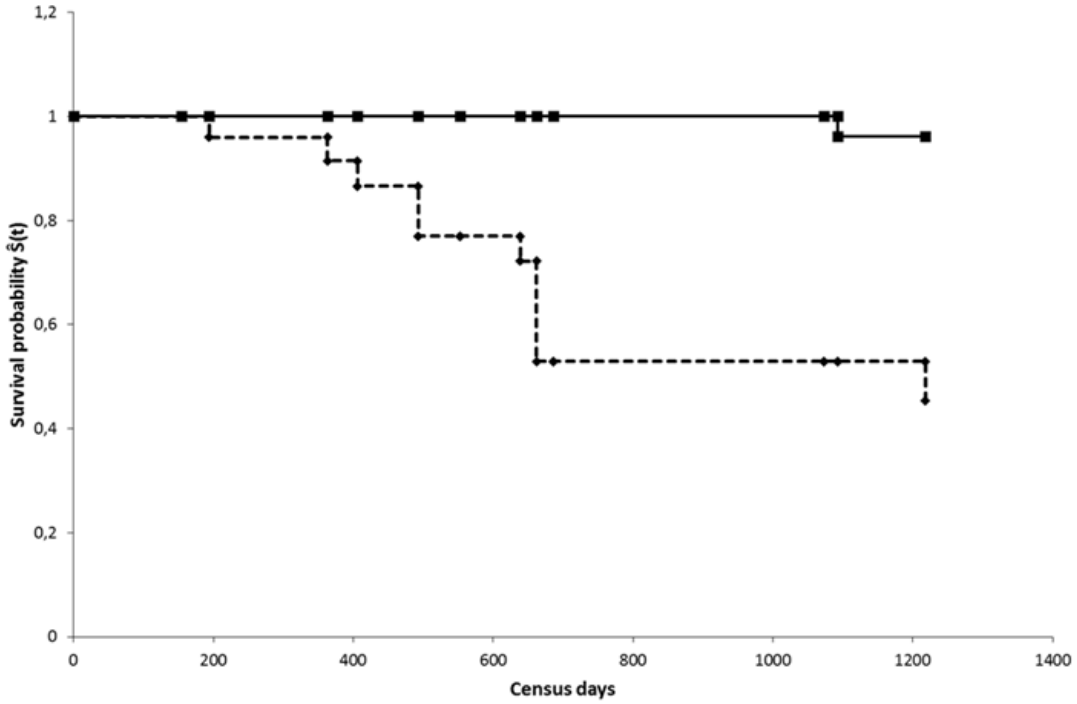


Figure 3.4 Kaplan-Meier probability of survival for the se1 (dashed line) and se2 (solid line) stage plants during the study period for Population B. Survival probability for juvenile and adult stages remains at 1 (not shown in this figure)

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 dense 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; $p < 0.05$; se = 0.015; lower = 0.0017; upper = 0.834). Survival against other environmental variables did not show any significant correlation.

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 2 females for every male. Information on coning frequency was not available for Population A. Coning frequency during the study period for Population B is shown in Table 3.3.

Table 3.3 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 (Plate 3.2 a). The plant experienced localised sprouting on the charred side of the stem and cone. In another instance, a female plant with 3 cones was infected with a pathogen (i.e. an unidentified fungus growing on all three cones), the female plant however survived. All three cones turned black and remained on the stem without disintegrating (Plate 3.2 b). The seeds on all these cones were malformed and unviable. Of the 9 cones produced by 6 females over the 5-year period, 1 cone was scorched by fire on one female and 3 cones (produced on three separate stems by another female) succumbed to a pathogenic fungus.

Plate 3.2 Localised sprouting from a charred area on the side of the stem and female cone in Population B: Site B6 (a). Black cones on female plant infected with a fungal disease (b)

The number of offspring per female in Population B ranged from 0 to 17 seedlings (Table 3.4). Site B6 consisted of two females with two males at a distance of 8 m and 17 m from the females respectively forming a close cluster of plants. The site however had no seedlings. Other female plants such as at site B4 had only one mature female plant with the closest male at a distance of 1439 m and 6 seedlings at the site. 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 ($r(8) = 0.23$, $p=0.28$).

Table 3.4 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

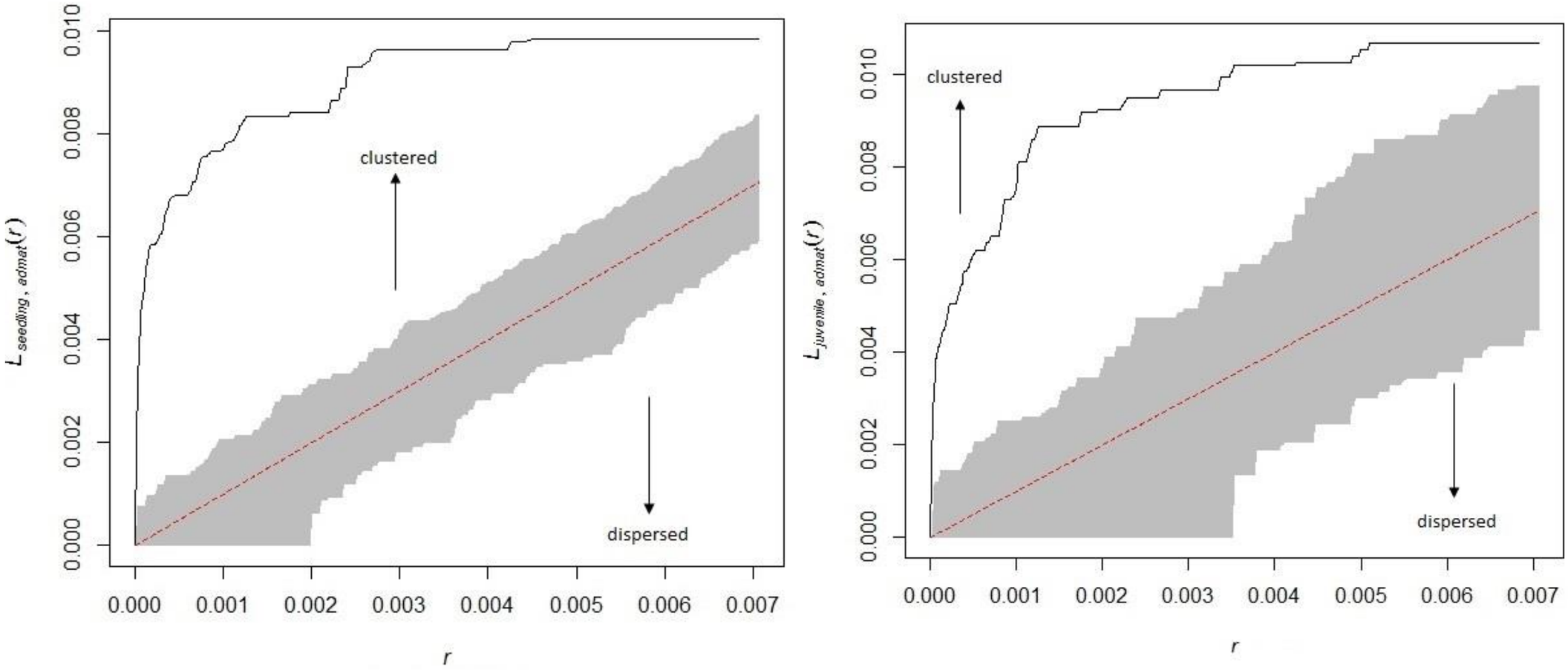
Spatial pattern

Overall, the ANN index value for Population B was 0.07 (z-score = -20.33, $p < 0.0001$) 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 3.5).

Table 3.5 ANN index of the different stage classes, z-score, and significance with observed and expected mean distances

Stage Class	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

Seedling and juvenile plants were strongly associated with the adult stages at all distances as shown by the Ripley K analysis in Population B (Figure 3.6).



F igure 3.6 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

Discussion

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* (Vovides 1990; Octavio-Aguilar et al. 2008), *Ceratozamia mirandae* (Pérez-Farrera et al. 2006), *Zamia debilis* (Negron-Ortiz and Breckon 1989), and *D. purpusii* (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 out is not known). There were however four natural seedlings recorded at site A2 before the poaching event in 1993. The estimated age of the seedlings was one years 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 however 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 less seedling numbers (Cousins et al. 2014).

Results of the life table analysis reveal that one population of *E. latifrons* is capable of natural regeneration, 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) is lower than other endangered cycad species such as *C. mirandae* at between 5.85 and 8.2 (Pérez-Farrera et al. 2006) but higher than populations of the Critically Endangered Mexican cycad *Ceratozamia zaragozae* 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* (Pérez-Farrera et al. 2006) and 0.89 for *C. zaragozae* (Castillo-Lara et al. 2017). This is in contrast to the endangered *D. sonorense* where all populations are showing signs of decline ($r < 1$ and $r < 0$) (Álvarez-Yépiz et al. 2011). The crucial difference between *E. latifrons* and the other 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* 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 unpredictable events including demographic stochasticity, environmental stochasticity, genetic stochasticity, or natural catastrophes (Gilpin and Soule 1986; Given 1994; Brook et al. 2002).

Fire survival strategies in *E. latifrons* in Population B can be compared to that of *Kumara plicatilis* in that both species display morphological characteristics that suggest fire tolerance and are not reprouters *per se* but apical sprouters (Cousins et al. 2016). It is suggested that *K. plicatilis* has a duel 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. Similarily, Cousins et al. (2016) found that postfire mortality of *K. plicatilis* increased with a decreasing percentage of rock cover within populations sampled. On these rocky outcrops, *E. latifrons* was associated with another resprouting endemic fynbos tree species, *Oldenburgia grandis*. Individuals of *O. grandis* are more likely to survive fire if growing on a rock (Swart 2008). This is particularly important for the *O. grandis* 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 (Marais et al. 2014). The same study found that on average, obligate Mountain Fynbos shrub resprouters 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 experiences a substantially different fire regime to Population B. According to the landowner, the last fire at the Population A site was over 15 years ago. This is a typical fire frequency in the far eastern coastal zone where patches of fynbos are small and fragmented (Rebelo et al. 2006; Kraaij et al. 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 different fire regime. Resprouting species such as *O. grandis* under different fire regimes displayed different adult survival rates under different fire regimes. Increased fire intensity due to a build-up of biomass in Mountain Fynbos combined with hot katabatic 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*. 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 between and within cycad populations differ remarkably and are often difficult to determine over short study period 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 to 1 female

(J.C. Basson survey report). 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 to 1.74 meters 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* where all populations (and the species as a whole) was 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, 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 first author was fortunate to witness a mast coning event, where the majority of plants in the Population B coned at the same time.

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 et al. 2014).

Successful coning, seed development and seed recruitment would 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 growth rate of *E. latifrons* reported here may represent an over-estimation of the realised growth rate of the species due to compression of the leaf bases as the plant gets taller (Vovides 1990). Growth rates are notoriously difficult to measure in cycad populations with sporadic leaf flushes and potential for measurement error. Giddy (1974) reported that in areas with higher rainfall, species such as *E. transvenosus* produces new leaves annually, are one of the tallest *Encephalartos* species reportedly reaching heights of up to 14 meters in the wild (Grobbelaar 2004)), whereas some records show *E. latifrons*, produces leaves every 4 to 5 years (Giddy 1974), assuming this is not taking into account sprouting after fire. Singh (2012) reported growth rates for *in situ* populations of *E. longifolius* at 1.1 cm yr^{-1}, with only 18% of the population displaying any observable increase in height over the 2-year study period. Under greenhouse conditions, *E. longifolius* grew at an annual rate of about 2.5 cm over the 185 years since it was planted in the Kew Gardens reaching a height of 3.4 m in 1960 (Giddy 1974). Reported growth rates in other cycad species vary from 4.5cm yr^{-1} for *C. armstrongii* (Watkinson and Powell 1997) compared to *D. edule* with a growth rate of 0.67cm yr^{-1} averaged across all stages (Vovides 1990). Fire stimulated growth in populations of *C. armstrongii* at frequently burnt sites with plants experiencing higher growth rates compared to unburnt sites (Watkinson and Powell 1997). Lower growth rates seen in the juvenile stage (0.63 cm yr^{-1}) of *E. latifrons* compared to the adult stages (1.50 and 1.75 cm yr^{-1}) is expected as juveniles will increase in diameter until the plant approaches its maximum number of leaves per flush. Although this was not directly measured, a flattening out in stem circumference was evident for plants reaching a stem height of approximately 116 cm while height continued to increase linearly.

The spatial pattern in the *E. latifrons* Population B displays a similar clustered pattern to the majority of 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 out of plants with an increase

in stage class. This is also observed in other cycad species such as *Macrozamia miquelli* (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).

Current and future threats

There is still a real poaching threat to *E. latifrons* populations that remain in the wild. Population A is considerably protected as it exists on private land and is constantly monitored with restricted access to the public. This population is not reproducing naturally; population survival is 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 the Population B has resulted in it being undisturbed than more exposed and well-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 a loss of biodiversity is to be accelerated by a changing climate (McCarthy et al. 2001). This is particularly evident in Mediterranean-type climate 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 however a large region characterised by east-west divisions in rainfall patterns, fire climate zones and temperatures as well as regional climatic gradients (Kraaij et al. 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* to this is currently unknown. Evidence does however 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, it is clear that timing of a fire will 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 unviable 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 possible other cycad species in similar environments. Given this potential for limited sexual recruitment, it has however 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 however 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).

Conclusion and future research

The discovery of an undocumented population of *E. latifrons* raises interesting questions regarding why there are such differences in recruitment ability between two populations of the same species. Reasons for these differences would need further investigation. Some possibilities include 1. Population B is larger and more intact and able to sustain plant-animal mutualisms such as pollination more effectively than Population A (although there is evidence that this population was able to naturally sustain itself according to survey reports of 1991). 2. Land management including the exclusion of fire/low fire frequencies, past disturbances, control of seed predators/herbivory may have reduced natural seed set in Population A. 3. Population

B does display certain morphological anomalies suggesting that the population may represent an introgression between *E. latifrons* and *E. longifolius* possibly resulting in hybrid vigour. Nonetheless, the discovery of an undocumented population of *E. latifrons* has given insights into the life-history of the species, particularly its response to fire and seedling recruitment and survival.

The construction of a life table for a viable *E. latifrons* population allowed the calculation of basic demographic parameters such as net reproductive rate and intrinsic population growth rate. While these results are useful, they are fairly limited in what they reveal about the state of a population over time. As an alternative, matrix models have been widely used in plant studies to estimate population growth rate over time as well as to determine how stochastic and deterministic factors affect the life history stages of a population or species (Esparza-Olguín et al. 2005; Kaneko et al. 1999; Monks et al. 2012). While these methods have been used to determine extinction risks for cycads (Álvarez-Yépiz et al. 2011; Octavio-Aguilar et al. 2008; Pérez-Farrera et al. 2006; Raimondo & Donaldson 2003) they are not without mathematical assumptions that render them problematic for studies on long-lived plant species (Stott et al. 2010; Zuidema et al. 2010). Intergral Projection Models (IPM) offer a solution to assumptions that sometimes cannot be met in matrix models (see Stott et al. 2010 on reducibility and erogodicity of population projection matrix models) and have become a popular method in recent plant demographic studies (Isaza et al. 2017; Sulis et al. 2018; Williams et al. 2015). In particular, the advantage of an IPM is the use of continuous variables to model population dynamics rather than the use of discrete stages as in matrix modelling (Merow et al. 2014; Mandle et al. 2015). An in-depth analysis was undertaken to test the feasibility of undertaking an IPM for *E. latifrons* for this study. While an estimate of growth rate for some individuals was obtained, it was not possible to determine the growth rate for all individuals, especially for the seedling stage at size t + 1 over the five-year period. An important step in the IPM is to construct the kernel (i.e. the function describing the state of an individual at one time and how it influences its states (and that of its offspring) at t + 1 (Merow et al. 2014). This includes mapping the size distribution of seedlings and how individual plants change in state (grow/shrink) between t and t + 1. Due to the difficulty in obtaining this information for *E. latifrons* over the 5-year census, it was decided to not to construct an IPM in this study, but to undertake this analysis as a separate study once robust growth data is available for

Population B. The annual monitoring of Population B by DEDEA staff is on-going, making this a possible future study

Despite challenges modelling the population dynamics of a viable population, new insights into the biology of *E. latifrons* revealed in this thesis 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 (Smith et al. 2011).

References

Adie H, Kotze DJ, Lawes MJ. (2017) Small fire refugia in the grassy matrix and the persistence of Afrotemperate forest in the Drakensberg Mountains. Sci Rep 7:6549

Altwegg R, West A, Gillson L, Midgley GF. (2014) Impacts of climate-change in the Greater Cape Floristic Region. In: Allsop N, Colville JF, Verboom GA (eds) Fynbos: ecology, evolution and conservation of a megadiverse region. Oxford University Press, pp 299–320

Álvarez-Yépiz JC, Búrquez A, Dovčiak M. (2014) Ontogenetic shifts in plant-plant interactions in a rare cycad within angiosperm communities. Oecologia 175:725–735

Álvarez-Yépiz JC, Dovčiak M, Búrquez A. (2011) Persistence of a rare ancient cycad: Effects of environment and demography. Biol Conserv 144:122–130

Baddeley A, Rubak E, Turner R. (2015) Spatial Point Patterns: methodology and applications with R. Chapman and Hall/CRC Press, London

Baddeley A, Turner R. (2005) spatstat: An R package for analyzing spatial point patterns. J Stat Softw 12:1–42

Basson M. (1991) Eerste verslag wat die bron en status van die *Encephalartos* spesies in die Trappe's Valley area in die Oos-Kaap aandui met spesiale verwysing na die *Encephalartos latifrons*. Cape Nature Conservation Survey Report, South Africa

Besag JE, Diggle PJ. (1977) Simple Monte Carlo tests for spatial pattern. Appl Stat 26:327–333

Bland JM, Altman DG. (1998) Statistics Notes: survival probabilities (the Kaplan-Meier method). BMJ 317:1572–1580

Bond WJ. (1983) Dead leaves and fire survival in southern African tree aloes. Oecologia 58:110–114

Bond WJ, Midgley JJ. (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51

Brigham CA (2003) Factors affecting persistence in formerly common and historically rare plants. In: Population viability in plants. Brigham, C.A. & Schwartz, M.W. (eds). Ecological Studies, 165: 59 – 97

Brook BW, Tonkyn DW, Grady JJO, Frankham R. (2002) Contribution of inbreeding to extinction risk in threatened species. Conserv Ecol 6:16–31

Caswell H (2001) Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland, Massachusetts

CITES (1973) Convention on Internatoinal Trade of Endangered Species of Wild Fauna and Flora. Entered into force July 1 1975. Text of the Convention 27 U.N.T.S. 243

Chamberlain CJ. (1919) The living cycads. Hafner Publishing Company, New York and London

Clark DA, Clark DB. (1987) Temporal and environmental patterns of reproduction in *Zamia skinneri*, a tropical rain forest cycad. J Ecol 75:135–149

Clarke PJ. (2002) Habitat islands in fire-prone vegetation: do landscape features influence community composition? J Biogeogr 29:677–684

Cousins SR, Witkowski ETF, Pfab MF (2014) Elucidating patterns in the population size structure and density of *Aloe plicatilis*, a tree aloe endemic to the Cape fynbos, South Africa. South African Journal of Botany 90: 20-36

Cousins SR, Witkowski ETF, Pfab MF. (2016) Beating the blaze: fire survival in the fan aloe (*Kumara plicatilis*), a succulent monocotyledonous tree endemic to the Cape fynbos, South Africa. Austral Ecol 41:466–479

Cowling R, Richardson D. (1995) Fynbos: South Africa's unique floral kingdom. Fernwood Press, Vlaeberg

Crosiers C, Malaisse FP. (1995) Ex situ pollination and multiplication *Encephalartos laurentianus* De Wild. (Zamiaceae, Cycadales). Biodivers Conserv 4:767–775

Da Silva J, Donaldson JS, Reeves G, Hedderson TA. (2012) Population genetics and conservation of critically small cycad populations: a case study of the Albany Cycad, *Encephalartos latifrons* (Lehmann). Biol J Linn Soc 105:293–308

Daly, B., Donaldson, J.S., Friedmann, Y., Hahndiek, Q., King, N. Newton, D. and Southwood, A. (editors) (2006) Population and habitat viability assessment for the Albany cycad (*Encephalartos latifrons*). Conservation Breeding Specialist Group (SSC /IUCN) / CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg

Deevey ES. (1947) Life tables for natural populations of animals. Q Rev Biol 22:283–314

Department of Environmental Affairs (2011) Biodiversity Management Plan for Albany Cycad, *Encephalartos latifrons*. National Environmental Management: Biodiversity Act (10/2004): South African Government Gazette No. 34388

Dixon PM. (2002) Ripley's K function. Encycl Environmetrics 3:1796–1803

Donaldson J. (2003) Cycads: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK

Donaldson J. (2008) South African *Encephalartos* species: NDF Workshop Case Study 4 (WG3)

Donaldson JS. (2010) *Encephalartos latifrons*. In: IUCN List of threatened species. http://www.iucnredlist.org/details/41892/0. Accessed 8 Sep 2017

Donaldson JS. (1995) Understanding cycad life histories: an essential basis for successful conservation. In: Donaldson JS. (ed) Cycad conservation in South Africa: Issues, Priorities and Actions. Cycad Society of South Africa, Stellenbosch, South Africa., pp 8–13

Engelbrecht CJ, Engelbrecht FA. (2016) Shifts in Köppen-Geiger climate zones over southern Africa in relation to key global temperature goals. Theor Appl Climatol 123:247–261

Enright NJ, Fontaine JB, Lamont BB, Miller BP and Westcott VC. (2014) Resistance and resilience to changing climate and fire regime depend on plant functional traits. J Ecol 102:1572–1581

Esparza-Olguín L, Valverde T, & Mandujano MC (2005) Comparative demographic analysis of three *Neobuxbaumia* species (Cactaceae) with differing degree of rarity. Population Ecology. 47(3): 229-245

ESRI (2012) ArcGIS: Environmental Systems Research Institute, Redlands California, USA

Fujita T and Mizuno K. (2015) Role of nurse rocks on woody plant establishment in a South African grassland. Tropics 24:57–64

Gerlach MA. (2012) The population structure and dynamics of *Macrozamia riedlei* within the Perth region. Unpublished thesis, Murdoch University

Giddy C. (1974) Cycads of South Africa. 1st Edition. Purnell and Sons Pty Ltd. Cape Town, South Africa

Gilpin ME, Soule ME (1986) Minimum viable populations: processes of species extinction. In: Soule ME (ed) Conservation biology: the science of scarcity and diversity. 1st Edition. Sinauer, Sunderland, Massachusetts, USA

Given DR. (1994) Principles and Practice of Plant Conservation. Timber Press, Inc., Portland, Oregon

Griffiths AD, Schult HJ, Gorman J. (2005) Wild harvest of *Cycas arnhemica* (Cycadaceae): Impact on survival, recruitment and growth in Arnhem Land, northern Australia. Aust J Bot 53:771–779

Grime JP. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Grobbelaar N. (2004) Cycads - with special reference to the southern African species, First Edit. Published by the author, Pretoria

Guimarães PR Jr, Galetti M, Jordano P (2008) Seed dispersal anachronisms: rethinking the fruits of extinct megafauna ate. PLoS One 3(3): e1745

Haase P. (1995) Spatial pattern analysis in ecology based on Ripley's K-function: Introduction and methods of edge correction. J Veg Sci 6:575–582

Hall JA, Walter GH. (2013) Seed dispersal of the Australian Cycad *Macrozamia Miquelii* (Zamiaceae): Are cycads megafauna-dispersed "grove forming" plants? Am J Bot 100:1127–1136

Hoare D, Mucina L, Rutherford MC, Vlok JH, Euston-Brown D, Palmer AR, Powrie LW, Lechmere-Oertel RG, Proches SM, Dold AP and Ward RA. (2006) Albany Thicket Biome. In: Mucina L, Rutherford MC (eds) The vegetation of South Africa, Lesotho and Swaziland, 1st edition. South African National Biodiversity Institute (Strelitzia 19), Pretoria, South Africa, pp 541–567

Hoffmann M, Hilton-taylor C, Angulo A, Böhm M, Brooks, TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Katariya V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vie J-C, Aguiar JM, Allen DJ, Allen GR and Amori G. (2010) The impact of conservation on the status of the world's vertebrates. Sci New Ser 330:1503–1509

Isaza C, Bernal R, Galeano G, & Martorell C (2017) Demography of *Euterpe precatoria* and *Mauritia flexuosa* in the Amazon: application of integral projection models for their harvest. Biotropica. 49(5): 653-664

Kaneko Y, Takada T & Kawano S (1999) Population biology of *Aesculus turbinate* Blume: A demographic analysis using transition matrices on a natural population along a riparian environmental gradient. Plant Species Biology: 14: 47 – 68

Kemp HJ (1986) *Encephalartos latifrons*. Encephalartos 8:8–15

Klein RG (1972) The late Quarternary mammalian fauna of Nelson Bay Cave (Cape Province: South Africa): its implications for megafaunal extinctions and environmental and cultural change. Quarternary Research 2: 135-142

Kottek M, Grieser J, Beck C, Rudolf B and Rubel F. (2006) World map of the Köppen-Geiger climate classification updated. Meteorol Zeitschrift 15:259–263

Kraaij T and van Wilgen BW. (2014) Drivers, ecology, and management of fire in fynbos. In: Allsop N, Colville JF, Verboom GA (eds) Fynbos. Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press, pp 47–72

Krishnamurthy V, Mandle L, Ticktin T, Gamesan R, Saneesh CS and Varghese A. (2013) Conservation status and effects of harvest on an endemic multi-purpose cycad, *Cycas circinalis* L., Western Ghats, India. Trop Ecol 54:309–320

Lamont BB and Downes KS. (2011) Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. Plant Ecol 212:2111–2125

Lamont BB, Enright NJ and He T (2011) Fitness and evolution of resprouters in relation to fire. Plant Ecol 212:1945–1957

Liddle DT (2004) The ecology of *Cycas armstrongii* and management of fire in Australia's tropical savannas. PhD thesis. Charles Darwin University, Darwin, Australia

Linder HP and Ellis RP. (1990) Vegetative morphology and interfire survival strategies in the Cape Fynbos grasses. Bothalia 20:91–103

Lopez-Gallego C and O'Neil P. (2010) Life-history variation following habitat degradation associated with differing fine-scale spatial genetic structure in a rainforest cycad. Popul Ecol 52:191–201

Lubke RA, Everard DA and Jackson S. (1986) The biomes of the eastern Cape with emphasis on their conservation. Bothalia 16:251–261

Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning J-C, Terborgh JW (2016) Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proceedings of the National Academy of Sciences 113(4): 838 – 846

Mandle L, Ticktin T and Zuidema PA (2015) Resilience of palm populations to disturbance is determined by interactive effects of fire, herbivory and harvest. Journal of Ecology 103(4):1032-1043.

Marais KE, Pratt RB, Jacobs SM, Jacobsen AL, Esler KJ. 2014. Postfire regeneration of resprouting mountain fynbos shrubs: differentiating obligate resprouters and facultative seeders. Plant Ecology 215: 195–208

McCarthy JJ, Canziani OF, Leary NA, Dokken DJ and White KS (eds). 2001 Climate Change 2001: Impacts, Adaptations, and Vulnerability. Cambridge Univ. Press, New York

Merow C, Dahlgren JP, Metcalf CJE, Childs DZ, Evans ME, Jongejans E, Record S, Rees M, Salguero-Gómez R and McMahon SM (2014) Advancing population ecology with integral projection models: a practical guide. Methods in Ecology and Evolution 5(2): 99-110.

Mills AJ and Fey M V (2003) Declining soil quality in South Africa: effects of land use on soil organic matter and surface crusting. S Afr J Sci 99:429–436

Mitchell A (2005) Spatial Measurements and Statistics. In: The ESRI Guide to GIS Analysis: Volume 2. ESRI Press, Redlands, USA

Monks L, Coates D, Bell T, Bowles M (2012) Determining success criteria for long-lived plants (pp 189-208) in Maschinski J and K. E. Haskins KE (editors). Plant reintroduction in a changing climate: promises and perils. Island Press

Mora R, Yáñez-Espinosa L and Flores J (2013) Strobilus and seed production of *Dioon edule* (Zamiaceae) in a population with low seedling density in San Luis Potosí, Mexico. Trop Conserv Sci 6:268–282

Negron-Ortiz V and Breckon GJ (1989) Population structure in *Zamia debilis* (Zamiaceae) I. Size classes, leaf phenology, and leaf turnover. Am. J. Bot. 76:891–900

Octavio-Aguilar P, Gonzalez-Astorga J and Vovides AP (2009) Genetic diversity through life history of *Dioon edule* Lindley (Zamiaceae, Cycadales). Plant Biol 11:525–536

Octavio-Aguilar P, González-Astorga J, Vovides AP (2008) Population dynamics of the Mexican cycad *Dioon edule* Lindl. (Zamiaceae): life history stages and management impact. Botancal Journal of the Linnean Society 157:381–391

Octavio-Aguilar P, Rivera-Fernández A, Iglesias-Andreu LG, Vovides AP, Núñez de Cáceres-González FF. (2017) Extinction risk of *Zamia inermis*: a demographic study in its single natural population. Biodivers Conserv 26:787–800

Ogwal JJ (2017) Population structure of the cycad along River Mpanga, Western Uganda. African J Rural Dev 2:95–103

Oostermeijer JGB (2003) Threats to rare plant persistence. In: Brigham CA, Schwartz MW (eds) Population viability in plants: conservation, management and modeling of rare plants. Springer, Berlin, Heidelberg, pp 17–58

Ornduff R (1985) Male-Biased Sex Ratios in the cycad *Macrozamia riedlei* (Zamiaceae). Bull Torrey Bot Club 112:393–397

Ornduff R (1987) Sex Ratios and Coning Frequency of the Cycad *Zamia pumila* L. (Zamiaceae) in the Dominican Republic. Assoc Trop Biol Conserv 19:361–364

Ornduff R (1990) Geographic Variation in Reproductive Behavior and Size Structure of the Australian Cycad *Macrozamia communis* (Zamiaceae). Am J Bot 77:92–99

Perez-Farrera MA, Vovides AP, Octavio-Aguilar P, González-Astorga J, de la Cruz-Rodríguez J, Hernández –Jonapá R and Villalobos-Méndez SM. (2006) Demography of the cycad *Ceratozamia mirandae* (Zamiaceae) under disturbed and undisturbed conditions in a biosphere reserve of Mexico. Plant Ecol 187:97–108

Pérez Farrera MA and Vovides AP. (2004) Spatial distribution, population structure and fecundity of *Ceratozamia matudai* Lundell (Zamiaceae) in El Triunfo Biosphere Reserve, Chiapas, Mexico. Bot. Rev. 70:299–311

Pickup M and Barrett SCH. (2013) The influence of demography and local mating environment on sex ratios in a wind-pollinated dioecious plant. Ecol Evol 3:629–639

Preece LD, Duguid AW and Albrecht DE. (2007) Environmental determinants of a restricted cycad in central Australia, *Macrozamia macdonnellii*. Aust J Bot 55:601–607

Quantum GIS Development Team (2015) Quantum Geographic Information System

Raimondo DC, Donaldson JS (2003) Responses of cycads with different life histories to the impact of plant collecting: Simulation models to determine important life history stages and population recovery times. Biological Conservation 111:345–358

Rebelo AG, Boucher C, Helme N, Mucina L and Rutherford MC (2006) Fynbos Biome. In: Mucina L, Rutherford MC (eds) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute., Pretoria, South Africa, pp 53–219

Rutherford MC, Mucina L, Lotter MC, Bredenkamp GJ, Smit JHL, Scott-Shaw R, Hoare DB, Goodman PS, Besuidenhout H, Scott L, Ellis F, Powrie LW, Siebert F, Mostert TH, Henning BJ, Venter CE, Camp KGT, Siebert SJ, Matthews WS, Burrows JE, Dobson L, van Rooyen N, Smidt E, Winter PJD, du Preez PJ, Ward RA, Williamson S and Hurter PJH. (2006) Savanna Biome. In: Mucina L, Rutherford MC (eds) The Vegetation of South Africa, Lesotho and Swaziland, First Edit. Strelitzia 19. South African National Biodiversity Institute., Pretoria, South Africa, pp 439–539

Schneider D, Wink M, Sporer F and Lounibos P (2002) Cycads: their evolution, toxins, herbivores and insect pollinators. Naturwissenschaften 89:281–294

Singh K (2012) Population dynamics of the Zuurberg cycad and the predicted impact of climate change. Unpublished M.Sc. thesis, Nelson Mandela Metropolitan University, South Africa

Smith MJ, Benitez-Diaz H, Clemente-Munoz MA, Donaldson J, Hutton JM, McGough HN, Medellin RA, Morgan DHW, O'Criodain C, Oldfield TEE, Schippmann U, Williams RJ (2011) Assessing the impacts of international trade on CITES-listed species: current practices and opportunities for scientific research. Biol. Conserv. 144: 82–91

Steele TE (2007) Vertebrate records: Late Pleistocene of Africa. In: Elias S (Ed) Encyclopedia of Quarternary Science 3139-3150

Stehlik I, Friedman J and Barrett SCH (2008) Environmental influence on primary sex ratio in a dioecious plant. Proceedings of the National Academy of Sciences of the United States of America 105:10847–52

Stott I, Townley S, Carslake D, Hodgson DJ (2010) On reducibility and ergodicity of population projection matrix models. Methods in Ecology and Evolution 1:242–252

Suinyuy TN, Donaldson JS and Johnson SD (2013) Variation in the chemical composition of cone volatiles within the African cycad genus *Encephalartos*. Phytochemistry 85:82–91

Sulis E, Bacchetta G, Cogoni D, and Fenu G Short-term population dynamics of *Helianthemum caputfelis*, a perennial Mediterranean coastal plant: a key element for an effective conservation programme. Systematics and Biodiversity (2018): 1-10

Swart C (2008) Life history, population dynamics and conservation status of *Oldenburgia grandis* (Asteraceae), an endemic of the Eastern Cape of South Africa. MSc Thesis, Rhodes University

Swart C (2017) The globetrotting Albany Cycad. Veld Flora 103:79–80

Swart C (2008) Life history, population dynamics and conservation status of *Oldenburgia grandis* (Asteraceae), an endemic of the Eastern Cape of South Africa. Unpublished M.Sc. thesis, Rhodes University, South Africa

Tang W (1990) Reproduction in the cycad *Zamia pumila* in a fire-climax habitat: an eight-year study. Bull Torrey Bot Club 117:368–374

TRAFFIC (2003) Review of Significant Trade Cycads. PC14 Doc. 9.2.2 Annex 1. Pp 3 - 44

Treurnicht M, Pagel J, Esler KJ, Schutte-Vlok A, Nottebrock H, Kraaij T, Rebelo AG and Schurr FM. (2016) Environmental drivers of demographic variation across the global geographical range of 26 plant species. J Ecol 104:331–342

Van Wilgen BW (2013) Fire management in species-rich Cape fynbos shrublands. Frontiers in Ecology and the Environment 11 (online issue 1): e35 – e44

Varley GC and Gradwell GR (1970) Recent advances in insect population dynamic. Annu Rev Entomol 15:1–24

Vesk PA and Westoby M (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. J Ecol 92:310–320

Vovides AP (1990) Spatial distribution, survival, and fecundity of *Dioon edule* (Zamiaceae) in a tropical deciduous forest in Veracruz, Mexico, with notes on its habitat. Am J Bot 77:1532–1543

Watkinson AR and Powell JC (1997) The life history and population structure of *Cycas armstrongii* in monsoonal northern Australia. Oecologia 111:341–349

Williams JL, Jacquemyn H, Ochocki BM, Brys R & Miller TE (2015) Life history evolution under climate change and its influence on the population dynamics of a long-lived plant. Journal of Ecology. 103(4):798-808

Wilson AM, Latimer AM and Silander JA (2015) Climatic controls on ecosystem resilience: postfire regeneration in the Cape Floristic Region of South Africa. Proc Natl Acad Sci 112:9058–9063

Wilson GW (2002) Insect Pollination in the cycad genus Bowenia Hook. ex Hook. f. (Stangeriaceae). Biotropica 34:438–441

Xaba P (2014) Pollination and germination as limiting factors in the propagation of threatened cycads, *Encephalartos* (Zamiaceae). MSc thesis. University of the Western Cape, South Africa, pp 1 - 138

Yáñez-Espinosa L and Sosa-Sosa F (2007) Population structure of *Dioon purpusii* Rose in Oaxaca, Mexico. Neotropical Biology and Conservation 2:46–54

Yeld J (2014) Thieves make off with cycads worth about R500 000. In: Cape Arg. https://www.pressreader.com/south-africa/cape-argus/20140807/282510066712732. Accessed 15 Sep 2017

Yessoufou K, Daru BH, Tafirei R, Elansary HO and Rampedi I (2017) Integrating biogeography, threat and evolutionary data to explore extinction crisis in the taxonomic group of cycads. Ecol Evol 7:2735–2746

Zamar D, Graham J and Mcneney B (2013) Exact Logistic Regression via MCMC: Package "elrm." 1–15 http://stat-db.stat.sfu.ca:8080/statgen/research/elrm. Accessed 08 August 2017

Zaiontz C (2017) Real Statistics Using Excel. www.real-statistics.com (accessed 17/05/2017)

Zuidema PA, Jongejans E, Chien PD, During HJ, Schieving F (2010) Integral projection models for trees: A new parameterization method and a validation of model output. Journal of Ecology 98:345–355

CHAPTER 4

Preliminary investigation into the reproductive ecology of *Encephalartos latifrons*

[Target journal: Current Science]

Abstract

A preliminary investigation of the reproductive ecology of *E. latifrons* is presented. Anecdotal evidence suggests that *E. latifrons* populations are functionally extinct, possibly due to the extinction of specialised weevil pollinators associated with the species. This is the first comprehensive analysis of cone fauna present in wild *E. latifrons* populations. This is also the first test of seed viability in wild populations under different management regimes. Fauna samples were taken from male cones in June/July of 2013. Seed samples from female cones were harvested in December/January of 2014/2015. Results from this study show that insect fauna within *E. latifrons* male cones is diverse with four different *Porthetes* weevil species found across all wild populations. Seed viability tests reveal that some *E. latifrons* wild populations are capable of producing viable seed under conditions of natural pollination. Seed malformation is high in some populations contributing up to 22% of seed loss. Seed germination trials reveal a staggered germination pattern in *E. latifrons* wild populations possibly as adaptive trait given the intra-annual variability in climate and fire regimes. Further research is needed to determine the success of weevil pollination in wild *E. latifrons* populations under natural conditions.

Keywords: plant-animal mutualisms, pollination, seed germination, seed viability

Introduction

Insect mutualisms between cycads and their specialist insect pollinators is likely to have evolved during the early Mesozoic era (250 – 65 mya) (Klavins et al. 2005; Labandeira et al. 2007) at a time when cycads were widespread (Schneider et al. 2002). All cycads are dioecious, with male cone (microstrobilus) acting as the breeding, mating and larval development site for their insect pollinators (Marler and Lindström 2015). Beetles of the Cucujoidea and Curculionoidea superfamilies are the primary pollinators for many cycad taxa including those belonging to the *Encephalartos* genus, representing the Zamiaceae in Africa (Cousins and Witkowski 2017). Evidence suggests that most pollinators feed on the male strobilus tissue rather than on the pollen directly (Norstog and Fawcett 1989; Marler and Lindström 2015). However, cycad ovules (carried by the megasporophylls on the female megastrobilus) are known to produce droplets that contain metabolites which may act as a reward for pollinators (Proches and Johnson 2009; Valencia-Montoya et al. 2017). Volatiles and thermogenesis also play a large role in regulating insect behaviour between the male and female cones in many cycad species during pollination (Terry et al. 2007; Suinyuy et al. 2010).

Terry (2001) was the first to demonstrate a dual-specialist pollination system in cycads with specialist pollinators of two different insect orders. Brookes et al. (2015) found that a single pollinator species can also be associated with more than one cycad species where populations overlap or are in close proximity. There are however no definitive studies showing a co-speciation of pollinators with their cycad hosts (Terry et al. 2012). Some studies have definitively demonstrated specific pollinator mutualisms in *Encephalartos* species such as the *Porthetes* sp. (Curculionidae) weevil in *Encephalartos villosus* (Donaldson 1997; *sensu* Downie et al. 2008), *P. hispidus*, *Erotylidae* sp. nov. (Cucujoidea), and *Metacucujus encephalarti* (Boganiidae) in *E. friderici-guilielmi* (Suinyuy et al. 2009). Although the *Porthetes* weevil was found to be the primary pollinator in *E. villosus*, other insects such as *Xenoscelinae* sp. (a languriid now placed among the erotylids – Leschen 2003) were responsible for up to 10% of pollination and less so *Antliarrhinus zamiae* (Donaldson 1997). Interestingly, under artificial conditions (i.e. dusting the beetles with pollen and releasing them onto the female cones) in the same study, *A. zamiae* was able to successfully pollinate a significant proportion of *E. villosus* ovules (Donaldson 1997). Regarded as a seed parasite, *A. zamiae* is often responsible for substantial loss of seed in many

Encephalartos species and are poor candidates for pollination as they do not visit the male cones under natural conditions (Donaldson 1993; Donaldson pers. comm.). The Antliarhinini are an exclusively African group of brentids unlikely to play a role as a pollination agent due to their wide host range specifically on species of *Encephalartos* that bear naked cones (Oberprieler 1995).

Cycads are a valuable horticultural group worldwide and artificial pollination of cycads has for long been a subject of great interest (Fourie 1986; Crosiers and Malaisse 1995; Donaldson 2003; Kay et al. 2011). In some species such as *Encephalartos latifrons* and *Microcycas calocoma*, artificial pollination is thought to be the only viable option for seed fertilization due to the apparent extinction or near extinction of the species-specific pollinators (Vovides et al. 1997; Daly et al. 2006). A potential pollinator was nevertheless discovered for *M. calcoma* (Chaves and Genaro 2005) and there are reports of some populations naturally recruiting seedlings (Vovides et al. 1997). The success of artificial pollination varies between species and plants in *ex situ* environments depending on method (wet/dry pollination), pollen storage, and timing (Crosiers and Malaisse 1995; Xaba 2014). Seed viability for artificially pollinated cones of *E. latifrons* is recorded as very low (< 10%) from various *ex situ* botanical garden collections (Whitelock 1995; Xaba 2014). This is in comparison to species such as *E. altensteinii*, where artificial pollination typically yields > 60 % viable seed in the same environments and by the same pollination and germination methods (Crosiers and Malaisse 1995; Xaba 2014). One *E. latifrons* landowner however reports seed viability percentages of ± 70 % (with an average of approximately 180 germinating seeds out of each cone) from artificially pollinating plants *in situ* (pers. comm. landowner, name withheld to protect the plants and wishes of the landowner). It is based on these good results and the fact that *E. latifrons* is considered functionally extinct, that artificial pollination of *in situ* plants was advocated as a viable and justified conservation strategy for *E. latifrons* (Donaldson 2003; Daly et al. 2006).

E. latifrons has been considered a species "on the verge of extinction" since the early 1900's (Pearson 1916). Its rarity was later confirmed by Chamberlain (1919) where, after visiting *E. latifrons* localities, he noticed that plants were isolated and far (a mile) apart from each other. Giddy (1974) was the first to suggest that natural regeneration in *E. latifrons* was not possible due to its "scattered distribution" and "no male and female clumps are within pollinating distance from each other". This was later echoed by Kemp (1986) who proposed that lack of natural regeneration in *E. latifrons*

possibly dated back to when it was first reported on by Pearson (1916) and Chamberlain (1919). Further reports on the lack of regeneration in *E. latifrons* was cited in Grobbelaar (2004), Daly et al. (2006), Da Silva et al. (2012) and published in the Biodiversity Management Plan for *E. latifrons* (Department of Environmental Affairs 2011). Reasons for lack of regeneration include anecdotal evidence pointing to the possible extinction of species-specific weevil pollinators for *E. latifrons*. This is in contrast to two unpublished records held by DEDEA (Department of Economic Development and Environmental Affairs) including information from an investigation and a survey report undertaken by the Department of Cape Nature Conservation, Eastern Cape Region (as it was called at the time). The first report was submitted as part of legal proceedings in the conviction and sentencing of a man found guilty in the Grahamstown Magistrates Court for the illegal possession and transportation of seven *E. latifrons* plants removed from a natural population near Grahamstown, South Africa. The report dated 1st April 1981 mentions three large clumps of *E. latifrons* (in excess of 20 plants) existing on the property (where the theft occurred) with male and female plants in close proximity. The report went on to mention that this is extremely rare and that that there was only one other *E. latifrons* population the author of the report knowns of where female *E. latifrons* are pollinated in a natural way producing *E. latifrons* seedlings. The second unpublished record was in the form of a survey report written in 1991. The survey was instigated in response to the harvesting pressure on natural cycads populations in the Eastern Cape Province of South Africa, particularly *E. latifrons* (Basson 1991). All known *E. latifrons* localities were surveyed, plants microchipped and photos taken. It was during this survey that 4 natural seedlings were found to be growing in one *in situ E. latifrons* population (a different population to the one referred to in the 1981 report). It was shortly after the survey was undertaken that a number of adult *E. latifrons* plants were illegally uprooted at the site, subsequently confiscated and relocated to a protected area (Vice 1995; Daly et al. 2006). Unpublished reports therefore do indicate that some populations were capable of natural regeneration as recently as 1991.

To date, no formal study of insect fauna in *E. latifrons* cones has been undertaken to determine if potential pollinators do exist and in what numbers. Insect samples from *E. latifrons* cones in one *in situ* population (Population A1 in Table 4.1) were however identified and published by Downie et al. (2008). Weevil species found in the male cones include *Amophocerus talpa* and *P. dissimilis* (*sensu* Downie et al.

2008). *Amorphocerus* is more commonly associated with female cones in *Encephalartos* species as is *P. dissimilis*, and are therefore unlikely to be important pollinators (Donaldson pers. comm.).

In this study I explore the diversity of insects inhabiting the male cones of three *in situ E. latifrons* populations and one translocated "population" and give an indication in what numbers insects species exist. I also investigate seed morphological characteristics of wild collected seed and determine if seed set under natural pollination is possible in wild populations.

Materials and methods

Study species

Encephalartos latifrons, is regarded as one of the slowest growing cycad species with long coning intervals (Whitelock 1995; Grobbelaar 2004). Listed as Critically Endangered (Donaldson 2010), *E. latifrons* is an arborescent cycad reaching heights of up to 2.8 meters with the mature plants having up to 8 stems by suckering. Male (microstrobili) and female (megastrobili) cones are produced on separate plants. The males generally cone more frequently than females and can have 1 to 5 cones per stem (Plate 4.1 d). The female plants cone sporadically with one cone per stem and a yield of 275 – 790 seeds per cone (Grobbelaar 2004). Female cone dimensions have been reported as 500 – 600 mm long with a diameter of 200 – 250 mm (Giddy 1974; Grobbelaar 2004). Female cones are usually shorter but thicker having fewer but larger sporophylls. Fertile sporophylls have two ovules attached to the bulla. The sporophylls open slightly when receptive to pollination. When the sporophylls open, pollen-bearing insects (if any) enter the cone through the cone fissures. The male cone dimensions are much smaller at 300 – 500 mm long and 80 – 170 mm in diameter (Giddy 1974; Grobbelaar 2004). Once matured, the pollen sacs (sporangia) on the male cones start to dehisce and release pollen around the winter months of July/August. When fertilised, the female cone develops for another 6 months starting to disintegrate around January/February the following year. Seed kernels are 27 – 33 mm long and 20 – 24 mm in diameter (Grobbelaar 2004). After fertilisation and release from the megasporophyll, seeds undergo a deep simple morphophysical dormancy period (Baskin and Baskin 2004; Xaba 2014). Due to this dormancy period, germination success in artificially pollinated seeds of *E. latifrons* is improved after a few months of dry storage recommended at 12 months (Xaba 2014).

Study sites

The study area exists with the eastern extreme of the Fynbos Biome in the Eastern Cape Province of South Africa, also known as the Greater Cape Floristic Region (GCFR; Bergh et al. 2014). The vegetation type associated with *E. latifrons* populations is referred to as Suurberg Quartzite Fynbos after the Witteberg Quartzite outcrops on which is occurs (Rebelo et al. 2006). Populations are spread out in an area spanning

approximately 40 kilometres (Table 4.1). Populations A, B and C include all known *E. latifrons* populations except for one other population where access to undertake research was not granted at the time of the study. This study does not include the few remaining scattered plants where once larger populations existed. Population A is divided into A1 and A2. This is as a result of plants in A2 that were originally part of Population A1 until they were illegally harvested, subsequently confiscated and replanted in a protected area.

Table 4.1 Table summarising information from the 3 populations studied. Locality information is not given to protect the remaining plants from theft.

Site	Population A1	Population A2	Population B	Population C
Known sex ratio (M:F)	2.6:1	1:2	1:2	1:1
Land Use	Private livestock and crop farm	Protected Area	Semi-protected area	Private livestock and crop farm
Management of cycads		No management	None	Some historical management
Fire Frequency	> 15 years	> 30 years	1 – 3 years	> 15 years
Disturbance History	Parental plants *in situ* artificially pollinated. Pollen and seed collected for propagation in nursery	Plants illegally removed from A1, confiscated and translocated to a protected area	Some parts affected by alien plant infestations that have now been cleared. Population remains relatively undisturbed by human activity.	A critically small population consisting of 2 mature plants. All other plants removed from wild decades ago according to the landowner with some of the original plants still in the garden on the property
Natural regeneration	No	No	Yes	No

Sampling insect fauna in male cones

The populations were monitored between 2013 and 2017 where coning plants were tagged (metal tags were placed on each plant with a unique number in order to identify them at each monitoring period) and GPS localities recorded. Insect fauna in male cones were sampled differently in the populations studied but all in the same year (June/July of 2013). Access to population A1 is restricted by the landowner making sampling insect fauna from the cones difficult. The landowner actively harvests the male cones just before the rupturing of the pollen sac. Cones are then placed in newspaper and "matured" until all the pollen is released into the newspaper and stored for artificial pollination of the female cones (the first author has first-hand knowledge of the methods involved after discussions with the landowner and visiting the nursery). The landowner was requested to collect any insects emerging from the male cone while harvesting pollen, as this is the only access to the plants available to the first author. For the remainder of the populations, cones were removed at each site (early to mid-morning) to sample for insect fauna (Plate 4.1a). Insects were removed from the male cone by beating the cones over some newspaper. The insects collected were recorded and counted before storing in vials containing 70% alcohol. Insects were later identified by JS Donaldson (second author of this paper) and voucher specimens housed at the South African National Biodiversity Institute (SANBI). Cones were sampled when the percentage of pollen shed was between 65 and 95%. The percentage pollen shed was estimated based on the extent to which the pollen sacs had ruptured compared to the sacs still intact. Insect fauna at Population C may be under-represented and/or reflect the insect population at a different life-cycle stage to the other cones sampled in this study for the following reason. The first visit to population C saw only 20% of the pollen on the male cone shed. It was decided that the cone was too 'unripe' to remove and sample but insects were collected between the microsporophylls while the cone was still attached to the plant making it difficult to collect a representative sample. The cone was revisited where it was found that 100% of the pollen was shed and the cone was beginning to blacken and decompose. Insects were therefore sampled twice at two different time periods from the same cone. No female plants were coning in 2013 in any of the populations sampled. In 2014 the following year, there was a mast coning event in all populations with simultaneous coning of male and female plants. It was therefore decided that no more male cones would be removed from the populations in

the study area in the monitoring period after 2013. This was to reduce the risk of artificially limiting any natural pollination that may occur in the studied populations. All cones (except those in Population A1) were sampled at mid-morning (10 – 11am) (Table 4.2).

Table 4.2 Male cones sampled from populations studied. An estimation of how much pollen shed had already taken place when the cone was harvested is given as a percentage

	Population A1	Population A2	Population B	Population C
No. of cones sampled	1	2	2	2
Sampling dates	01/07/2013	06/08/2013	30/07/2013	23/08/2013 (a) 02/10/2013 (b)
% pollen shed at time of sampling	unknown	80 – 95%	65 – 70%	a – 20% b – 100%

Testing the seed viability of female cones

Given the low coning frequency reported in *E. latifrons* populations (Kemp 1986), the first author was fortunate to witness a mast-seeding event in 2014 in all populations. Seed samples were collected from all populations including Population A1 (Table 4.3). Although all cones are artificially harvested in Population A1 and the seeds collected for germinating in the nursery, one female cone was not artificially pollinated (by mistake) and offered to the first author for this research project. The cone had already disintegrated at the time the seeds were collected but the seeds were still relatively fresh. In this case, all seeds from the entire cone were collected rather than a just a sample. Population A2 had two female plants and two male plants coning in 2014. A seed sample was harvested as soon as the female cone started to disintegrate in early 2015 (Plate 4.1b). Population B had 56% of females and 80% of males coning in 2014. Timing the disintegration of the female cone was challenging as the plants were difficult to access (due to rough terrain and the long distances to get to all the plants) to allow for weekly monitoring. In total, five female cones were sampled for seed upon their

disintegration in early 2015. Both male and female cone dimensions, wherever possible, were also measured in all populations.

Table 4.3 Summary of female cones sampled from each population including the coning ratio, number of cones sampled, sampling dates, number of seed collected and mean number of seed sampled per cone. The summary table also includes fire disturbance and other influencing factors

	Population A1	Population A2	Population B	Population C
Coning ratio in sampling year (M:F)	unknown	1:1	4:5	1:1
No. of cones sampled	1	2	5	1
Sampling dates	13/01/2015	16/01/2015	06/01/2015 – 25/01/2015	01/02/2015
Number of seed collected	113	89	176	62
Mean no of seed sampled per cone	113	44	35	62
Fire disturbance	N/A	N/A	2 female cones burnt in the 2014 fire	N/A
Other influences	Not known	N/A	3 female cones on one plant succumbed to fungal infection	N/A

Seeds were soaked in water for a week to soften the sarcostesta. The fleshy sarcostesta was then removed from the stony sclerostesta by scrubbing with an abrasive sponge. Once clean, seeds were dried and treated with a fungicide powder and stored in breathable paper bags. The seed kernels were measured with a digital calliper to record length and width. The coronula protrusion was not included in the measurement of seed length. Seed kernels were also weighed in grams to the nearest 2 decimal places. Malformed seeds were counted but not included in the measurements of length and

width and were also not weighed. Malformed seeds were small, undeveloped and easily distinguished from seed that appeared normal and fully developed (Plate 4.1c). One female cone sampled from Population B had 3 cones, all of which were attacked by a fungal pathogen and subsequently turned black. The black cones did not disintegrate making sampling the seed difficult. Other factors resulted in a poor seed sample from the cones in Population B, with fire being one of the main causes. Fire scorched one of the developing female cones in 2014, causing partial disintegration of the cone on the side of the cone not burnt. All fully formed seeds sampled were rested for 10 months to allow for embryo development (Xaba 2014). It was decided that seeds would be tested for germinability by planting out all seeds rather than undertaking the flotation test where seeds are discarded if the float and retained if they sink. Seeds were not dissected to determine viability by confirming the presence of an embryo as any viable seed were considered a source for restoration should any seeds germinate.

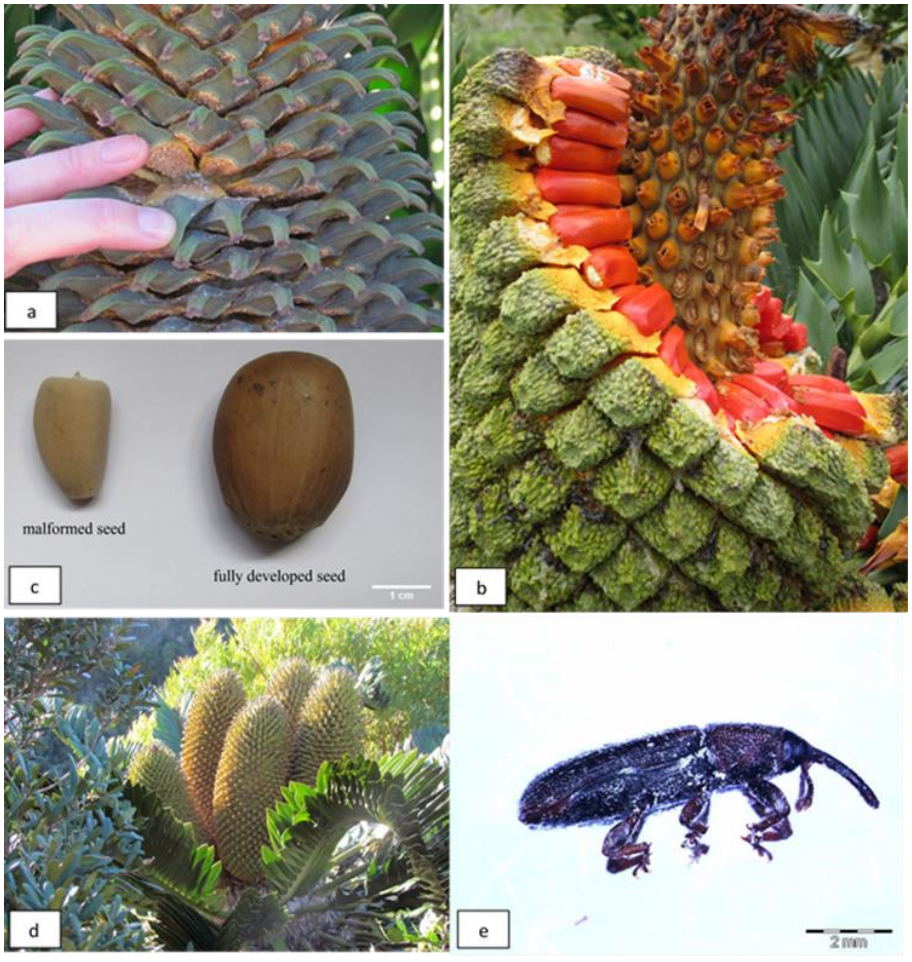


Plate 4.1 *Encephalartos latifrons* male cone showing ruptured pollen sacs (a). Disintegrating *E. latifrons* female cone showing exposed brightly coloured seed (b). The difference in appearance between a malformed seed (left) and a fully developed seed (right) (c). *Encephalartos latifrons* male plant with 5 cones (d). *Porthetes* sp. 2 weevil found in the male cone in Population B (e). Photo (d) courtesy of R. Rowswell

Germinating seed

After the 10 month resting period, seed kernels were sown in a sterilised mixture of vermiculite and seedling soil mix (a fine sandy soil mixture) in individual seedling bags, in November of 2015. Malformed and underdeveloped kernels were not included in the germination experiment as it was clear that these did not contain an embryo and therefore were not viable. Seedlings were kept in a polytunnel structure and watered weekly or bi-weekly when necessary to prevent drying out. Seeds were monitored every day for signs of germination. Seed were considered as germinated when the coleorhiza emerged through the coronula and the date noted. Seeds were monitored for 41 weeks with the experiment terminated in September 2016. This is 11 weeks longer than other *E. latifrons* germination trials conducted (Xaba 2014). The seed samples from all populations experienced the same environmental conditions and watering regime during the germination trial. Seeds that did not germinate during the experimental period were considered not to be viable. They were however retained and were placed in a suitable environment conducive to germination (no more seeds have germinated to date).

Statistical analysis

Variation in seed characteristics

The majority of data were not normally distributed (determined by means of the Shapiro-Wilks test) as samples were of unequal size and variances differed substantially. The Kruskal Wallis non-parametric test was therefore used to test for significant differences between populations based on the three measured seed characteristics. A Mann-Whitney U follow up test was done to determine any significant difference between the groups in a pairwise comparison. For both tests, effect size was calculated to allow the evaluation of the magnitude and importance of the significant result, if obtained (Sullivan and Feinn 2012).

Time to event analysis (germination probability)

The seed data analysed for this paper is right-censored as well as continuous, representing exact germination times. Time-to-event analysis (i.e. survival analysis) was the non-parametric test used to characterise the temporal pattern of germination by means of the Kaplan-Meier estimator of the survivor function S(t) (Bland and Altman 1998) or in this case, the germination probability. As a comparison to other germination studies with *E. latifrons* seed under artificial pollination in the nursery environment, the mean time to germination (MTG) was also calculated. It has been argued however that MTG is a misleading phrase and does not measure the real time to germination but should rather be interpreted as an index of germination speed (Soltani et al. 2015). Most other germination indices such as germinability and germination value are also problematic and do not maximise the use of germination data or do not characterise the temporal pattern of germination (McNair et al. 2012; Soltani et al. 2015).

Results

Microstrobili (male cone) fauna

The insect fauna in the *E. latifrons* microstrobili sampled was diverse with 4 species belonging to the *Porthetes* genus found in male cone across all populations (Table 4.4). Results show that the cones sampled in Population A2 were mostly sterile with a large number of cockroaches for some reason attracted to the cones. One *Porthetes* weevil specimen was found and identified to closely resemble *P. bulboscapus* (Donalson pers. comm.). The insect fauna in Population B comes with the discovery of a new unidentified species of *Porthetes* weevil (*Porthetes* sp. 2) not documented elsewhere in substantially larger numbers than any other *Porthetes* species found on the other cones in other populations in this study (Plate 4.1e). The fauna found in the cones of population B also had by far the most diverse range of insects (flying insects, earwigs) and unidentified spiders found in any other the other cones in this study. Cones sampled from Population C contained 6 *Porthetes* sp. no 3 weevil specimens and a number of unidentified erotylid beetles. One *Porthetes zamiae* weevil was collected by the landowner in cones harvested from Population A1.

Table 4.4 Insect fauna sampled within the microstrobili of *Encephalartos latifrons* male cones from three populations across the species distribution range and one translocated "population". Total number of individuals found on number of cones sampled in brackets. Population C cone sampled twice at 20% pollen shed[a] and again at 100% pollen shed[b].

Site	Date	*Porthetes* species	Total number of *Porthetes* individuals (number of cones sampled in brackets)	*Porthetes* sp. found on other *Encephalartos* species	Total number of Erotid beetles (number of cones sampled in brackets)	Erotid beetles found on other Encephalartos species	Total number of Amorphocerus species (number of cones sampled in brackets)	Amorphocerus species found on other Encephalartos species	Other fauna found in microstrobili
Population A1	unknown	*Porthetes zamiae*	1 (1)	*E. longifolius* (female cone) (Downie et al., 2008); *E. horridus*, E. *lehmannii*, E. *longifolius* (female cone) (R G Oberprieler, 1995)	11 (1)	*E. cycadifolius* (Donaldson et al. 1995); *E. friderici-guilielmi* (Suinyuy et al. 2009)	0 (1)	Amorphocerus found on the female sporophyll and cone axes of the following cycads: *E. cycadifolius*, *E. friderici-guilielmi*, *E. altensteinii*, *E. horridus*, *E. lehmannii*, *E. longifolius, E. middelburgensis*, *E. trispinous*, *E. caffer* and *E. lebomboensis* and on the male and female cones of *E. villosus* (RG Oberprieler, 1995)	
Population A2	06/08/2013	*Porthetes* sp.1 (resembles *P. bulboscapus*)	1 (2)	*E. caffer* (Vorster 1999)	0 (2)		0 (2)		Numerous cockroaches
Population B	30/07/2013	*Porthetes* sp. 2	123 (2)	New unidentified species not documented elsewhere	156 (2)		14 (2)		1 *Phacecorynes variagutus* (usually found in and on decaying trunks)
Population C (wild)	23/08/2013	*Porthetes* sp. 3	6 (1) [a] 0 (1) [b]		48 (1) [a] 31 (1) [b]				

Cone morphology

The mean male cone height for cones sampled in all populations was 501 mm (n = 11; SD ± 57 mm) and the female cone shorter at 421 mm (n = 6; SD±67 mm). The mean circumference of the male cones was narrower at 521 mm (n = 11; SD ± 34 mm) than the female at 755 mm (n = 6; SD ± 96 mm).

Seed morphology

Population B had 22% malformed seeds out of the 227 collected. The female plant with the 3 black cones had 96% of malformed seed in the sample of 47 seeds. The seed collected from the blackened cones contributed to 20% of the malformed seeds in the total sample for Population B. Population A1 had no malformed seed while 14% of the seed sampled from Population A2 were malformed and 4% of the seed in Population C.

Correlation tests of the measured seed characteristics show a relation ($r(438) = 0.78$, $p < 0.0005$)) between seed mass and width for pooled data. Comparison of seed characteristics between populations show that seed width, length and mass were significantly different in their means ($p < 0.0005$; effect size for width = 0.70, length = 0.47 and mass = 0.67). A follow up Mann-Whitney test provides more detail regarding the pair-wise differences in seed characteristics between populations (Table 4.5).

Table 4.5 Mann-Whitney tests (one tailed) for significance between populations based on seed characteristics. P-value reported with effect size in brackets. NS = not significant; WS = Shapiro-Wilk test; m = median; n = number of seeds

Source of variation		Population A1	Population A2	Population B	m	n	Normal distribution (SW)
Length (mm)	A1				30.3	112	No
	A2	< 0.0005 (0.33)			29.8	88	No
	B	< 0.0005 (0.73)	< 0.0005 (0.60)		27.9	170	No
	C	=0.0001 (0.28)	NS	< 0.0005 (0.51)	29.8	59	No
Width (mm)	A1				22.4	113	Yes
	A2	< 0.0005 (0.86)			18.3	89	Yes
	B	< 0.0005 (0.84)	0.007 (0.15)		18.5	175	No
	C	< 0.0005 (0.77)	< 0.0005 (0.72)	< 0.0005 (0.63)	20.8	62	No
Mass (g)	A1				6.8	113	Yes
	A2	< 0.0005 (0.82)			4.6	87	No
	B	< 0.0005 (0.75)	< 0.0005 (0.36)		5.0	171	No
	C	=0.04 (0.13)	< 0.0005 (0.84)	< 0.0005 (0.74)	7.0	60	No

Probability of germinating

Out of the four sites from which seeds were sampled, only one resulted in seed germinating. The smallest population with only two individuals (a male and female coning simultaneously in Population C) had a germination success of 41% out of 62 seeds sampled. The seed sampled from the other populations did not germinate over the experimental period. There was a 5.5-week delay in onset of germination in population C (Table 4.6). After this delay, germination probability decreased steadily until 28 weeks when the last seed germinated. Once 35% of the seed had germinated at 15 weeks, there was a resting period where no seeds germinated for 6 weeks until into the 21st week when the remainder of the 26 seeds out of the sample germinated. The last seed germinated at 28 weeks (a second resting period). The MTG index was calculated as 11 weeks.

Table 4.6 Time-to-event analysis of germinating seed from population C showing the Kaplan-Meier estimator of the survivor function (germination probability) at time t; d = the number of seeds germinating at time t; n = the number of seeds at time t; s.e. = standard error and 95% confidence intervals = lower and upper values

t (weeks)	*Germination percentage*	*Germination success*	*n*	*1-d/n*	*Germination probability*	*s.e.*	*lower*	*upper*
0	0	0	62		1			
5.5	13	8	62	0.87	0.87	0.04	0.76	0.93
7	18	3	54	0.94	0.82	0.05	0.70	0.90
8	21	2	51	0.96	0.79	0.05	0.67	0.87
9	26	3	49	0.94	0.74	0.06	0.61	0.83
11.6	27	1	46	0.98	0.73	0.06	0.60	0.82
12.6	29	1	45	0.98	0.71	0.06	0.58	0.81
14.6	32	2	44	0.95	0.68	0.06	0.55	0.78
15.2	35	2	44	0.95	0.65	0.06	0.51	0.75
21.3	37	1	40	0.98	0.63	0.06	0.50	0.74
22.3	39	1	39	0.97	0.61	0.06	0.48	0.72
23.5	40	1	38	0.97	0.60	0.06	0.47	0.71
28	42	1	37	0.97	0.58	0.06	0.45	0.69

Discussion

Insect fauna in male cones

This is the first comprehensive survey of insect fauna in *E. latifrons* male cones across a number of populations. Previous samples of weevil species on *E. latifrons* male cones are only included from Population A1 (Downie et al. 2008). The weevil found in Population A1, *Porthetes zamiae*, has also been found in the female cones of *E. longifolius* (Downie et al. 2008). This adds another species sampled for the A1 population to the *P. dissimilis1* found in 2004 (Downie et al. 2008). The translocated A2 population A2 is considered sterile with only one *Porthetes* specimen resembling *P. bulboscapus* (J. Donaldson pers. comm.), a species also associated with *E. caffer* (Vorster 1999), found in one of the two cones sampled. The Grahamstown Cycad, or *Encephalaros caffer* has a relatively widespread distribution extending from Humansdorp and into the former Transkei region as far east as Willowvale (Kemp 1985). Specimens of *E. caffer* also have an affinity to rocky outcrops in open grassland areas and have been found growing close to *E. latifrons* Population B. It is likely that there are *E. caffer* populations close to the translocated A2 "population". Insect samples from this study indicate that if there was a weevil population associated with the cones of population A2 it no longer exists. The reason for the large number of cockroaches found in the fresh male cones is unknown but this is not unusual as they are regularly found in cones of other *Encephalartos* species (J. Donaldson pers. comm.) such as those found to be attracted to the decomposing female cones of *E. friderici-guilielmi* (Suinyuy et al. 2009).

The health of the weevil population in the cones of Population A2 before the plants were stolen from the original population (A1 Population) was never determined, but a survey of the *E. latifrons* A1 Population (including the A2 plants before they were uprooted at the site) undertaken in 1991 indicated that the population was naturally recruiting with 4 natural seedlings found at the site (Basson 1991). Natural self-recruitment was also confirmed by the recent discovery of an *in situ* population of *E. latifrons* that is producing numerous seedlings through natural pollination (Population B - first author unpublished data). The insect fauna found in the male cones of Population B was the most diverse compared to the other populations and had by far the highest number of *Porthetes* specimens (123) in the two cones sampled. The cones also harboured a variety of other insects such as *Amorphocerus* weevils, unidentified

erotylid beetles, a *Phacecorynes* weevil (stem-borer) and other insect fauna. The stem-borer weevil is almost exclusively associated with dead or dying trunks of Encephalartos where it tunnels in the old leaf bases and lives a realtively elusive life inside the stem of the cycad (RG Oberprieler 1995) and its interesting that this is the first published record of a specimen found in the male cone of a cycad.

The *Porthetes* weevil in the cones of Population B was identified as a new undocumented species (Donaldson pers. comm). The presence of *Porthetes* and erotylid beetles in the male cones of Populaiton B, as well as natural seedlings in the population means that functional pollination systems could still be intact within some *E. latifrons* populations. The role of erotylid beetles in the pollination of cycads is often underplayed (Oberprieler 2004) but definitive studies have shown that they play an important role in the pollination of some South African species (Donaldson et al. 1995; Donaldson 1997; Suinyuy et al. 2009) and may be the exclusive pollinators in several Asian species of cycads (Tang et al. 1999), as well as important pollinators in certain *Zamia* species in the Americas (Chaves and Genaro 2005; Valencia-Montoya et al. 2017). Recent fossil evidence also suggests that erotylids may have been a widespread and diverse group of insects in the Mesozioc and their association with cycads may be older than previously thought (Liu et al. 2017). This was the only population where Amorphocerus weevils were found (albeit in low numbers). This is not unusual as Amorphocerus are found predominantly on female cycad cones where the larvae feed and tunnel in the cone axis and play an important role in the distintegration of the female cone rather than play the role of a pollinator (Oberprieler 1995).

The male cones in Population C matured later than cones in other populations. A relatively low number (6 specimens) of *Porthetes* weevil specimens were found in the male cones at 20 – 25 % pollen shed. A large number of unidentified erotylid beetles were however found in the cone (48 specimens) at the same stage of cone dehiscence. Resampling the cone resulted in no further *Porthetes* weevils found but a number of eryotid beetles still remained. The insects were initially sampled with the cone still attached to the plant which may have resulted in an underepresentative sample of insect fauna compared to Population B. Most *Porthetes* weevils (with the exception of *P. zamie*) develop in the microsporophylls once the cone has matured and shed pollen (Oberprieler, 1995). Pupation occurs in sporophyll cavities with the adult remaining in the cativities until the next coning season (Oberprieler 1995). It is possible that because the male cone was re-sampled while it was at an advanced stage of dessication, explains

the fact that no *Porthetes* weevils were visible as they had already pupated and were present but not obvious in the sample.

The insect fauna found in these *in situ E. latifrons* cones reveal that the cones may be host to a range of insect species, some of them potential specialist and/or generalist pollinators. In other southern African cycads, species of cycad are known to share the same pollinator species such as *Metacucujus encephalarti* implicated in the pollination of *E. cycadifolius* (Donaldson et al. 1995) and *E. friderici- guilielmi* (Suinyuy et al. 2009). Research has shown that a diversity of insects is involved in the pollination of cycad species within the genus *Encephalartos,* some appearing to be generalists while others specialist pollinators (Terry et al. 2012). The presence of *Porthetes* and erotylid beetles in self-pollinating (Population C) populations give hope to the idea that pollinator transfer might be possible where the original pollinator population has declined or disappeared (Donaldson 1995).

Seed malformation

Population B had the highest number of underdeveloped seeds yet it is the only known self-sustaining *E. latifrons* population known to exist with seedlings making up 55% of the population (first authors unpublished data). Fungal pathogen attacking three cones contributed to the high number (22%) of malformed seeds in this population (relative to the other populations sampled). One cone was also partially burnt destroying the cone and undoubtedly the seeds which did not germinate. A suite of fungal species is known to affect cycad populations in the *Encephalartos* genus not uncommon in wild populations (Nesamari et al. 2017). Reports of seed loss through aborted and malformed seeds are however limited in the published literature. One study by Mora et al. (2013) though reported that 42.5% of seed loss in the Mexican cycad, *Dioon edule*, was attributed to abortive ovules and malformed seeds, possibly as a result of limited pollination. Species of *Encephalartos* are nonetheless different in that unpollinated ovules remain fulled developed and are not aborted if they are not pollinated (Donaldson 1997). Similarities in the morphologies of abortive vs. developed seeds are however evident in the *D. edule* and *E. latifrons* populations (Mora et al. 2013; this study). Other populations in the study had either no malformed seeds (one cone from Population A1), or a limited number malformed seeds (Populations A2 and C). Reasons for the development of malformed seeds in the cones from Populations A2 and C is unknown but cannot be attributed to fire or any noticeable disease as with Population

B. The cone structure in some cases may contribute to the formation of sterile omnules (sensu Grobbelaar 2004) where seeds at the very top or bottom of the cone may be malformed (J. Donaldson pers. comm). It was difficult to determine if this was the reason for the malformed seeds as samples were often collected on the ground from an already disintegrated female cone. Futher investigation is needed to determine what factors may result in malformed seeds on a maturing female cone exploring the possible effects of fire and pathogens.

Seed morphology and germination

There were significant differences in seed characteristics (length, width and mass) among all populations. The only sample of seeds to germinate was from Population C (two plants in the population a few meters apart). The seed characteristics of Population C compared to the other populations where none of the seeds germinated is therefore focussed upon in this paper to determine if characteristics of the germinating seeds differ from non-germinating seeds. Seed characteristics of Population C showed the most significant difference from the other populations in width and mass. Population A seeds were visibly larger and measured significantly wider than Population C, while seeds from Population A2 and B measured significantly shorter in width from the seeds sampled in Population C. The mass of seeds in Population C were however significantly heavier than seeds from the other populations with a median measurement of 7 grams. It was at this mass that seeds were more likely to germinate from the Population C sample. Mass as predictor of potential germiniability therefore shows more promise than either length or width of the seeds. A germination success rate of 41% in Population C through natural pollination considered excellent compared to the low germination rates of *E. latifrons* achieved by artificial pollination in *ex situ* collections (Whitelock 1995; Xaba 2014). There is no natural seedling recruitment occurring in Population C but the results from this study confirm that lack of natural pollination is unlikely to be the cause. The seedlings germinated from the Population C sample in this study were planted around the male and female plants as part of an attempt to restore the seedlings back into the population. Subsequent monitoring of the site revealed intense grazing on the new leaves of the seedlings where the entire seedling would be uprooted by grazing livestock (primarily sheep revealed by camera traps placed at the site). It is not uncommon for livestock to graze on cycads (Hooper 1978; Schneider et al. 2002) sometimes resulting in severe cycad toxicosis (Reams et al. 1993; Hall and

McGavin 1968; Shimizu et al. 1986). Reams et al (1993) identified *Zamia puertoriquensis* as the primary cause of death in dairy heifers on a farm in Puerto Rico and noted that the new leaves on the cycads were grazed extensively and sometimes the kernels also eaten.

After 10 months of storage, the mean germination time of 11 weeks for the Population C seeds was less than those reported for the germination of seeds pollinated artificially in botanical garden collections at 19 weeks after 8 months of storage and 15 weeks at 6 months of storage (Xaba 2014). The time to event analysis indicated that germination in the *E. latifrons* sample was staggered with two resting periods of between 5 to 6 weeks. The first resting period occurred at 15.2 weeks after 35 % of the seeds had germinated and the second at 23.5 weeks after 40% of the seeds had germinated. The temporal pattern and dispersion in time of cycad seeds germination is lacking in the published literature. We do however know that in other species such as those belonging to the genus Eugenia (evergreen trees found in the dry forests of Jamaica) display a similar staggered germination pattern with two peak periods of germination at 4 and 8 weeks after planting (Mclaren and Mcdonald 2003). Mclaren and Mcdonald (2003) attributed this temporal pattern of germination to the fact that seeds become permeable to water at different times resulting in the staggered germination of seeds from the same cohort. This ultimately results in staggered seedling recruitment particularly important in some regions of South Africa given the intra-annual variability in climate and occurrence of fires (Wilson et al. 2010). This bet-hedging increases the probability of seeds surviving and germinating when conditions are favourable (Khurana and Singh 2000; Hudson et al. 2015). As this study included only a small sample of seed displaying a staggered germination pattern, further germination studies will confirm if this is a common germinaton pattern for *E. latifrons* (and cycads in general).

Conclusions

Results from this study indicate that there is a diversity of insect fauna associated with the male cones in wild *E. latifrons* populations. A number of different *Porthetes* species were found to be associated with different *E. latifrons* populations in the wild. Investigation into the role these potential pollinators play and the host-pollinator relationship is needed for *E. latifrons*. Further entomological studies are also

recommended with the inclusion of an in-depth taxonomic and molecular investigation of this finding.

This study also reveals that *E. latifrons* is capable of natural seedling recruitment in some wild populations as well as seed set under conditions of natural pollination. Lack of recruitment cannot always be attributed to lack of pollination and seed set in wild populations. Likewise, successful fertilization of ovules by natural pollination in wild populations is not the only determinant of germination success. Germination response (seed survival/seedling emergence) in many natural plant populations in fire prone landscapes is regulated by fire cues, environmental stress (including temperature and water availability), herbivory, pathogens, and inbreeding depression amongst others (Bell et al. 1993; Schupp and Jordano 2010; Thomas et al. 2010; Li et al. 2012).

E. latifrons appears to display certain traits that may indicate a certain resilience to disruption in the pollinator mutualisms (Bond 1994) given the fact that populations are not demographically dependant on seeds due to asexual reproduction by suckering, long-life span of hundreds of years of individual plants and capacity to resprout vegetatively after a fire. Nevertheless, artificial pollination of *in situ* populations (a possible threat to pollinator populations) should be done in a manner where the methods involved do not pose a risk to pollinator populations that may exist or become re-established in wild populations. It is important that when advocating artificial pollination as a conservation strategy in wild cycad populations (Grobbelaar 1992) that the cautionary principle is adopted (Marler and Lindtrom 2017) not to disrupt the delicate plant-pollinator mutualisms that may still exist or have the potential to recover from disturbances. Population A was naturally recruiting as recently as 1991 and lack of recruitment in the population may not only be due to a lack of natural pollination. Cycad populations may take years to recover from disturbances such as the theft of adult plants from a population (Vice 1995) and this cannot be discounted as a possible reason for lack of seedlings recruitment at a site. Further research into the impact of livestock grazing on cycad populations needs further study.

Seed malformation is common in some wild *E. latifrons* populations. External factors such as pathogens and fire during coning periods may play a role in the formation of underdeveloped seeds. The viability of seeds is also difficult to determine from the morphological characterises of seeds but seed mass necessities further exploration as an indicator of seed viability. The germination of a sample from a single

wild female cone did not allow for the comparison of the timing and temporal pattern of germination between populations. There are indications however that *E. latifrons* may exhibit a staggered germination pattern of seeds in wild populations, possibly an adaptive evolutionary trait ensuring that some seeds survive to germinate in stochastic environments such as fire-prone regions.

References

Baskin JM, Baskin CC (2004) A classification system for seed dormancy. Seed Sci Res 14:1–16

Basson M (1991) Eerste verslag wat die bron en status van die *Encephalartos* spesies in die Trappe's Valley area in die Oos-Kaap aandui met spesiale verwysing na die *Encephalartos latifrons*. Cape Nature Conservation Survey Report, South Africa

Bell DT, Plummer JA, Taylor SK (1993) Seed Germination Ecology in southwestern western Australia. Bot Rev 59:24–73

Bergh NG, Verboom GA, Rouget M, Cowling RM (2014) Vegetation types of the Greater Cape Floristic Region. In: Allsop N (ed) Fynbos: Ecology, evolution and conservation of a megadiverse region. Oxford University Press, pp 1–25

Bland JM, Altman DG (1998) Statistics notes—time to event (survival) data. Br. Med. J. 317: 468–469

Bond WJ (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Phil. Trans. R. Soc. Lond. B. 344:83–90

Brookes DR, Hereward JP, Terry LI, Walter GH (2015) Evolutionary dynamics of a cycad obligate pollination mutualism – pattern and process in extant *Macrozamia cycads* and their specialist thrips pollinators. Mol Phylogenet Evol 93:83–93

Chamberlain CJ (1919) The living cycads. Hafner Publishing Company, New York and London

Chaves R, Genaro JA (2005) A new species of *Pharaxonotha* (Coleoptera: Erotylidae), probable pollinator of the endangered Cuban cycad, *Microcycas calocoma* (Zamiaceae). Insecta mundi 19:143–150

Cousins SR, Witkowski ETF (2017) African cycad ecology, ethnobotany and conservation: a synthesis. Bot Rev 83:152–194

Crosiers C, Malaisse FP (1995) *Ex situ* pollination and multiplication *Encephalartos laurentianus* De Wild. (Zamiaceae, Cycadales). Biodivers Conserv 4:767–775

Da Silva J, Donaldson JS, Reeves G, Hedderson TA (2012) Population genetics and conservation of critically small cycad populations: a case study of the Albany Cycad, *Encephalartos latifrons* (Lehmann). Biol J Linn Soc 105:293–308

Daly B, Donaldson JS, Friedmann Y, Hahndiek Q, King N, Newton D and Southwood A (editors) (2006) Population and habitat viability assessment for the Albany cycad (*Encephalartos latifrons*). Conservation Breeding Specialist Group (SSC /IUCN) / CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg

Department of Environmental Affairs (2011) Biodiversity Management Plan for Albany Cycad, *Encephalartos latifrons*. National Environmental Management: Biodiversity Act (10/2004): South African Government Gazette No. 34388

Donaldson JS (1993) Mast-seeding in the cycad genus *Encephalartos*: a test of the predator satiation hypothesis. Oecologia 94:262–271

Donaldson JS (1995) The Winterberg cycad: surviving against the odds. Veld Flora 81:36–39

Donaldson JS, Nanni I, de Wet Bosenberg J (1995) The role of insects in the pollination of *Encephalartos cycadifolius*. In: Vorster P (ed) Proceedings of the Third International Conference on Cycad Biology. Cycad Society of South Africa, Stellenbosch, South Africa., pp 423–434

Donaldson JS (1997) Is there a floral parasite mutualism in cycad pollination? The pollination biology of *Encephalartos villosus* (Zamiaceae). Am J Bot 84:1398–1406Donaldson J (2003) Cycads: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK

Donaldson JS (2010) *Encephalartos latifrons*. In: IUCN List Threat. Species. http://www.iucnredlist.org/details/41892/0. Accessed 8 Sep 2017

Downie DA, Donaldson JS, Oberprieler RG (2008) Molecular systematics and evolution in an African cycad-weevil interaction: *Amorphocerini* (Coleoptera: Curculionidae: Molytinae) weevils on *Encephalartos*. Mol Phylogenet Evol 47:102–116

Fourie SP (1986) The Transvaal (South Africa) Threatened Plants Programme. Biol. Conserv. 37:23–42

Giddy C (1974) Cycads of South Africa, First Edit. Purnell and Sons Pty Ltd, Cape Town

Grobbelaar (1992) A more realistic conservation strategy for the South African cycads. Encephalartos 32:15-18

Grobbelaar N (2004) Cycads - with special reference to the southern African species, First Edit. Published by the author, Pretoria

Hall WTK and McGavin MD (1968) Clinical and neuropathological changes in cattle eating the leaves of *Macrozamia zucida* or *Bowenia serrulata* (family Zamiaceae). Pathol. Vet 5: 26 - 34

Hooper PT (1978) Cycad poisoning in Australia: etiology and pathology. In: Keeler R, van Kampen KR, James LF (eds) Effects of poisonous plants on livestock. Academic Press, New York, pp 337–347

Hudson AR, Ayre DJ and Ooi MKJ (2015) Physical dormancy in a changing climate. Seed Sci Res 25:66–81

Kay J, Strader AA, Murphy V, Nghiem-Phu L, Calonje M and Griffith MP (2011) *Palma corcho*: A case study in botanic garden conservation horticulture and economics. Public Hortic 21:474–481

Kemp HJ (1985) Focus on *Encephalartos caffer*. Encephalartos 3: 6-11

Kemp HJ (1986) Focus on *Encephalartos latifrons*. Encephalartos 8:8–15

Khurana E, Singh JS (2000) Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ Conserv 28:39–52

Klavins SD, Kellogg DW, Krings M, Taylor EL and Taylor TN (2005) Coprolites in a Middle Triassic cycad pollen cone: evidence for insect pollination in early cycads? Evol Ecol Res 7:479–488

Labandeira CC, Kvaček J, Mostovski MB (2007) Pollination drops, pollen and insect pollination of Mesozoic Gymnosperms. Taxon 56:663–695

Leschen RAB (2003) Erotylidae (Insecta: Coleoptera: Cucujoidea): phylogeny and review. Fauna of New Zealand 47: 108pp

Li Y-Y, Tsang EPK, Cui M-Y, Chen X-Y (2012) Too early to call it success: An evaluation of the natural regeneration of the endangered *Metasequoia glyptostroboides*. Biol Conserv 150:1–4

Liu Z, Slipinski A, Lawrence JF, Ren D, Pang H (2017) Palaeoboganium gen. nov. from the Middle Jurasic of China (Coleoptera: Cucujoidea: Boganiidae): the first cycad pollinators? Journal of Systematic Palaeontology 16(4): 351 - 360

Marler TE, Lindström AJ (2015) Carbohydrates, pollinators, and cycads. Commun Integr Biol 8:6–9

Marler TE and Lindstrom AJ (2017) First do no harm. Communicative and Integrative Biology, 10:5-6, e1393593

Mclaren KP, Mcdonald MA (2003) The effects of moisture and shade on seed germination and seedling survival in a tropical dry forest in Jamaica. For Ecol Manage 183:61–75

McNair JN, Sunkara A, Frobish D (2012) How to analyse seed germination data using statistical time-to-event analysis: non-parametric and semi-parametric methods. Seed Sci Res 22:77–95

Mora R, Yáñez-espinosa L, Flores J (2013) Strobilus and seed production of *Dioon edule* (Zamiaceae) in a population with low seedling density in San Luis Potosí, Mexico. Trop Conserv Sci 6:268–282

Nesamari R, Coutinho TA, Roux J (2017) Investigations into *Encephalartos* insect pests and diseases in South Africa and identification of *Phytophthora cinnamomi* as a pathogen of the Modjadji cycad. Plant Pathol 66:612–622

Norstog KJ, Fawcett PKS (1989) Insect-cycad symbiosis and its relation to the pollination of *Zamia furfuracea* (Zamiaceae) by *Rhopalotria mollis* (Curculionidae). Am J Bot 76:1380–1394

Oberprieler RG (1995) The weevils (Coleoptera: Curculionoidea) associated with cycads. I. Classification, relationships, and biology. In: Vorster P (Ed). Proceedings of the third international conference on cycad biology. 295 – 334. Cycad Society of South Africa, Stellenbosch, South Africa

Oberprieler RG (2004) "Evil weevils" – the key to cycad survival and diversification? In. Lindstrom A (Ed). Proceedings of the 6th International Cycad Conference on Cycad Biology. Pattaya, Thailand 2002: 170 – 197. Nooch Tropical Botanical Garden, Thailand

Pearson HHW (1916) The Kirstenbosch Cycads. J Bot Soc 2:7–13

Proches S, Johnson SD (2009) Beetle pollination of the fruit-scented cones of the South African cycad *Stangeria eriopus*. Am J Bot 96:1722–1730

Reams RY, Janovitz EB, Robinson FR, Sullivan JM, Casanova CR, Más E (1993) Cycad (*Zamia puertoriquensis*) toxicosis in a group of dairy heifers in Puerto Rico. J Vet Diagn Invest 5:488–494

Rebelo AG, Boucher C, Helme N, Mucina L and Rutherford MC (2006) Fynbos Biome. In: Mucina L, Rutherford MC (eds) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, South Africa. pp 53–219

Schneider D, Wink M, Sporer F, Lounibos P (2002) Cycads: their evolution, toxins, herbivores and insect pollinators. Naturwissenschaften 89:281–294

Schupp EW, Jordano P (2010) Tansley review: seed dispersal effectiveness revisited: a conceptual review. New Phytol 188:333–353

Shimizu T, Yasuda N, Isaburo K Shimizu T, Kono I, Yagi F, Tadera K, Kobayashi A. (1986) Hepatic and spinal lesions in goats chronically intoxicated with cycasin. Jpn. J. Vet. Sci. 48:1291 - 1295

Soltani E, Ghaderi-Far F, Baskin CC, Baskin JM (2015) Problems with using mean germination time to calculate rate of seed germination. Aust J Bot 63:631–635

Suinyay TN, Donaldson JS, Johnson SD (2010) Scent chemistry and patterns of thermogenesis in male and female cones of the African cycad *Encephalartos natalensis* (Zamiaceae). South African J Bot 76:717–725

Suinyay TN, Donaldson JS, Johnson SD (2009) Insect pollination in the African cycad *Encephalartos friderici-guilielmi* Lehm. South African J Bot 75:682–688

Sullivan GM, Feinn R (2012) Using effect size - or why the p value is not enough. J Grad Med Educ 4:279–282

Tang W, Oberprieler RG, Si_lin Y (1999) Beetles (Coleoptera) in cones of Asian Cycas: diversity, evolutionary patterns, and implications for Cycas taxonomy. In: Chen CJ (Ed). Biology and conservation of cycads. Proceedings of the 4th International Conference on Cycad Biology pp 280 – 297. International Academic Publishers, Beijing

Terry I (2001) Thrips and weevils as dual, specialist pollinators of the Australian cycad *Macrozamia communis* (Zamiaceae). Int J Plant Sci 162:1293–1305

Terry I, Tang W, Taylor Blake AS, Donaldson JS, Singh R, Vovides AP and Jaramillo AC (2012) An overview of cycad pollination studies. Mem New York Bot Gard 106:352–394

Terry I, Walter GH, Moore C, Roemer R, Hull C (2007) Odor-mediated pollination push-pull in cycads. Sci New Ser 318(5847):70

Thomas PB, Morris EC, Auld TD, Haigh AM (2010) The interaction of temperature, water availability and fire cues regulates seed germination in a fire-prone landscape. Int Assoc Ecol 162:293–302

Valencia-Montoya WA, Tuberquia D, Andres Guzman P, Cardona-Duque J (2017) Pollination of the cycad Zamia incognita A. Lindstr. & Idarraga by Pharaxonotha beetles in the Magdalena Medio Valley,

Colombia: a mutualism dependent on a specific pollinator and its significance for conservation. Arthropod-Plant Interactions 11(5): 717-729

Vice A (1995) *Encephalartos altensteinii*: A massive rape and recovery. Encephalartos 1:15–19

Vorster (1999) A review of the arborescent tropical species of *Encephalartos* In: Chen CJ (Ed). Biology and conservation of cycads. Proceedings of the 4th International Conference on Cycad Biology. Panzhihua, China. Academic Publishers, Beijing

Vorster, P. & Oberprieler RG (1999) Entomological evidence for and against taxonomical decisions in *Encephalartos*. In: Chen, C.J. (ed). Biology and conservation of cycads. Proceedings of the 4th International Conference on Cycad Biology, Panzhihua, China. International Academic Publishers, Beijing

Vovides AP, Ogata N, Sosa V, Peña-García E (1997) Pollination of endangered Cuban cycad *Microcycas calocoma* (Miq.) A. DC. Bot J Linn Soc 125:201–210

Wilson AM, Latimer AM, Silander Jr. JA, Gelfand AE and Klerk H (2010) A Hierarchical Bayesian model of wildfire in a Mediterranean biodiversity hotspot: implications of weather variability and global circulation. Ecological Modelling 221: 106 - 112

Whitelock LM (1995) Cycad Conservation in the past and the need for improvements in the future. In: Vorster P (ed) Proceedings of the Third International Conference on Cycad Biology. Cycad Society of South Africa, Stellenbosch, South Africa., pp 1–8

Xaba P (2014) Pollination and germination as limiting factors in the propagation of threatened cycads, *Encephalartos* (Zamiaceae). MSc thesis. University of the Western Cape, South Africa, pp 1 - 138

CHAPTER 5

Augmentation of a wild *Encephalartos latifrons* population: lessons for future conservation efforts

[Target journal: Biological Conservation]

Abstract

Cycads are one of the most globally threatened organisms, with some species experiencing little to no recruitment in the wild. For such species, species recovery in the form of restoration or augmentation of populations may be the only conservation solution left to save species from extinction in the wild. Restoration/augmentation programmes are stressed as a priority for *E. latifrons* which is considered functionally extinct. This study comprises the augmentation of an *E. latifrons* population consisting of 2 individuals, a male and female adult plant, with 25 seedlings originating from the female plant as part of a seed viability experiment. The population occurs on a commercial livestock farm where livestock activity is considered a threat to the persistence of the small population. The threat from livestock was mitigated for by fencing off the population as part of the recovery experiment. Seedlings were planted both inside and outside the fenced area and survival monitored over 391 days. Kaplan-Meier estimates of the survivor function was calculated for the two planting sites to determine if there is a difference in survival rates of seedlings inside and outside the fence. A high percentage of seedling mortality was experienced on both sides of the fenced enclosure with only 8% of seedlings surviving the monitoring period in total. None of the seedlings survived in the exposed site outside the fenced enclosure while 12% (n = 2) seedlings survived inside the fenced enclosure over the monitoring period. The primary cause of seedling deaths at both sites included: uprooting, defoliation and in some cases seedlings were missing altogether. This study found that lack of seedling recruitment in this population was as a result of livestock activity at the site. Grazing poses a significant threat to cycad recovery at this site. Alternative recovery methods are suggested including the use of seeds placed in suitable microhabitats (e.g. rock fissures) inaccessible to grazing livestock, important in the early seedling developmental stages.

Keywords: restoration, herbivory, livestock, survival analysis

Introduction

Previously regarded as an ancient group of gymnosperms, modern-day cycads are now known to have recently diversified from a few ancestor species in late Miocene (Crisp and Cook 2011; Nagalingum et al. 2011; Yessoufou et al. 2014). Cycads are one of the most globally threatened group of organisms (Hoffmann et al. 2010) with some species experiencing little to no recruitment in the wild (Cousins and Witowski 2017). Habitat restoration as a conservation intervention may not be adequate on its own where the natural recovery of a species is restricted by lack of regeneration (Godefroid et al. 2011). In such situations, population augmentation may be required to mitigate against extinction in the wild (Maunder 1992). In this study, augmentation (also known as reinforcement), is defined as the attempt to increase the size of a population by adding individuals to an *in situ* population (Ackeroyd and Wyse Jackson 1995; IUCN/SSC 2013). Reintroduction is the controlled planting of material (seeds/propagules) into a natural or managed ecological site and to enable populations to become self-sustaining where the species had once occurred but is now extirpated (Ackeroyd and Wyse Jackson 1995; IUCN/SSC 2013). Both definitions are included in the general concept of species recovery - an attempt to improve the survival prospects of an endangered species across its natural distribution range either by the augmentation or reintroduction of propagules/seedlings.

The life history of a species, as well as the type and size of propagule used for recovery, determines the survival success and persistence of a restored plant population (Albrecht and Maschinski 2012). Cycads are generally long-lived woody perennials with slow life histories (Donaldson 1995, 2003; Whitelock 2002; Cousins and Witkowski 2017). Consequently, there are certain challenges for recovery plans involving cycads making such plans difficult to implement (Donaldson 2003). There are very few successful reintroduction projects reported in the published literature such as the successful restoration of *Cycas debaoensis* populations in China (Ren et al., 2012). Other recent species recovery programmes such as the planting of 6 400 seeds of *Encephalartos whitelockii* in Western Uganda and the establishment of new populations of *Zamia* species in Colombia are in their early stages and its too early to tell of their success (http://www.saveourspecies.org/our-projects/our-projects/plants accessed 14-08-2018).

The use of whole plants, preferably larger older propagules, increases the probability of recovery success for long-lived perennials (Albrecht and Maschinski 2012). Albeit, the time and costs involved in growing and sustaining cycad propagules to reach the ideal age and size would be a limiting factor for any cycad recovery programme. Due to their slow growth and long times to maturity, the success of a recovery project and assessment of self-sustainability by natural recruitment would take decades to determine (Maunder 1992; Maschinski and Duquesnel 2006). Furthermore, if pollination failure is the primary cause for lack of regeneration in certain populations of threatened and endangered cycad species (Vovides et al. 1997; Donaldson 2003; Daly et al. 2006; Octavio-Aguilar et al. 2017), pollinator restoration would have to be incorporated into the recovery plan for it to have any chance of success (Dixon 2009). This is in addition to the usual considerations for any recovery programme involving threatened plants such as the choice of suitable habitat, climate requirements, founder source and size, genetics and legislative requirements (IUCN/SSC 2013; Maschinski and Haskins 2012).

The notion of latent extinction was referred to by Janzen (2001) to explain how some trees in the Cosa Rican rainforest constitute what is termed "the living dead". These are non-reproductive rainforest trees living out their physiological lives with no young trees to replace them once they die. This is because the circumstances that once allowed them to reproduce (though pollination/seed dispersal/sapling survival) no longer exists. This is the situation for other threatened species such as *Pinus sylvestris* where regeneration is prevented by high levels of seed predation (Castro et al. 1999) and the previously threatened *Taxus baccata* where recruitment is inhibited by lack of nurse plants to facilitate germination and establishment of seedlings (Garcia et al. 2000; see also conclusion in Chapter 7). Examples of "living dead" cycads include *Encephalartos latifrons* (Cousins and Witowski 2017; Donaldson 2003; Daly et al. 2006; see also Chapter 3 and 4), *Microcycas calocoma* (Vovides et al. 1997) and *E. middelburgensis* (Xaba 2014), where recruitment failure in the wild is purportedly caused by pollinator extinctions in the populations that remain. Recovery programmes in South Africa involving *E. latifrons* and *E. middelburgensis* have met with little success (Donaldson 2003; Daly et al. 2006; Rousseau and Rousseau 2011; Swart et al. 2018; see also Chapter 2). One *E. latifrons* landowner however reports a high germination rate from artificial pollination of an *in situ* population on his property (Xaba 2014) and subsequent high survival percentage of planted *E. latifrons* propagules

in the wild near the existing population on his property (*E. latifrons* owner pers. comm.). It is from these informal attempts at species recovery that there is hope for the future success of recovery efforts for CR cycads around the world.

The Biodiversity Management Plan (BMP-S) for *Encephalartos latifrons* (Department of Environmental Affairs 2011) encourages the manipulation and artificial pollination of *in situ* populations on private land on the premise that the species is considered to be "living dead" without successful seed set. The primary aim of the BMP is therefore to create and maintain an enabling environment for an *E. latifrons* breeding programme to produce seedlings for reintroduction/augmentation of existing populations or the reintroduction of populatios where the species has been extirpated. This is further supported by the National Strategy and Action Plan for the Management of Cycads in South Africa, where a need to determine suitable sites for cycad introduction and/or reintroduction to increase the reproductive success of cycads in the wild was identified (DEA 2014). This is in line with South Africa's Strategy for Plant Conservation which aims to have at least 1% of all threatened species in active reintroduction programmes by 2020 (Raimondo 2015) and underpinned by the Global Strategy for Plant Conservation (2011 – 2020) to have at least 20% of threatened species available for recovery and restoration programmes (Convention on Biological Diversity 2011a). This is further supported by Aichi biodiversity target 12 to prevent the extinction of known threatened species and improve their conservation status by 2020 (Convention on Biological Diversity 2011b).

There are currently (at the time of this study) over 160 propagules (ranging from seedlings to juveniles) of *E. latifrons* available to conservation authorities for reintroduction and/or augmentation programmes (Q. Hahndiek pers. comm.). An attempt by the author at initiating a recovery programme with this material, primarily for this research project, has been unsuccessful for a number of reasons (Chapter 2). It was thus fortunate that 25 seedlings resulting from the seed viability experiment (Chapter 4: Population C) were available for augmenting an existing *in situ* population of only two adult plants, a male and female. The seedlings used in this research project are a product of natural pollination between these two plants on privately owned land (Chapter 4). There is no natural recruitment (i.e. no seedling or juvenile plants) at this site, supporting the notion that the population is too small to be a viable naturally recruiting population (Cousins and Witkowski 2017).

The primary aim of this augmentation project was to determine the possible cause for lack of regeneration at a site where two *in situ* adult plants (making up what remains of the population) are successfully producing viable seeds by natural pollination. The extensive grazing activity at the study site is considered to be a major threat to seedling recruitment and natural regeneration. The second aim of the study was to determine if the survival of planted seedlings at the site was improved by removing the livestock threat.

Materials and methods

Study species and site

Encephalartos latifrons is a long-lived perennial, dioecious cycad having the reputation of being one of the slowest growing member of the Cycadales (Kemp 1986). Female plants growing in the wild reach reproductive maturity at approximately 35 cm stem height (see Chapter 3). The size at first coning for male plants has not yet been reported. Male plants cone more frequently than female plants (pers. obs.). Female plants cone infrequently (3 – 5 years between coning episodes) and after the cones ripen they spontaneously disintegrate in December/January releasing the seeds (Grobbelaar 2004). Seeds require a resting period of at least six months before they are ready to germinate (see Chapter 4). Throughout its distribution, *E. latifrons* grows predominantly on Quartzite outcrops associated with Suurberg Quartzite Fynbos vegetation (SQF - Rebelo et al. 2006; see also Chapter 2). Only four populations of the species are known to remain, three of which are not self-sustaining and do not naturally recruit seedlings. One of these three 'living dead' populations consists of only two individuals (hereafter referred to as Population C introduced in Chapter 4). The fourth population, recently discovered, consists of a healthy population that is naturally recruiting (hereafter referred to as Population B introduced in Chapter 3). In addition to these four known populations, there are individual plants scattered throughout the species distribution range where once larger populations existed.

The study site exists on a privately owned cattle and livestock ranch where a larger *in situ* population of *E. latifrons* once occurred (personal communication with the landowner whose family has lived on the farm for over 100 years). The remaining two adult plants (male and female), grow a meter apart on a rocky outcrop. The vegetation is SQF on the upper escarpment of the property where the cycads are found at 750 meters above sea level. Over a century of rainfall data collected on the property shows a mean of 512 mm rain per annum (land owner's personal rainfall records). This is slightly less than the mean annual precipitation reported for the vegetation type at 544 mm (Rebelo et al. 2006). The fires in fynbos are frequent events in the surrounding area, sometimes occurring every 4 – 6 years. Fires at this site are however carefully monitored and controlled on the property and do not occur as frequently as other *E. latifrons* sites in the area (see Chapter 3). The land owner keeps livestock (sheep, goats, and cattle) and the vegetation surrounding the cycads is intensively grazed. Visits to the

site saw animal droppings in substantial quantities. The adult cycads at the site were also grazed upon where leaves had suffered substantial damage at certain times over the monitoring period (Plate 5.1). The cycads at this site have not produced any young plants for a number of years – there is no record of when the last seedling was seen at the site. Viability tests of the seeds produced by the female cone at the site harvested in 2015 indicate that an absence of natural pollination is not the cause of the lack of seeding recruitment (see Chapter 4). The 25 seedlings resulting from the germination experiment were used for this augmentation project. There were two influencing factors that resulted in young seedlings (as opposed to older propagules) planted at the site: 1. Timing: the seedlings were not maintained for longer in the growing tunnel as the project was part of this PhD study. As such the timeframe of the project did not allow for maintaining the seedlings in the tunnel for longer than a year. And 2: the advantage of planting young seedlings is to allow them to acclimate to the environment from an early stage, which is particularly important for developing drought resistance (drought stress hardening off period - Palma and Laurance 2015), possibly requiring less aftercare support once they are established. At the time that a sample of seeds wwere harvested from the female plant for seed viability testing, a few extra seeds were scattered in the rocky crevices just below the male plant. This was not done in any systematic way and did not form part of the recovery experiment as it was not expected that any of the seeds would germinate at the time.

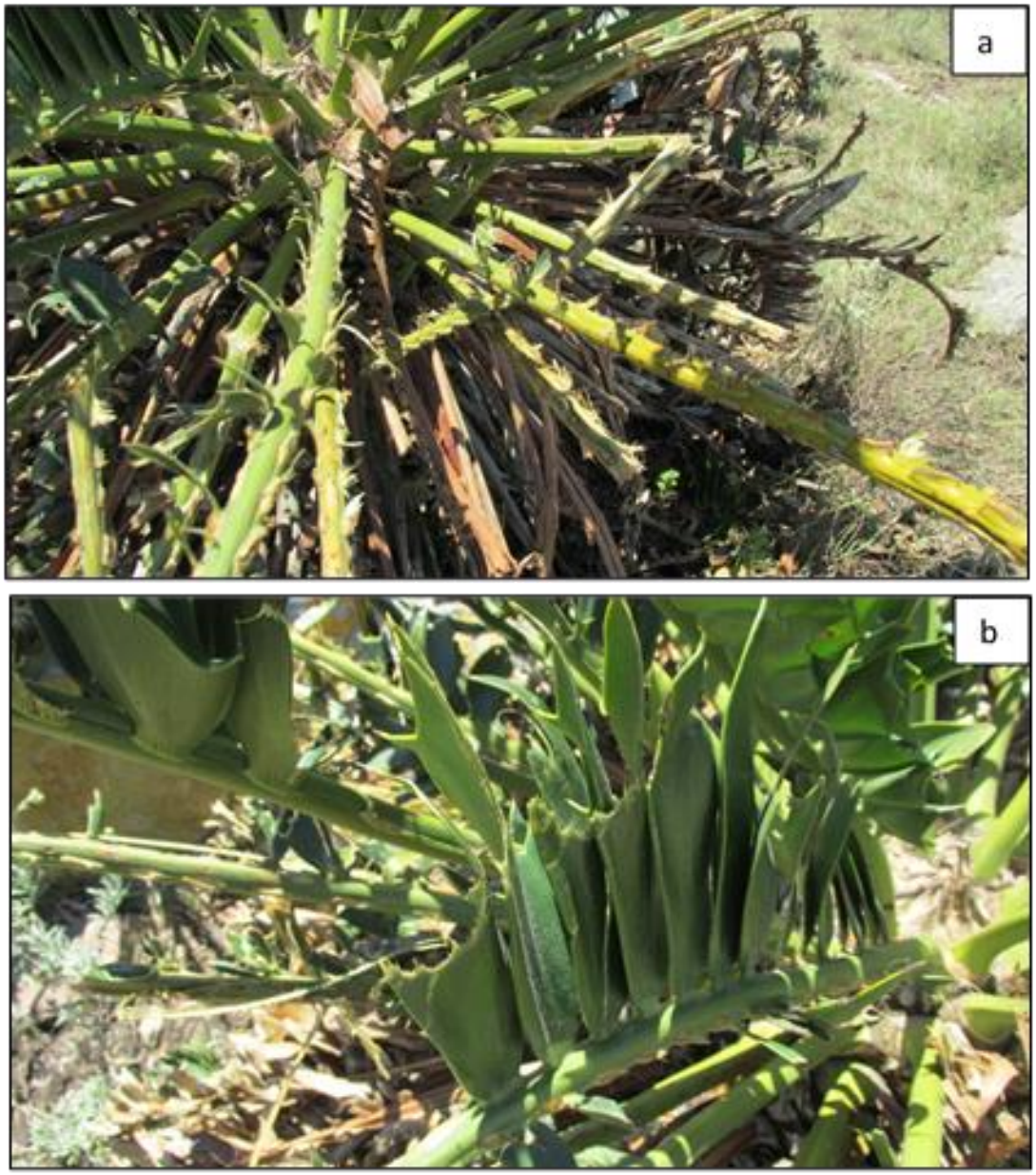


Plate 5.1 Photos of *Encephalartos latifrons* adult male plant at the restoration site showing signs of damage by a large animal (a) and damage to adult leaves (b)

Planting, monitoring and analysis

It was evident that livestock activity around the cycads was a possible threat to the recovery plan for this population, either by herbivory or trampling. A decision was therefore made to fence off the male and female plants from any livestock activity before the recovery project commenced. This was done by erecting a standard stock fence constructed to a height of 1.4 meters using 2.24 mm fully galvanised high strain wire placed in keeping with the fencing specifications for game in the Eastern Cape Province (DEDEA 2016). To investigate if livestock activity made a difference to the

survival of planted seedlings, propagules were planted both inside and outside the fenced area and survival of individual seedlings monitored. Due to the limited number of seedlings available for the project, replication of the experiment was not possible at either site. The first phase of planting was done in March/April 2016 and the second phase in November 2016. This corresponds to the expected peak in rainfall for the study area. Planting dates were relatively staggered (rather than planting all the seedlings at the same time) because seed germination in the growing tunnel was staggered (see Chapter 4) and the size of seedlings available for planting varied. To ensure that all seedlings were approximately the same height and had the same number of leaves, those not ready for planting remained in the tunnel until the first leaf emerged.

Field surveys of *in situ E. latifrons* population's show that seedlings are found close to the female plants and are significantly clustered (see Chapter 3). Seedlings are most often found associated with rocks and it is this relationship that increases survival during a fire (see Chapter 3). Seedlings were therefore planted next to a rock (over a meter in length and/or width) in each instance (Plate 5.2). There were a limited number of suitable rocky sites next to the female plant. Seedlings were consequently spaced out at a distance of 4 to 36 meters from the female inside the fenced area along a rocky ridge and 38 to 40 meters from the female plant outside the fenced area, all next to a rocky outcrop in sheltered sites. Seedlings were planted to a depth of 10 to 15 cm and covered with soil from the site and a layer of sterile vermiculite before being watered. Metal tags with unique numbers were placed around each seedling using a thin wire. Unique numbers corresponding to the tag numbers were also painted onto nearby rocks making the seedlings easier to find. At the time of planting, the seedlings were on average 137 days old (from date the radicle emerged upon germination) with an average leaf length of 7.9 cm. All seedlings were planted at the one leaf stage, except for two seedlings aged 265 and 205 days old with two leaves. The mean size and age of seedlings planted in the outside fenced area was 6.9 cm and 110.2 days old from time of germination respectively (N = 8). The mean size and age of seedlings inside the fenced area was 8.8 cm and 158.6 days old from time of germination respectively (N = 17).

Plate 5.2 A single-leafed *Encephalartos latifrons* seedling planted near a rock at the restoration site

Seedlings were planted inside the fenced area in March 2016 and November 2016. Seedlings were planted outside the fenced area in April 2016. Sites were monitored again in April 2016, May 2016, September 2016, November 2016, and April 2017 sometimes twice in on month. Camera traps were placed at both sites and images downloaded at the same time seedling survival was monitored. The camera trap outside the fenced area started recording images in April 2016 while the camera trap at the site inside the fenced area started recording in May 2016. Seedlings were considered not to have survived the experiment if they were uprooted or were missing altogether. Some seedlings were re-planted but their deaths were confirmed with subsequent monitoring events.

Survival analysis for seedlings planted inside and outside the fenced area was based on just over a year (391 days) of right censored data. A seedling's surviving (0) or dying (1) was recorded at each census period as a binary number. The Kaplan-Meier estimator was used to calculate the non-parametric estimates of the survivor function (Bland and Altman 1998) for the two sites (inside and outside the fenced area) combined. Survival data from the two sites were combined as the separate curves for each site violated the proportional hazards assumption making comparison testing of the two sites statistically problematic (Li et al. 2015). The assumption is therefore that the two sites experienced the same environmental pressures/threats and that the fence

made no difference to the survival of seedlings. This was confirmed by the evidence captured on the camera traps where the herd of livestock breached the fence. Similar livestock pressure was witnessed in both the inside and outside fenced areas. Survival data was analysed using the Real Statistics Resource Pack software (version 4.14) Zaiontz (2017).

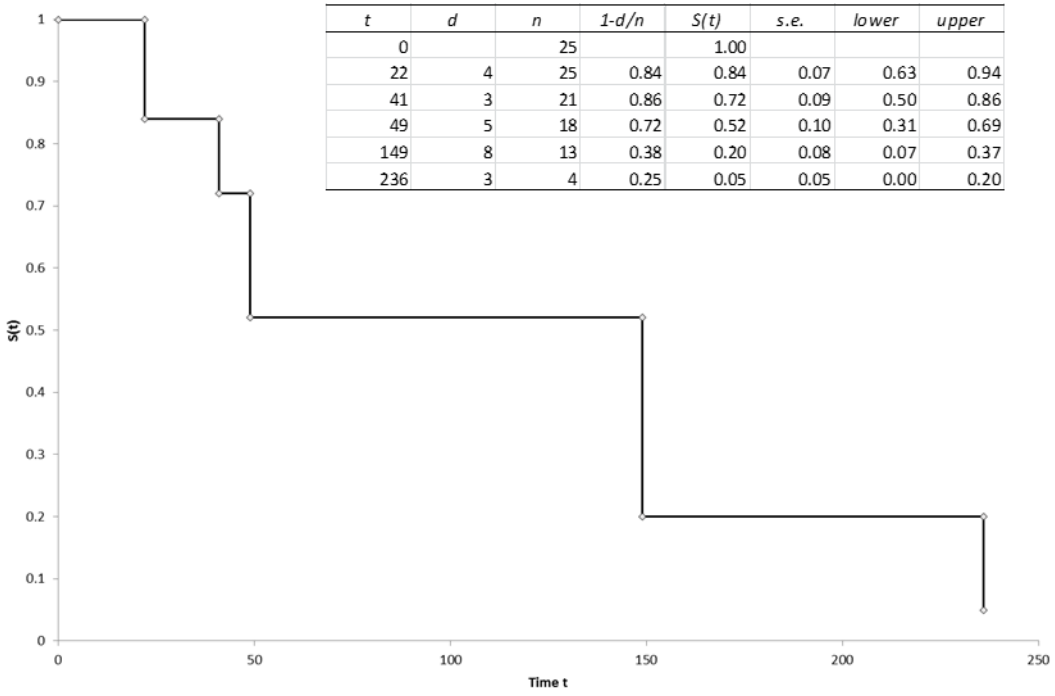
Results

Overall, there was high mortality of planted seedlings with only 8% of planted propagules (2 seedlings survived out of 25 planted) surviving in the outside and inside fenced areas combined. Not part of the recovery project but worth mentioning is one seed from the naturally disintegrating cone under the female plant germinated (naturally) and subsequently died. The germinated seed was exposed and did not survive past the radicle emergence stage. Of the seeds randomly placed deep rock fissures/crevices (scattered by the author when harvesting the seeds for the viability experiment in Chapter 4), one germinated and survived to the end of the monitoring period. None of the seedlings planted outside the fenced area survived the restoration attempt. Two (12%) of the seedlings survived the restoration effort only once they were placed in individual cages to deter further herbivory. The cause of death for all seedlings inside and outside the fenced area included: uprooting (70%), defoliation (4%) and 26% of seedlings planted were missing from where they were originally placed (Plate 5.3).

Plate 5.3 Uprooted *Encephalartos latifrons* seedling at the restoration site. Uprooting was the primary cause of the low survival rates seen at the restoration site

Survival analysis

The seedlings outside the fenced area experienced a rapid decline in survival just 40 days after planting. The decline in survival was sudden, signifying that most seedlings suffered the same fate at the same time by the same cause. At 41 days, 38% of the seedlings had perished, and after 49 days, 63% of the seedlings were recorded as dead. The decline in survival of the seedlings planted inside the fenced area was more gradual with 24% of deaths occurring at 22 days, 47% of deaths at 149 days and 18% of deaths occurring at 236 days after planting. At the end of the monitoring period however, the fate of the seedlings planted inside and outside the fenced area resulted in similar overall low survival (Figure 5.1). Significance testing on the survival curves was not done due to the violation of the proportional hazards assumption (i.e. the curves cross when the sites are plotted separately) (Li et al. 2015).



t	d	n	1-d/n	S(t)	s.e.	lower	upper
0		25		1.00			
22	4	25	0.84	0.84	0.07	0.63	0.94
41	3	21	0.86	0.72	0.09	0.50	0.86
49	5	18	0.72	0.52	0.10	0.31	0.69
149	8	13	0.38	0.20	0.08	0.07	0.37
236	3	4	0.25	0.05	0.05	0.00	0.20

Figure 5.1 Kaplan-Meier curves and corresponding table generated for the survival of *Encephalartos latifrons* seedlings planted inside and outside the fenced area (combined) at the restoration site. Time (t) in days on the horizontal axis with the survivor function (S(t)) plotted on the vertical axis. The table inset contains the graph values (t = time in days; d = the number of plants dying at time t; n = the number of plants at time t; s.e. = standard error and 95% confidence intervals = lower and upper values)

Camera traps at both sites recorded a variety of wild individual grazers and browsers, all solitary individuals. Wild ungulates at the site included: Kudu (*Tragelaphus strepsiceros*), Springbok (*Antidorcas marsupialis*), Common Duiker (*Sylvicapra grimmia*) and Warthog (*Phacochoerus aethiopicus*) (Plate 5.4c). A resident hare, most likely a scrub hare (*Lepus saxatilis*) was also caught on the camera trap. It was not surprising that Merino sheep (*Ovis aries*) were active at the site outside the fenced area as this was expected. This site forms part of a camp the landowner uses for grazing. A large herd of sheep were caught on camera, grazing the site and surrounding area from the 24/05/2016 to the 30/05/2016. Six days of intensive grazing coincided with the death of most of the seedlings planted at this site (Plate 5.4a). The last monitoring date at the site (26/05/2016) saw all seedlings at the site perish by being uprooted or were missing.

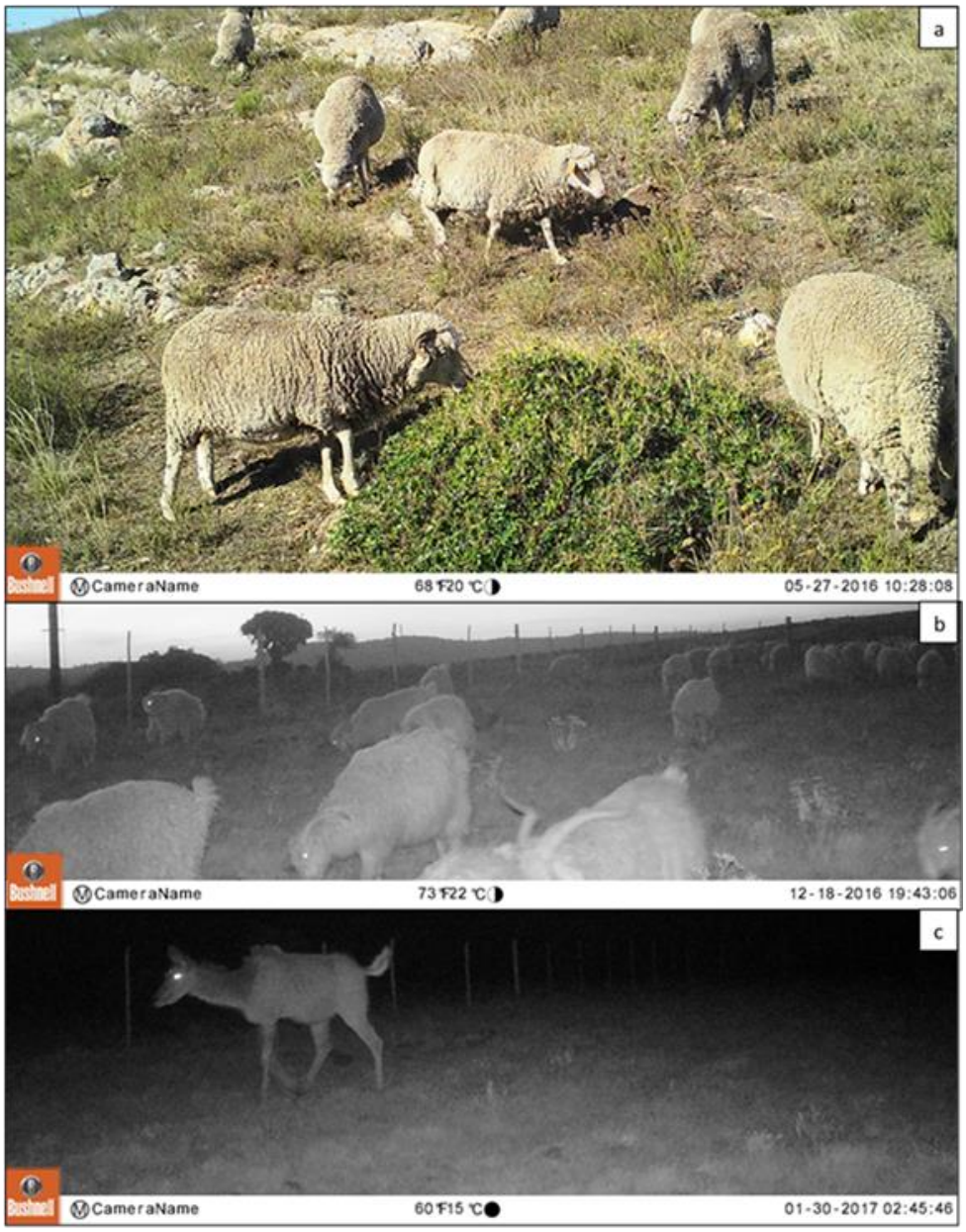


Plate 5.4 Domestic and wild herbivorous mammals caught on the camera trap outside the fenced area (a) and inside the fenced area (b and c)

It was however surprising that the camera trap recorded a breach in the fence on the 18/12/2016 and again on the 09/03/2017 by a herd of Angora goats (*Capra aegagrus hircus*). There was a delay in placing the camera trap inside the fenced area resulting in 63 days of no camera trap monitoring from when the seedlings were first planted. There may have been some activity missed at the site over this period. The death of the seedlings planted inside the fenced area however co-incided with the breaching of the

fence by the goats as recorded on the camera (Plate 5.4b). Goats were very active in this area on the 09/03/2017 with all seedlings recorded as dead on the 05/04/2017. The two seedlings remained alive at this site when individual cages were constructed and placed around the seedlings to deter further herbivory (see appendix 5.1 for cage construction). This is excluding the one seedling that germinated naturally at the site in the rock fissure and survived the entire monitoring period.

Discussion

Toxic effects of cycads on livestock are reported in the literature, published primarily in veterinary and animal health journals (Hooper 1978; Reams et al. 1993; Hall and McGavin 1968; Shimizu et al. 1968). This is contradictory to reports that cycads are generally unpalatable to livestock and herbivores in general, as the sclerophyllous leaves are spiny and difficult to chew (Cousins and Witkowski 2017). Animal health specialists however point out that the new leaves (rather than the older sclerophyllous leaves) are more often targeted by grazing livestock (Reams et al. 1993; Hooper et al. 1974). This would include cycad seedlings whose leaves are young, soft and still developing the characteristic sclerophyllous wavy leaflets, making them more vulnerable to mechanical damage compared to juvenile and adult plants (Álvarez-Yépiz et al. 2014). In particular, *E. latifrons* seedlings have not yet developed the characteristic hardened basal remains of the epidermal hairs which make the adult leaflets characteristically rough to the touch (Grobbelaar 2004). Personal observations from this study however confirm that adult plants are not invulnerable to herbivory (Plate 5.1). Similar incidences of herbivory on wild cycad populations of *Encephalartos friderici-guilielmi* have been reported by conservation authorities in the north-eastern parts of the Eastern Cape Province (D. Ricketts pers. comm.) and *E. lehmannii* and *E. trispinosus* by goats (Donaldson pers. comm) where damage to adult plants can be substantial.

It is often reported that lack of natural seedling regeneration in some cycad populations is as a result of little to no natural pollination occurring between male and female plants due to the possible extinction of pollinators. This was reportedly the case for all *E. latifrons* populations (Daly et al. 2006). This study however confirms that such conclusions cannot be made without first testing the viability of seeds under conditions that promote natural pollination. If natural pollination is possible (as reported in Chapter 4), other factors that may play a role in lack of natural recruitment need to be explored. Whether the pollinators at Population C are specialist *E. latifrons* weevils or more generalist pollinators substituting the pollinator role is unknown and warrants further study, but natural pollination is nevertheless occurring at this site. The lack of seedling recruitment/survival after germination in Population C is likely a result of intense herbivory by livestock (goats and sheep). This was confirmed by the recordings on the camera traps that coincided with the simultaneous death of planted

seedlings by uprooting and possibly some of the kernels eaten although this cannot be confirmed. This is similar to the findings of Álvarez-Yépiz et al. (2011) on the negative impact of grazing and trampling by cattle and livestock on the seedling and juvenile survival of wild *Dioon sonorense* seedlings in the tropical dry forests of north-western Mexico. Seedling herbivory was also seen in the reintroduction of 20 *E. middelburgensis* seedlings under 10 years old, where the majority of exposed seedlings (those planted away from rocks in areas more accessible to herbivores) were uprooted and did not survive the attempted recovery (Rousseau and Rousseau 2011).

Preference for feeding on cycad immature leaves has been reported for Red Colobus Monkeys feeding on *Encephalartos hildebrandtii* in Zanzibar (Nowak and Lee 2011). It is known that native herbivorous mammals in other countries feed on cycad leaves in Australia (Schneider et al. 2002). It is not inconceivable that the herbivorous mammals caught on camera at the restoration site may have fed on the young seedling leaves in the same way. However, it is unlikely that this was the cause of death of the majority of seedlings because the deaths occurred almost simultaneously. Considerable activity of native wildlife was caught on the traps but individuals were mostly solitary animals (one Kudu cow had a calf with her; all other sightings were of solitary animals). Herbivory on wild cycad *E. latifrons* seedlings in another naturally recruiting population (Population B) was very rarely recorded in an area that does not have livestock but has abundant natural game coexisting with the population.

The construction of fences to reduce herbivory and human disturbances has proven successful in improving survival rates of restored propagules and in turn, improved long-term survival, reproductive success and seedling recruitment of restored plants (Guerrant 2012; Fenu and Cogoni 2016; see also Gordefroid et al. 2011). This is particularly important for restoration sites outside of formal protected areas (Fenu and Cogoni 2016). In the successful introduction of the Cherry Palm (*Pseudophoenix sargentii*) in the Florida Keys, heavy herbivory of young plants (> 4 years old) was recorded, even within the fenced restoration site (Maschinski and Duquesnel 2006). It was only once individual plants were caged, that the survival of young plants improved (Maschinski and Duquesnel 2006). Similarly, the survival of the two remaining *E. latifrons* seedlings was improved by the construction of individual cages over the seedlings. It is uncertain at this early stage whether this will improve the long-term survival prospects of the seedlings, but short-term propagule survival by the elimination of herbivory is crucial when livestock poses a threat to planted propagules at the

recovery site. Given the fact that *E. latifrons* is slow growing and recruitment events may be extremely rare in some populations, even light grazing or trampling may have a negative impact on seedling recruitment. This recovery experiment gives an extreme example of the impact of grazing on an *E. latifrons* population and planted propagules. It would need to be determined to what extent the threat from livestock pose to other wild *E. latifrons* populations occurring on livestock ranches (e.g. Population A). A survey report undertaken by Nature Conservation Authorities in 1991 reported the occurrence of 3 natural seedlings near the adult plants in Population A (Basson 1991). The cause of lack of recruitment since 1991 in Population A has not been determined, although it has been suggested that lack of pollination is the reason (Daly et al. 2006). Further investigations are needed to ascertain the role of livestock and herbivory and/or trampling around the plants in this population. Seed viability under conditions that enable natural pollination (e.g. by not removing the male cones out of the population and initiating artificial pollination of the female cone) should be tested. Seed viability testing should be done under natural non-disruptive conditions before lack of natural pollination is identified as a factor inhibiting natural recruitment.

The private landowner on whose property Population A exists, reports a high survival rate for propagules planted as part of the *ad hoc* recovery project on his property. The current age of restored propagules varies between 11 and 12 years old. The landowner reports no mortalities of planted propagules to date. Having said this, monitoring of propagules is done on an *ad hoc* basis not following a structured monitoring programme (landowner pers. com). Nevertheless, the prospects of propagules surviving are likely to be much improved with increasing age and/or size as reported in restoration projects across the globe (Dalrymple et al. 2018). The survival of larger *E. latifrons* propagules is therefore expected to be higher compared to the planting of seedlings less than two years old as was the case in this study. The level of herbivory on the property and around the plants of Population A has not been studied and the threats to the population may differ. Similar survival rates were reported for planted propagules of *E. dyerianus* seedlings (92%) and *E. cupidus* (80%) as part of a restoration project in what was formerly known as the Transvaal in South Africa (Boyd 1995).

In areas where grazing is a threat, the disadvantage of using very young seedlings is that the cost and effort of the project increases with the need to protect individual seedlings. It is uncertain whether the use of larger propagules would increase

the chances of the restoration success in this case. The young seedlings used in this study were vulnerable to uprooting as their roots had not yet established. Longer term research is needed on the effects of herbivory on established plants and populations. The alternative to the use of young or older propagules would be the use of seeds for recovery. There are many advantages and disadvantages with using seeds in recovery programmes. In a global assessment of plant reintroductions, Godefroid et al. (2011) found that recruitment from seed in the wild was rare for most recovery efforts. In addition, Dalrymple et al. (2018) found that seed-based reintroductions had the lowest mean proportion of survival compared to adult and juvenile survival from another assessment of reintroductions around the globe. There is however an advantage to using seeds for population recovery efforts, particularly for a plant with a life-history such as *E. latifrons*. Seeds placed in rock fissures and crevices around the adult plants in the population are more likely to be inaccessible to grazing livestock. The seeds would benefit from the microhabitat provided by the sheltered position, which will enable it to establish a root system. This may increase its chances of surviving if grazed upon once the leaves are exposed. An example of this can be seen at the recovery site when the author scattered a few seeds in some crevices around the male and female cluster. One seed germinated successfully and has survived without the need for additional protection (Plate 5.5). If seeds are to be used for recovery, it is however recommended that the potential viability of the seed is determined initially in order to maximise the chance of germination. This is a low-cost, low effort option to recovery projects involving cycads with similar life histories to *E. latifrons*; provided the seeds are processed, stored correctly, and tested for viability before sowing. The advantage of using seeds in certain instances outweighs the higher establishment rates by the use of seedlings and juveniles (Guerrant and Kaye 2007).

Plate 5.5 *Encephalartos latifrons* seed sown in rocky fissure at the time the female cone was disintegrating. The seed germinated and the seedling survived throughout the monitoring period as it was inaccessible to grazing herbivores

The low number of propagules used in this study was limited by what was available. The recommended minimum number of propagules to use for most restoration programmes is 50 individuals (Albrecht and Maschinski 2012). *E. latifrons* has always been innately rare according to early reports on its distribution (Donaldson 2003) making it difficult to determine the ideal number of propagules sufficient for species recovery (Tear et al. 2005; Neel et al. 2012). In the self-sustaining *E. latifrons* Population B, seedlings make up just over 50% of the population. Given that Population C consists of 2 plants, the survival of 3 seedlings (two caged and one naturally germinated in rock crevice) is considered a positive start. It is clear that natural seedling recruitment under natural pollination will not occur with the current livestock activity on the property, even with the fence around the plants. It is recommended that future coning events are carefully monitored at this population, seeds collected from the disintegrating cone and processed for sowing. Once the seeds are checked for viability, it is recommended that they are sown in rocky fissures/crevices surrounding the adult plants. There may be a need to create artificial rocky features (possibly using available material from the site) to facilitate the establishment and survival of seeds. The fact that the population has the potential to be self-recruiting and that natural pollination is taking place, is half the battle won in the recovery of the species at this site.

Lessons learnt

The most important lesson to take from this research is that lack of seedling recruitment in *in situ E. latifrons* populations cannot always be attributed to natural pollination failure. Seed viability testing should be done under conditions that enable natural pollination. Threats such as livestock activity around populations need to be considered as possible causes of recruitment failure in populations where this threat exists. Where herbivory threat is high, planted seedlings need to be individually protected in order to improve their survival. In this case, fencing a population did not reduce the threat from livestock herbivory, and seedlings needed to be caged individually.

Augmentation using seeds may provide a solution in situations where the threat from herbivory is high and the funds for recovery programmes are low. Seed viability testing would be important prior to sowing, as well as finding microsites favourable to seed germination that provide natural barriers to herbivory. Seeds need to be sown into fissures and between rocks where they will be inaccessible to livestock until they have established a large enough root mass to withstand some defoliation. How much defoliation a seedling can withstand would be the subject of another research project. Other costly options would be to construct an electric strand, mesh wire fence around Population C, but this comes with costs and maintenance. It may also be worth exploring the use of nurse plants to increase seedling survival where rocky microsites are limited. The use of unpalatable nurse plants, as part of the recovery project, may protect seedlings against herbivory as seen in other restoration studies (Padilla & Pugnaire 2006).

Although considered an ecological failure, the outcome of the research was successful in guiding further protocols for *E. latifrons* recovery at this and other sites. Population C is an ideal site to start a recovery programme for *E. latifrons* (see appendix 5.2 for a complete *ad hoc* assessment of the site). Natural pollination is already occurring at the site increasing the chances that the population will become self-sustaining compared to sites where natural pollination may be limited. Minimal effort will be required to harvest the seeds from the female cone, process, store and test for viability before sowing. It is recommended that systematic and scientific monitoring of introduced plants at the site is undertaken in order to analyse the outcomes which will inform future recovery programmes for the species.

Future research at the site could include a genetic study (inbreeding/outbreeding of propagules at the site), pollination studies to determine specificity and vigour of the current pollinator population, the impact of climate change and biome shifting on the population at the site, and the long-term population demographics and survival of *E. latifrons*.

References

Ackeroyd J, Wyse Jackson P (1995) A handbook for botanic gardens on the reintroduction of plants to the wild. BGCI, Richmond.

Albrecht MA, Maschinski J (2012) Propagule stages, and life history on the survival of reintroduced plant populations. In: Maschinski J, Haskins KE (eds) Plant reintroduction in a changing climate: promises and perils. Island Press, pp 171–188

Álvarez-Yépiz JC, Búrquez A, Dovčiak M (2014) Ontogenetic shifts in plant-plant interactions in a rare cycad within angiosperm communities. Oecologia 175:725–735

Álvarez-Yépiz JC, Dovčiak M, Búrquez A (2011) Persistence of a rare ancient cycad: Effects of environment and demography. Biol Conserv. 144: 122-130.

Basson M (1991) Eerste verslag wat die bron en status van die *Encephalartos* spesies in die Trappe's Valley area in die Oos-Kaap aandui met spesiale verwysing na die *Encephalartos latifrons*. Cape Nature Conservation Survey Report. Grahamstown, South Africa

Bland JM, Altman DG (1998) Statistics Notes: survival probabilities (the Kaplan-Meier method). BMJ 317:1572–1580

Boyd WM (1995) The translocation and re-establishment of priority *Encephalartos* species in the Transvaal, South Africa. In: P. Vorster (ed) Proceedings of the Third International Conference on Cycad Biology. Cycad Society of South Africa, Stellenbosch, South Africa., pp 39–43

Castro J, Gomez JM, Garcia D, Zamora, R and Hodar JA (1999) Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecol 145:115–123

Convention on Biological Diversity (2011a) Global strategy for plant conservation (2011 - 2020). In: Conf. Parties to CBD, by Decis. X/17. https://www.cbd.int/gspc/default.shtml Accessed 23 Feb 2018

Convention on Biological Diversity (2011b) Conference of the Parties Decision X/2: Strategic Plan for biodiversity 2011-2020. https://www.cbd.int/decision/cop/?id=12268 Accessed 27 Oct 2017

Cousins SR, Witkowski ETF (2017) African cycad ecology, ethnobotany and conservation: a synthesis. Bot Rev 83:152–194

Crisp MD, Cook LG (2011) Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. New Phytol 192:997–1009

Dalrymple SE, Banks E, Stewart GB, Pullin AS (2012) A meta-analysis of threatened plant reintroductions from across the globe. In: Maschinski J, Haskins KE (eds) Plant reintroduction in a changing climate: promises and perils. Island Press, pp 31-50

Daly, B., Donaldson, J.S., Friedmann, Y., Hahndiek, Q., King, N. Newton, D. and Southwood, A. (editors) (2006) Population and habitat viability assessment for the Albany cycad (*Encephalartos latifrons*). Conservation Breeding Specialist Group (SSC /IUCN) / CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg

DEDEA (2016) Game fence specifications: operational policy guideline of the Chief Directorate of Environmental Affairs. King Willimams Town

Department of Environmental Affairs (2011) Biodiversity Management Plan for Albany Cycad, *Encephalartos latifrons*. National Environmental Management: Biodiversity Act (10/2004): South African Government Gazette No. 34388

DEA (2014) National Strategy and Action Plan for the Management of Cycads. Pretoria, South Africa

Dixon KW (2009) Pollination and Restoration. Science 325:571–573

Donaldson J (2003) Cycads: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK

Donaldson JS (1995) Understanding cycad life histories: an essential basis for successful conservation. In: Donaldson JS (ed) Cycad conservation in South Africa: issues, priorities and actions. Cycad Society of South Africa, Stellenbosch, South Africa., pp 8–13

Fenu G, Cogoni D (2016) The role of fencing in the success of threatened plant species translocation. Plant Ecol 217:207–217

Garcia D, Zamora R, Hodar JA, Gomez JM, Castro J (2000) Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. Biol Conserv 95:31–38

Godefroid S, Piazza C, Rossi G, Buord S, Stevens A-D, Aguraiuja R, Cowell C, Weekley CW, Vogg G, Iriondo JM, Johnson I, Dixon B, Gordon D, Magnanon S, Valentin B, Bjureke K, Koopmanq R, Vicens M, Virevaire M, Vanderborght T (2011) How successful are plant reintroductions? Biol Conserv 144:672–682

Grobbelaar N (2004) Cycads - with special reference to the southern African species, First Edit. Published by the author, Pretoria

Guerrant EO (2012) Characterizing two decades of rare plant reintroductions. In: Maschinski J, Haskins KE (eds) Plant reintroduction in a changing climate: promises and perils. Island Press, pp 9–50

Hall WTK and McGavin MD (1968) Clinical and neuropathological changes in cattle eating the leaves of *Macrozamia zucida* or *Bowenia serrulata* (family Zamiaceae). Pathol. Vet 5: 26 – 34

Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks, TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Katariya V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vie J-C, Aguiar JM, Allen DJ, Allen GR and Amori G (2010) The impact of conservation on the status of the world's vertebrates. Sci New Ser 330:1503–1509

Hooper PT, Best SM and Campbell A (1974) Axonal dystrophy in the spinal cords of cattle consuming the cycad palm, Cycas media. Australian Veterinary Journal 50 (4): 146 – 149

Hooper PT (1978) Cycad poisoning in Australia: etiology and pathology. In: Keeler R, van Kampen KR, James LF (eds) Effects of poisonous plants on livestock. Academic Press, New York, pp 337–347

IUCN/SSC (2013) Guidelines for reintroductions and other conservation translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission

Janzen D (2001) Latent Extinction — The Living Dead. Encyclopaedia of Biodiversity 4:590-598

Kemp HJ (1986) *Encephalartos latifrons*. Encephalartos 8:8–15

Li H, Han D, Hou Y, Chen H, Chen Z (2015) Statistical inference methods for two crossing survival curves: a comparison of methods. PLoS One 10: e0116774

Maschinski J, Duquesnel J (2006) Successful reintroduction of the endangered long-lived Sargent's cherry palm, *Pseudophoenix sargentii*, in the Florida Keys. Biol Conserv 134:122–129

Maschinski J, Haskins KE (eds) (2012) Plant reintroduction in a changing climate: promises and perils. Island Press.

Maunder M (1992) Plant reintroduction: an overview. Biodivers Conserv 1:51–61

Nagalingum NS, Marshall CR, Quental, TB, Rai HS, Little DP and Mathews S (2011) Recent synchronous radiation of a living fossil. Science 334: 796 - 799

Neel MC, Leidner AK, Haines A, Goble DD, Scott JM (2012) By the numbers: how is recovery defined by the US Endangered Species Act? Bioscience 62:646–657

Nowak K, Lee PC, Lee PC Consumption of cycads *Encephalartos hildebrandtii* by Zanzibar Red Colobus *Procolobus kirkii*. Journal of East African Natural History 100 (1-2):123–131

Octavio-Aguilar P, Rivera-Fernández A, Iglesias-Andreu LG, Vovides AP, Núñez de Cáceres-González FF. (2017) Extinction risk of *Zamia inermis*: a demographic study in its single natural population. Biodivers Conserv 26:787–800

Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Front Ecol Environ 4:196–202

Palma AC and Laurance SGW (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Appl Veg Sci 18:561–568

Raimondo D (ed) (2015) South African strategy for plant conservation. South African National Biodiversity Institute and the Botanical Society of South Africa, Pretoria

Reams RY, Janovitz EB, Robinson FR, Sullivan JM, Casanova CR, Más E (1993) Cycad (*Zamia puertoriquensis*) toxicosis in a group of dairy heifers in Puerto Rico. J Vet Diagn Invest 5:488–494

Rebelo AG, Boucher C, Helme N, Mucina L and Rutherford MC (2006) Fynbos Biome. In: Mucina L, Rutherford MC (eds) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute., Pretoria, South Africa, pp 53–219

Rousseau R, Rousseau P (2011) *Encephalartos middelburgnesis* on site propagation project: progress and prospects with lessons learnt. Encephalartos 104:20–24

Schneider D, Wink M, Sporer F and Lounibos P (2002) Cycads: their evolution, toxins, herbivores and insect pollinators. Naturwissenschaften 89:281–294

Shimizu T, Yasuda N, Isaburo K Shimizu T, Kono I, Yagi F, Tadera K, Kobayashi A. (1986) Hepatic and spinal lesions in goats chronically intoxicated with cycasin. Jpn. J. Vet. Sci. 48:1291 – 1295

Swart C, Donaldson J, Barker N (2018) Predicting the distribution of *Encephalartos latifrons*, a critically endangered cycad in South Africa. Biodivers Conserv. (in press)

Tear TH, Kareiva P, Angermeier PL, Comer P, Czech B, Kautz R, Landon L, Mehlman D, Murphy K, Ruckelshaus M, Scott JM, Wilhere G (2005) How much is enough? The recurrent problem of setting measurable objectives in conservation. Bioscience 55:835–849

Vovides AP, Ogata N, Sosa V, and Peña-García E (1997) Pollination of endangered Cuban cycad *Microcycas calocoma* (Miq.) A. DC. Bot J Linn Soc 125:201–210

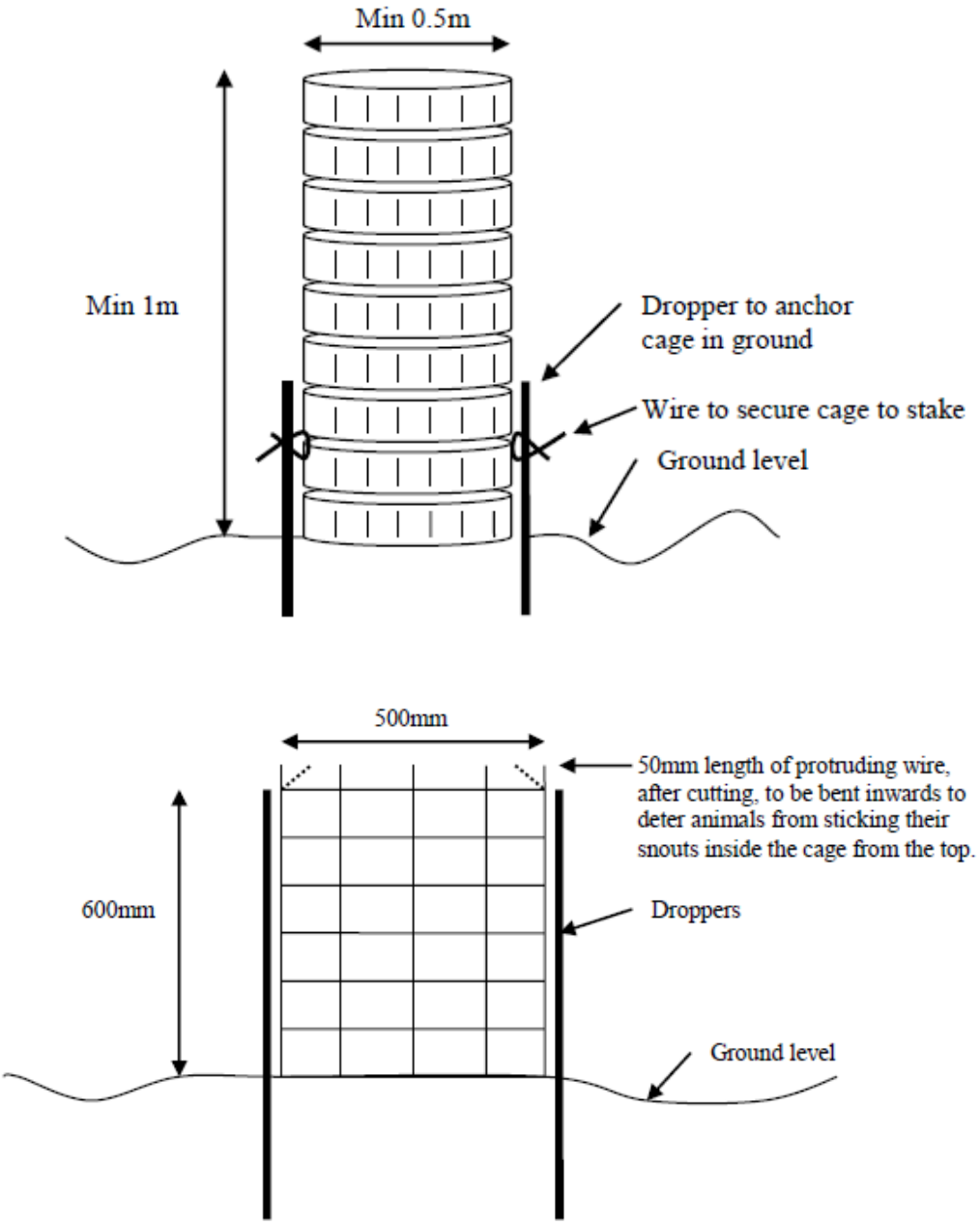
Whitelock LM (2002) The Cycads. Timber Press, Inc.

Xaba PM (2014) Pollination and germination as limiting factors in the propagation of threatened cycads, *Encephalartos* (Zamiaceae). MSc thesis. University of Western Cape

Yessoufou K, Bamigboye SO, Daru BH and van der Bank M (2014) Evidence of constant diversification punctuated by a mass extinction in the African cycads. Ecology and Evolution 4: 50 - 58

Zaiontz C (2017) Real Statistics Using Excel. www.real-statistics.com (accessed 17/05/2017)

Appendix 5.1 Cage design for *Encephalartos latifrons* seedlings (design and diagram courtesy of R. Rowswell). The top diagram illustrates the overall dimensions of the cage. The lower diagram depicts the protruding wire at the top of the cage to prevent livestock utilising the open part of the cage to access the seedlings.



Appendix 5.2 Ad hoc recipient site assessment based on questions posed by Maschinski and Haskins (2012).

Planning future recovery projects for Population C can be guided by this *ad hoc* assessment. It can also be used as an example of what process to follow for other *E. latifrons* recovery programmes. Recipient sites will differ and will need to be assessed separately. This assessment was done with the benefit of hindsight.

Is this an augmentation, reintroduction or introduction?

Augmentation

What are the legal, logistical and land management issues?

Legal: The harvesting of seeds from the female cone requires a permit in terms of the Threatened and/or Protected Species Regulations (NEMBA Act 10 of 2004). Restricted activities on the permit are listed in NEMBA Act 10 of 2004: Chapter 1.1. Definitions of restricted activities (ii, iii, vi, vii, viii). Conditions to the permit should include strict record keeping. The researcher should allow unrestricted access to conservation authorities who ensure compliance to permit conditions. Challenges would include the approval of such as permit from the relevant conservation authorities.

Logistical: The site is relatively easy to access without the need for a 4 x 4 vehicle. There are logistical implications depending on if the augmentation is to be done using seeds or seedlings. Harvesting, processing and sowing seeds would be logistically easier than harvesting seeds, finding space to germinate seeds and maintain seedlings as well as replanting seedlings back at the site. Securing cages around each seedling in the population will come at a financial and logistical cost. Finding sufficient microsites to sow the seeds may be a challenge if the decision to use seeds rather than seedlings is chosen, but the creation of artificial seed microhabitats is possible using the numerous rocks available at the site.

Land management issues: The land on which population C exists is a well-managed and a well-run privately owned farm. The farm is extensively used for livestock grazing and this is a threat to the current population on the property.

Are the biology and ecology of the species understood?

Yes, the biology, ecology and life history of the species is better understood and reported in Chapter 3 of this thesis.

Have germination protocol and propagation methods been determined?

The germination protocols and propagation methods have been studied (Xaba 2014; Chapter 4) and practised by individual landowners with considerable success (land owner pers. com.).

Has a recipient suitable site been identified, and is the land manager supportive?

The *ad hoc* identification of the recipient site was based on the germination of viable seeds harvested from the female plant at the recipient site (see Chapter 4). The landowner is particularly supportive of the recovery project and offered labour (the staff working on his property) for the construction of the fence. The land owner also agreed to set aside a portion of the property to fence off the site from grazing livestock. The recovery trial would not have been possible without land owner support.

Have threats been reduced or eliminated?

An attempt to reduce the threats failed. Further re-enforcement of the fence with mesh or electric wiring may be the only solution to protect the adult plants and future planted propagules from further damage. Constructing individual cages (seedlings) or ensuring seed are placed in protected microsites will reduce the threat from herbivory in the short term. It is not known how seedlings will survive once the leaves are more exposed as they grow larger with age.

How many plants are available and how many are needed?

For this experiment, there were only 25 seedlings available. It is expected that the female will cone in the future and produce more viable seeds though natural pollination in the coming years. Female *E. latifrons* plants may typically cone every 5 - 10 years, which would potentially be 25 seeds available for reintroduction every 5 - 10 years. Artificial pollination of the female cone is a possibility provided the ecological integrity of the pollinator environment is maintained (i.e. by not harvesting male cones when the pollen is collected).

What question is being addressed, and does your experiment answer the question?

Chapter 4 of this thesis discovered that seeds collected from the female plant at the recipient site are viable and that regeneration through natural pollination is possible. The question was to determine other probable causes of lack of seedling recruitment at the site. The experiment did answer this question by showing that herbivory is a major threat to seedling recruitment in this population.

How will success be measured?

The short term success was measured by monitoring seedling survival over the monitoring period (March 2016 – April 2017). The experiment was a success in that it answered the research question and provided further information to inform recovery protocols for *E. latifrons*. The recovery project was not a success in that almost all of the planted seedlings did not survive the experiment.

What kind of aftercare for plant and site management will be needed and how frequently?

If seeds are sown at the site, aftercare and site management will be minimal, besides monitoring germination and survival (every 3 months would suffice). If seedlings are planted at the site, aftercare and site management efforts increase as well as monitoring intervals. Seedlings are also a challenge to plant due to the rocky nature of the substrate at the site; they would need to be watered during hot dry spells and periods of drought. Cages would need to be constructed and secured over the seedlings. Monthly monitoring would be required to assess damage to the cages and/or seedlings.

What is the involvement of the land manager?

In this case, the land manager was very involved and supportive of the project. In many other cases, land managers are suspicious of conservation authorities and do not allow access to their land (researchers personal experience). Recovery programmes will only be successful if land managers are supportive of the project and intentions of the researcher and/or conservation authorities are well understood.

What is the monitoring design and plan for reporting results?

In this case, plants were monitored every 1 to 3 months. Camera traps were also placed at the site to monitor livestock activity. Seedlings were marked individually and survival/death reported per seedling (right censoring). Results were kept in an excel spreadsheet and monitoring dates, watering dates, survival, cause of death etc. was reported for individual seedling.

In what ways will/should you involve the public in your project?

The public should not be involved in the project in any way. Knowledge of the locality of the cycads (seedlings and adults) would increase the risks to the recovery programme and the population as a whole as the plants are sought after by the horticultural trade and theft of plants is an existent threat.

Experimental design

What additional knowledge is needed about the species' biology or other factors?

Further research is needed regarding the pollination ecology and population demographics (matrix/integral projection models) for *in situ* populations that exist throughout the species distribution range.

How much replication is needed for adequate statistical power? How will the study be analysed?

The experimental design is dependent on how many viable seeds are harvested from the female plant in the future. There is no certainty around what future yield to expect. The experiment will have to be replicated on a temporal scale rather than on a spatial scale due to the limited material available for recovery projects at the site. Monitoring long-term population dynamics of the restored population would require many years (10 - 20) of census data. Analysis of the reintroductions of the endangered long-lived Sargent's cherry palm, *Pseudophoenix sargentii*, in the Florida Keys (Maschinski and Duquesnel 2006) is an example of what type of analysis can be done under a similar monitoring regime for *E. latifrons* at the recipient site.

Who will conduct the analysis?

The researcher would conduct the analysis. If the project is undertaken by conservation authorities, the analysis can be done through the South African National Biodiversity Institute, the National Cycad Task Team or alternatively the scientific section of the provincial conservation department undertaking the recovery project.

Using the reintroduction population as a cohort, will you examine natural variation in survival, mortality and recruitment and tie these to environmental factors?

It was not possible to examine which environmental factors influenced variations in survival etc. This would form part of the long-term recovery project once the threat of herbivory is substantially reduced or eliminated.

Will the underlying environmental drivers of λ be measured?

This was not part of the short-term study but should a recovery programme be initiated for this population, underlying drivers of λ need to be measured in the absence of herbivory.

Will genetic factors be part of the experimental design?

Genetic factors were not part of this experimental design but should be incorporated into a longer term recovery project for this site.

Are you testing factors within a single site or across multiple sites?

Due to the limited number of propagules/viable seeds available, testing factors across a single site would be most appropriate for future population augmentations. If this population is included in future genetic studies to determine if it belongs to the single panmictic population identified by Da Silva (2012)

Will a monitoring plan be developed? How long will monitoring be conducted? Have you considered an adaptive monitoring plan? What will the duration of the experiment be?

The time frame of the current recovery experiment depended on the PhD thesis (limited to 1 year in this case). A monitoring plan should be developed and linked to the revised Biodiversity Management Plan for *E. latifrons*. Adaptive monitoring should be ongoing as part of the BMP (which is revised every 5 years). If/once a recovery project is initiated, monitoring should be at least between 10 and 20 years before any realistic results can be expected.

How will plants be mapped, marked or numbered?

If using seedlings for augmentation, the best way to mark plants is by using a metal tag with a unique number punched into it. The metal tag is then secured to the plant using thin wire. This is the best approach in the event of a fire. An alternative method would be to hammer a tent peg or similar metal object into the ground next to the seedling and to secure the tag with the wire into the peg. Alternatively, the metal tag can be secured onto the wire cage. If seeds are to be used for the recovery project, scrubbing

the closest rock to the position of the seed using a wire brush to remove lichen and debris before marking the rock with a unique number for each seed. A stencil can be used to paint the rock using durable/weatherproof paint (road paint used to mark hiking trails would work best). It is also useful to have a hand-drawn map of the seeds/seedlings to refer to when undertaking the monitoring as well as a GPS reading of each locality. The site in question is fairly small and contained and it would be relatively easy to find seeds/seedlings over the monitoring period. If any of the seeds have not germinated within a year of sowing, it would be safe to assume that the seed is not viable and the position used for future seeds harvested from the female plant.

If the plants are susceptible to herbivory, will their response be included in the design or should the plants be protected?

Plant material should be protected against herbivory at all costs. The impact of herbivory could possibly be incorporated into the design at a later stage when the plants are older and possibly able to withstand some form of herbivory.

Wild populations

What is the genetic structure of the wild populations?

The genetic structure of wild populations is published in Da Silva (2012). This did not include all wild populations (as well as Population C at the recipient site) and further research is needed to include newly discovered *E. latifrons* populations.

What is the dispersal capability of the species?

The dispersal capability of the species is extremely poor in the wild as for most species of cycad including *E. latifrons* (Chapter 3).

Is hybridisation a concern?

Yes, hybridisation is a concern. Individuals on neighbouring farms show variations in leaf morphology that may indicate natural hybridisation is occurring in the immediate vicinity.

Based on special ecology, unique morphology, or spatial disconnection from other populations, do you suspect that the population has local adaptation?

It is possible that the population has local adaptation but this would need further investigating.

Based on the presence of a congener in the wild population or variable morphology, do you suspect that the species is hybridising with a congener?

There is suspicion that the species is hybridising with a congener (*E. longifolius*) in some areas of its distribution. Having said that, based on visible morphology, there is no indication that this population has elements of a congener but this can only be determined through genetic analysis.

Genetics of source material

From which wild populations will/should the material be collected for use in reintroduction?

The material collected for this augmentation originated from the same population to which is was returned. It is recommended that seeds collected from Population C only be used for augmentation of Population C until further genetic research is available.

What is the basis for collecting source material from a particular location?

The seeds collected from the female at this recipient site germinated unexpectedly resulting in this ad hoc augmentation project. Other than Population B (Chapter 3 and 4), this is the only recorded population where natural pollination is observed. Although research does indicate that existing *in situ E. latifrons* populations are part of a single large panmictic population, further genetic testing needs to be undertaken in this part of the *E. latifrons* distribution range where seedlings from closer populations, such as Population B may prove to be a useful source of propagules for restoration.

What is the genetic composition of the reintroduced material?

This is still to be determined with further research.

Should material come from an ex-situ source, only one wild source population, or mixed population sources?

It is advisable that the material come from the source population until further genetic testing confirms that material from an ex situ/other *in situ* population will not cause harm. The cautionary principle is advised in this case.

Reintroduction location

Have you researched the history of the recipient site?

Yes, the landowner's family has owned the farm for generations. There was once a larger population of *E. latifrons* where only two now remain. Some of those transplanted from the wild (generations ago) are now in the land owners garden.

Have you ranked several potential suitable recipient sites to determine the best place for the reintroduction to occur?

The best place for augmentation is the source of the material collected. The recipient site has an existing pair of male and female naturally cross-pollinating plants at the site. This makes the ranking recipient sites an unnecessary task in this case. Should a change of land ownership occur and the attitude towards the augmentation project change, ranking recipient sites may become necessary.

Is there still suitable habitat left within the species' range?

See Chapter 2.

Are recipient sites of sufficient quality and with sufficient long-term protection to ensure the long-term security of the reintroduced population?

See Chapter 2.

Are threats absent or adequately managed at the site?

Herbivory by livestock is a considerable threat at this site. Attempts to remove this threat were not successful. Greater measures need to be put in place to reduce this threat but this will require funding.

What were the previous threats that may have caused the species to become extirpated from the site?

Previous threats included the removal of adult plants from the population (before this became a prohibited activity). This was undoubtedly the biggest threat to the population. Lack of natural regeneration and seedling recruitment is exacerbated by herbivory and livestock activity at the site.

What is the potential for future threats?

Future threats include the expansion of infrastructure for the construction and expansion of the network of wind turbines in the area. Future threats may also include biome shifting due/fire regime changes due to climate change (Kraaij et al. 2014; Guo 2017; Chapter 2).

Is the current and future land use of the recipient site and surrounding sites compatible with sustainability of the reintroduced populations?

The current land use of the recipient site is not compatible with the sustainability of the restored population unless threats from livestock activity are successfully removed from the population.

Are potential hybridising congeners present at the recipient site? Which ones? Are they present at nearby sites? Are they present within the target species range?

There are no potential hybridising congeners at the recipient site. They may however present at sites a few kilometres away although it will only be through genetic testing to determine if they pose a real threat to the population.

In the recipient site within the species' climate envelope now? Do models suggest that the location will be safely within the climate envelope in the future?

Further research will need to be undertaken but Gou et al. (2017) predicts that the Fynbos Biome will shift under future climate change scenarios in the area. Sites representing climate change refugia need to be identified in future distribution modelling scenarios for the species.

What site preparation is needed before the plants can be installed? What habitat manipulation will continue after reintroduction?

Other than excluding grazing goats, cattle and sheep from the site, not much site preparation is required. Finding sufficient suitable microsites for seeds (in the event that an electric fence cannot be installed and maintained around the population) may present a challenge to future recovery projects.

Does the species need habitat conditions that no longer exist at the site e.g. fire? Can those conditions be mimicked?

Fire is a natural occurrence in the Fynbos Biome and is a natural disturbance in the area. Fire frequencies at nearby *E. latifrons* sites (approximately 8 kilometres away) experience frequent fires (see Chapter 3).

Fires are however more controlled on private land and do not occur as frequently as in other *E. latifrons* sites in the north-western part of the species distribution.

Habitat or landscape level considerations

Does the recipient site contribute to natural patterns of heterogeneity in the species' distribution?

The recipient site is in the western part of the species distribution in a core area considered as suitable habitat for *E. latifrons* (see Chapter 2 - southwest of Grahamstown, in an extension of the Highlands Range towards Howieson's Poort). The potential exists to augment this population further reinforcing the species presence in the area as it is relatively close (8 km) from a naturally self-sustaining larger *E. latifrons* population.

Have you considered habitat connectivity? Is healthy suitable habitat nearby that will allow the reintroduced population to expand in area and number of individuals? Is adjacent property suitable habitat? Is adjacent property protected?

The expansion of the population is possible as properties adjacent to the recipient site are suitable in terms of habitat and land management (a neighbouring property is a wildlife reserve keeping indigenous as well as livestock). There is however a property 4km from the recipient site that serves as a private wildlife protected area. See answer to answer to next question for further explanation.

Are there metapopulation possibilities? Have you accounted for between site factors as well as within site factors? Is the site located close to extant populations or other reintroduced populations?

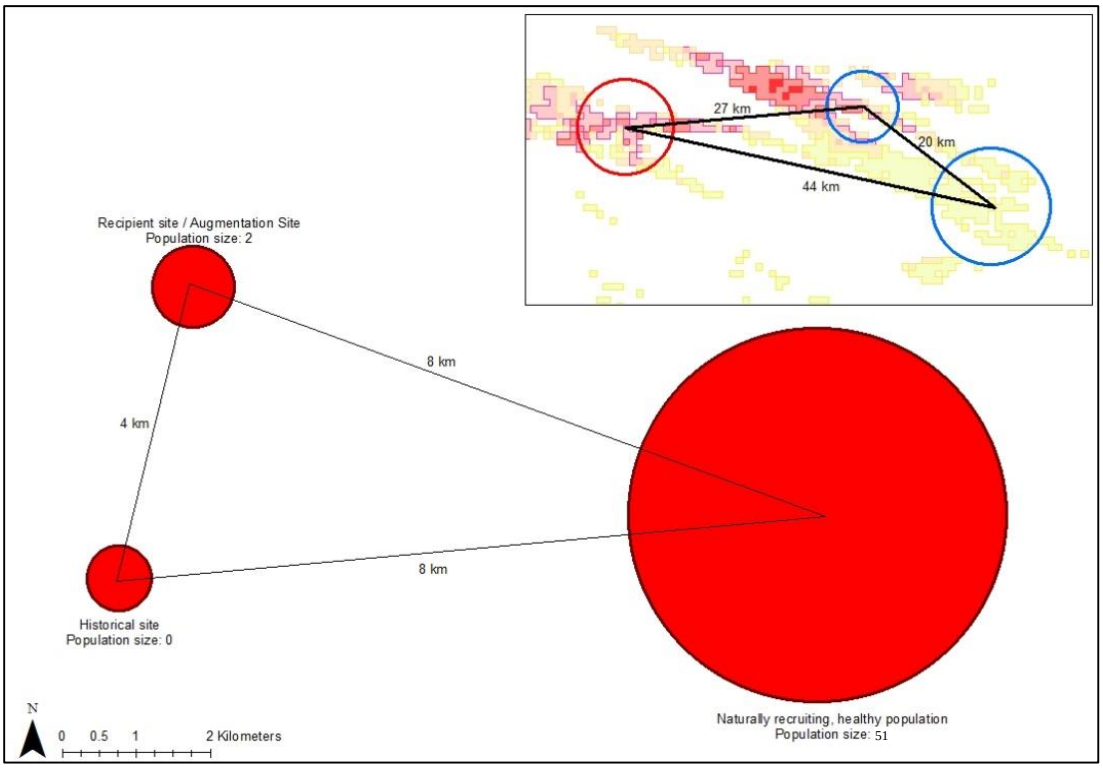


Figure 5.2.1 Metapopulation and connectivity possibilities of the re-establishment of the *Encephalartos latifrons* recipient site (smaller red circle at the top left of diagram). Population expansion/connectivity possibilities include a site 4km from the recipient site (smaller red circle on the bottom left of the diagram) where there is a historical record for *Encephalartos latifrons* in the wild. Both recipient and historical sites are 8km from a larger self-sustaining *Encephalartos latifrons* population (large red circle on the right of the diagram). Insert indicates the species distribution and suitable habitat described in Chapter 2. Blue circles indicate existing *in situ* populations of *Encephalartos latifrons* in relation to the recipient and historical sites that are both included within the red open circle

The historical site has great potential as reintroduction site for material from the current recipient site (depending on the outcome of genetic testing on the material). It falls within an area that is suitable for

E. latifrons. The current land use of the historical site is a private conservation area and the current land managers would be highly supportive of such an initiative. Augmentation at the recipient site and reintroduction at the historical site will positively contribute to the metapopulation dynamics of the species in the western part of the species distribution (Figure 5.2.1). In a broader overview of the species distribution, this cluster of existing and potential augmentation/reintroduction sites will contribute to the metapopulation dynamics of existing sites 27 and 44 km away towards the east of the species distribution (inset in figure 5.2.1).

What are the distances between proposed reintroduction and nearby wild populations? What advantages or disadvantages do nearby sites give the reintroduced population?

See previous answer

<u>Population Biology</u>

What founder population size will be used?

This depends on what is available and viable once the female plant cones again.

What size and stage structure of plants will be used?

The best choice given logistics and threats would be the used of seeds (once tested for viability).

How will the founding population be spatially configured to favour demographic persistence and stability?

Spatial configuration would depend on microsites available. Clustering of seedlings due to poor dispersal is often seen in wild populations, but intraspecific mortality is expected to play a role in seedling survival if the seedlings are too clustered (Chapter 3).

What is known about population growth, recruitment and survivorship in wild habitats and what environmental or community factors are correlated with population growth rates?

An integral projection/matrix model study on long-term census data will provide more insight into the population growth rates etc. at the metapopulation and population levels.

How will population growth, recruitment and survivorship be monitored in the reintroduced population and by whom?

Population growth, recruitment and survivorship will be monitored by census of individual propagules.

Implementation logistics

What is the best season to transplant seedlings?

The site experienced a Cfb climate with two rainfall peaks (September to November and March to April). This is the ideal time to sow seeds/plant seedlings.

Are permits acquired and up to date?

Permits will have to be required from DEDEA.

How will you ensure that the plants will be able to be tracked for many years into the future? Are plants tagged and coordinates recorded?

Tagging system already mentioned.

How will you transport plants to the recipient site?

Material to the site can be transported using an average high-rise vehicle, 4 x 4 is not necessary and access to the site is reasonable.

What is the planting layout design?

An assessment of the site can be undertaken to determine how many microsites are available for sowing seeds. The use of GIS and satellite photos will assist when designing a layout plan. It may be necessary to include construction of artificial microsites by creating rock barriers and fissures to protect seedlings from herbivory and creating a conducive environment for seed germination.

Post planting considerations

There are no post planting considerations for sowing seeds. Seedlings would require the construction of cages as well as watering during dry periods.

What aftercare is needed and how frequently will plants need attention?

If seeds are planted – one every 3 months, if seedlings are used, at least once a month.

What habitat management and threat abatement are needed? How frequently?

Control of livestock can only be achieved if there are funds available to electrify the fence. It would also be important to determine the importance of fire and to implement a fire regime strategy at the site if necessary.

References

Da Silva J, Donaldson JS, Reeves G, Hedderson TA. (2012) Population genetics and conservation of critically small cycad populations: a case study of the Albany Cycad, *Encephalartos latifrons* (Lehmann). Biol J Linn Soc 105:293–308

Guo D, Desmet PG, Powrie LW (2017) Impact of the future changing climate on the southern Africa biomes, and the importance of geology. J Geosci Environ Prot 5:1–9

Kraaij T, Wilgen BW Van, Van Wilgen BW (2014) Drivers, ecology, and management of fire in fynbos. In: Allsop N, Colville JF, Verboom GA (eds) Fynbos: ecology, evolution, and conservation of a megadiverse region. Oxford University Press, pp 47–72

Maschinski J, Duquesnel J (2006) Successful reintroduction of the endangered long-lived Sargent's cherry palm, *Pseudophoenix sargentii*, in the Florida Keys. Biol Conserv 134:122–129

Xaba PM (2014) Pollination and germination as limiting factors in the propagation of threatened cycads, *Encephalartos* (Zamiaceae). MSc thesis. University of Western Cape

CHAPTER 6

Population viability risk management (PVRM) of *Encephalartos latifrons in situ populations*

[Target journal: Journal for Nature Conservation]

Abstract

A holistic approach is needed when developing conservation plans for threatened and endangered species. One that takes into account what little is known about the biology and/or ecological requirements of the species concerned by factoring in uncertainty, as well as having the flexibility to include non-biological criteria such as socio-economic or political influencers which may become important when implementing the conservation plan. Multi-Criteria Decision Making (MCDM) is one such approach where multiple objectives and criteria based on multi-stakeholder inputs can be incorporated to come to an overall decision when faced with many conservation management alternatives. The Analytical Hierarchy Process (AHP) is one such MCDM approach used in this study to decide the best management strategy for *E. latifrons*. As part of this process, a sensitivity analysis was completed to test the robustness of the decision and to identify which criteria influenced the original results. Alternative management strategies are discussed including inherent risks and advantages associated with each strategy. The Population Viability Risk Management (PVRM) of *E. latifrons* using the AHP method is suggested as a viable method when developing conservation plans for the species. This technique is particularly practical when non-biological criteria need to be included in the decision-making process when they may influence the effective management of threatened and endangered species or when the traditional Population Viability Analysis (PVA) approach is not feasible.

Keywords: MCDM, AHP, conservation decision-making, PVRM

Introduction

Conservation managers and decision makers often lack information on endangered species due to their rarity and small geographic ranges (Regan et al. 2005; Schaub et al. 2007; Gibbs 2009; Pimm et al. 2014). Insufficient information on the demographic and ecological requirements of such species may hinder the development of conservation management plans where urgent conservation action is often required (Razgour et al. 2011; Di Minin and Moilanen 2012). This leads to a conservation paradox where the need to take urgent action is met with hesitancy associated with making conservation decisions in the face of uncertainty (Canessa et al. 2015).

Population viability analysis (PVA) is often suggested as a quantitative tool to assess the persistence of rare and endangered species under different management scenarios (CBSG 2010) but very few examples of PVA for long-lived perennial plant species exist in the published literature (Monks et al. 2012). The PVA approach to determine overall population growth rate and how management strategies influence population persistence requires demographic data collected over long time periods (depending on the study species 4 years is considered the minimum) for long-lived perennial plant species (Garcia 2003; Raimondo and Donaldson 2003; Dhar et al. 2008) and has limited use for management of threatened and endangered species where uncertainty is high (Moore et al. 2011). Moreover, if realistic models are to be developed then the traditional PVA analysis is a time-consuming process, which is problematic when conservation decisions need to be made quickly. In addition, the PVA approach does not take into account the socio-economic and political factors that may play a role in implementing conservation strategies, often not considered in conservation plans (Di Minin and Moilanen 2012). Tinch et al. (2018) identify problems hampering biodiversity conservation across all policy sectors including inadequate governance and administrative capacity as well as insufficient funding, to name a few. A holistic approach is therefore needed when developing conservation plans for threatened species; one that takes into account what little is known about the biology and ecological requirements of the species as well as non-biological factors such as logistic feasibility/socio-economic/political factors. Tinch et al. (2018) advocate a multi-way interaction process when developing and implementing conservation policies rather than a one-way approach where knowledge is transferred from science to policy in a linear fashion.

Multi-Criteria Decision Making (MCDM) is a decision making process that includes multiple objectives and criteria based on a variety of information (opinion, expert knowledge, objective facts) sourced from stakeholder input, in order to come to an overall decision when faced with many alternatives (Kangas and Kangas 2005; Ananda and Herath 2009; Young et al. 2011; Forsyth et al. 2012). In this way, decision analysis often incorporates conflicting interests affecting the decision making process to present a holistic evaluation of different decision alternatives (Kangas and Kangas 2005). The Analytical Hierarchy Process (AHP) is a MCDM method developed by Saaty (2008) and widely used in natural resource management, and more commonly in strategic forest planning (Segura et al. 2014). Other applications of AHP in conservation management include prioritising areas for alien species control and improved management of invasions (Roura-Pascual et al. 2009; Forsyth et al. 2012), examining the geographic factors influencing the poaching risk of a rare plant (Young et al. 2011), evaluating conservation strategies regarding the viability of an endangered tree species (Dhar et al. 2008), and in restoration planning (Kukrety et al. 2013).

The AHP method has many advantages including its ease of use (complex decisions are reduced to a series of pairwise comparisons), its less complex nature compared to other techniques (see Regan et al. 2005 and Canessa 2015 for examples of other methods) and the fact that different types of information can be considered together such as objective information and subjective opinion (Kangas and Kangas 2005; Mu and Pereyra-Rojas 2017). Stakeholder opinion is combined into an unbiased model that includes all viewpoints (Ramanathan 2001), which is particularly applicable where there is a need to resolve conflicting ideas in the decision-making process (Regan et al. 2005). One of the most important benefits is the fact that each participant's judgements are taken into account making it impossible for one group or participant to dominate the decision-making process (Tinch et al 2018). The advantages of using AHP process far outweigh the disadvantages which include the fact that the construction of the decision-hierarchy (and how the comparisons are constructed) will influence the outcome of the AHP (Kangas and Kangas 2005; Ananda and Herath 2009). An overview of MCDM methods including advantages and disadvantages is reviewed by Kangas and Kangas (2005) and Ramanathan (2001).

The need to develop a conservation plan for the critically endangered Albany cycad (*E. latifrons*) was identified in July 2006 due to its critically low population sizes and concern that the species is on the verge of extinction, if not already functionally

extinct (Daly et al. 2006). It was imperative that the viability of the current populations was assessed and actions determined for species recovery and ongoing conservation (Basson 1991). However, there was limited formal scientific information on the biology and ecological requirements of the species available at the time. In response to the call to develop a formal conservation plan for the species, a multi-stakeholder workshop including 21 participants (representing conservation authorities, private landowners, cycad collectors and nurseryman, members of the Cycad Society of South Africa, conservation NGOs and researchers) resulted in the development of the Population Viability Habitat Assessment (PHVA) for *E. latifrons* (Daly et al. 2006). The methodology used for the development of the PHVA was based on the Conservation Breeding Specialist Group (now known as the Conservation Planning Specialist Group – CPSG) approach to designing and implementing management plans for endangered species (CBSG 2010). The CPSG approach is based on the PVA method that integrates stakeholder input, which includes not only biological interactions affecting the population dynamics of threatened species, but socio-economic and other factors that may play a role in conserving the species concerned as well. The VORTEX program (Lacy and Pollak 2014) is the choice tool for quantifying extinction risks using the CPSG PHVA approach. However, modelling population dynamics for *E. latifrons* using the VORTEX program was not successful and the PVA model was not included in the final PHVA decision-making process (Daly et al. 2006). The PHVA ultimately led to the development of the Biodiversity Management Plan (BMP) for *E. latifrons* (Department of Environmental Affairs 2011) gazetted in terms of the National Environmental Management: Biodiversity (NEMBA) Act 10 of 2004. The BMP, with the overall aim to enhance the conservation status of *E. latifrons* and secure its existence in the wild, is aligned to the National Strategy and Action plan for the management of cycads in South Africa intended to secure the persistence of *in situ* viable populations of all indigenous cycad species by 2020 (DEA 2014). This is further supported by South Africa's Strategy for Plant Conservation to have at least 75% of known threatened plant species conserved *in situ* by 2020 (Raimondo 2015). The BMP for *E. latifrons* facilitates and favours a certain management strategy for the species where private land owners are legally permitted to artificially manipulate wild plants (e.g. through artificial pollination and seed germination) in order to establish a breeding programme intended to improve the persistence of wild populations. The rationale is that this management solution has a clear conservation benefit; in that by using the propagated seedlings for

restoration/augmentation programmes, species persistence in the wild is likely to improve over the long term. This also provides an incentive for the land owners to protect plants against poaching by generating revenue from the sale of a certain percentage of the seedlings propagated. The BMP stipulates that land owners are required to carry out appropriate management actions to ensure that necessary ecological processes are in place for the species persistence in the wild, but what constitutes such actions is not elaborated on in the plan (DEA 2011).

Aims

The aim of this chapter is to revisit the PHVA process for *E. latifrons* and to determine how this method may be strengthened in the face of uncertainty and lack of research information, without the need to include a formal traditional PVA for the species. Included in this assessment is to outline an integrative method which includes all stakeholder judgements into the decision-making process in a fair and un-biased manner. In this way, the PVRM could act as a precursor to the development of management strategies for *E. latifrons* before the BMP for the species is revised. This can be applied to other threatened cycad species in South Africa where appropriate. This process is simple and easy to understand, which is important for stakeholders who may not have a background in computer modelling.

Methods and results

The methods outlined in Dhar et al. (2008), a similar decision making process for the dioecious conifer *Taxus baccata*, were used in this analysis as a general step by step approach to guide conservation decision makers on how to best manage an *in situ* population of *E. latifrons*. This was linked to the formal AHP process as part of the decision-making framework. In this case, population viability in the PVRM process does not point to any formal PVA process but rather to evaluate threats that may limit the ability of a population to persist by identifying management strategies that mitigate or limit their impact.

Identifying the species/population at risk and relevant regulations

A detailed legislative framework for the species was outlined in the PHVA and again in the Biodiversity Management Plan for *E. latifrons* (Daly et al. 2006; Department of Environmental Affairs 2011). The target population, to determine the best management scenarios given the current threats, in this chapter is referred to Population A in this and other chapters in this thesis. Population A is divided by a game fence with a portion of plants on one side of the fence (referred to as A1 in this chapter) and the remainder of the population on the other side of the fence (referred to as A2). Population A1 occurs on a pineapple and livestock farm and Population A2 on a game farm. This population therefore experiences two different land use practices depending on which side the fence the plants occur. The BMP for *E. latifrons* was gazetted in 2011, and it was around this time that one land owner (on whose property A1 exists) started a formal breeding programme in line with the legal requirements as stipulated in the BMP. The breeding programme included Population A1 and A2 with neighbouring land owners both participating in the programme. It was in 2015/2016 that a change of land ownership occurred and Population A2 is now no longer part of the breeding programme. At the time of this thesis, Population A1 and A2 are not only experiencing separate land use practices but also different conservation management styles. Population A2 is now in a resting phase where the plants are not manipulated and natural ecological processes continue without anthropological interference. The current A2 land owners do however realise the importance of the role they need to play in order to protect the plants on their property but are not interested in cultivating cycads. As the property has changed hands relatively frequently, there is a great deal of uncertainty regarding the conservation management style of the different land owners for the A2 population on the property.

Population A1 is still managed intensively and part of the long-term breeding programme at the time of this study.

Description of the ecological conditions of the target species and its environment

Detailed information of what is currently known about the life history of *E. latifrons* is included in Table 6.1. Each life history or ecophysiological characteristic is assessed against its potential to increase or decrease the species' risk of extinction. Table 6.1 includes information from research detailed in the chapters of this thesis based on all known *E. latifrons* populations in the wild. Census information collected as part of this thesis is not sufficient to model a robust PVA in order to determine how the species might respond to different management scenarios. Long-lived perennials with slow life histories such as *E. latifrons* are more suited to stage –structured (rather than age) projection matrices (Lefkovitch 1965). For such species, there will be little to no movement of plants between stages (e.g. an immature plant becoming an adult) in a short term (4-6 year) study. This creates the problem of a reducible matrix (no transitions between stages) and therefore likely to be ergodic i.e. stable asymptotic growth remains unchanged (Stott et al. 2010). Integral Projection Modelling (IPM) provides another method to simulate the viability of plant populations under different management scenarios which also has its own limitations requiring the fitting of growth curves (Zuidema et al. 2010). Accurate measurable growth of individual plants (if any) is problematical for *E. latifrons* over a short term study (see Chaper 3).

Table 6.1 Importance of life history/ ecophysiologcial characteristics of *Encephalartos latifrons* measured against extinction risk susceptibility and population viability.

Life history and ecophysiological characteristics of *E. latifrons*	Comments	Influence on extinction risk
Small population size	*E. latifrons* populations are critically small increasing the risk of extinction (Matthies et al. 2004; Schemske et al. 1994).	↑↑↑
Slow growth	Slow growing species such as *E. latifrons* often trade off seed recruitment for growth and persistence making the species/population particularly vulnerable to adult plant mortality (Raimondo and Donaldson 2003).	↑↑↑
Fire response	*E. latifrons* plants are apical sprouters and respond well to fire damage from the seedling to adult stage (see Chapter 3). Fire is not considered a threat to *E. latifrons* populations at high frequencies (see Chapter 3) but this needs to be confirmed by longer term studies including the effects of fire regime change under a changing climate (Guo et al. 2017; Kraaij et al. 2014)	0
Asexual reproductive capability	In addition to apical sprouting, *E. latifrons* produces suckers (subterranean lateral branches) readily from the base capable of producing its own root system increasing the persistence and longevity of adult plants in the wild.	↓↓
Sexual reproductive capability	Research suggests that *E. latifrons* is capable of sexual reproduction in some wild populations. This needs to be tested for Population A before concluding that the Population is not capable of natural regeneration as reported in the PHVA and elsewhere. Some cycad species are however vulnerable to the loss of the mutualistic relationship with their pollinators which may be the case for *E. latifrons* in Population A (Cousins and Witkowski 2017; Donaldson 2003; Vovides et al. 1997).	↑↑
Drought tolerance	The distribution of *E. latifrons* is associated with Suurberg Quartzite Fynbos where summer droughts are less pronounced compared to Fynbos in the Western parts of South Africa (Campbell 1986; Cowling 1983; Rebelo et al. 2006). However, different life history stages may have different levels of resistance to drought (Álvarez-Yépiz et al. 2014). Further research is needed to determine the drought resistance of *E. latifrons* particularly with a changing climate.	0
Dioecious sexual system	Wild populations of *E. latifrons* display high levels of genetic diversity indicating a single panmictic population, high levels of gene flow between populations and a sexual mode of reproduction (Da Silva et al. 2012). Higher levels of genetic diversity may increase reproductive success (Noel et al. 2010) and the negative effects of inbreeding depression is less of a threat in dioecious plants (Ainsworth2000; Freeman et al. 1997). Conversely, the loss of one sex or a skewed sex ratio may increase the risk of extinction in small populations making them more prone to genetic drift (Hilfiker et al. 2004).	↑
Susceptibility to disease and pests	Diseases and pests are not a major concern in *E. latifrons* populations but evidence does point to occasional fungal infections of female cones (see Chapter 3). The landowner of Population Ai does report occasional infestation of the leopard moth (*Zeronopsis leopardina*) where the wild plants are sprayed with pesticide. Leopard moth infestations were not recorded in any other wild *E. latifrons* populations.	↑
Narrow physiological/habitat requirements	Narrow physiological and habitat requirements of *E. latifrons* restrict populations to quarzitic outcrops in the Suurberg Quartzite Fynbos vegetation (see Chapter 2). Regionally rare species with narrow habitat requirements may be more vulnerable to environmental and land use changes (Lavergne et al. 2005). On the other hand, restricted endemic species such as *E. latifrons* occur in harsh inaccessible habitats in areas with difficult terrain and low human disturbance increasing the probability of persistence for some populations (Lavergne et al. 2005; see also Population B in Chapter 3)	↑
Susceptibility to browsing/grazing/trampling	Grazing/trampling has not been recorded as a threat to *E. latifrons* populations in the past. Lack of natural recruitment however has been identified as caused by livestock herbivory and is considered an important and often overlooked threat to *E. latifrons* (see Chapter 5). Population A1 exists on a cattle farm. The population is not fenced off from grazing activity on the property and the landowner reports that livestock are active in the area surrounding the population. Threats by livestock on the property require further research.	↑↑

0 = no influence on extinction risk or undetermined; (↑) Increasing risk of extinction); (↓) decreasing risk of extinction.

Development of management strategies

Three management strategies are proposed for *E. latifrons* Population A based on factors that enhance the viability of the population (overall objective) with the primary goal to decrease the extinction risk to the species. More specifically, the primary aim of management strategies described below is to improve the prospects of Population A by restoring ecological processes necessary for the population to become self-sustaining (DEA 2011).

The first management strategy (MS I) is relatively passive allowing for the population to recover naturally and to create a conducive environment for the pollinator population to recover from intensive sexual reproductive management currently experienced by Population A1. The plants in the population are recorded to have recently recruited naturally according to a 1991 survey report by the conservation authorities (Basson 1991). Viability of seeds in the population under natural conditions has not been tested and it cannot be concluded that the population is not capable of natural recruitment until further research is available. The population experienced an extreme disturbance two years after the 1991 survey, where the illegal harvesting and theft of adult *E. latifrons* plants occurred on the property in 1993 (Vice 1995). It is unlikely that the seedlings mentioned in the survey report survived this disturbance and it is undetermined how long the population will take to recover from this severe disruption. This management strategy promotes the long-term self-sustainability of the population, an important inclusion in management plans for rare and threatened species where important and possibly endangered mutualisms are at play (Kearns et al. 1998). Pollinators have certain environmental requirements in order to complete their life cycle such as the availability of food sources, nesting material and nest sites (Menz et al. 2011). For cycads, most pollinators feed on the male strobilius tissue rather than on the pollen directly (Norstog and Fawcett 1989; Marler and Lindström 2015). The male cone is therefore an important breeding site for pollinators. Removing male cones out of the population will therefore negatively affect pollinator populations at the site. Socio-economic criteria do not apply to this management strategy except that alternative land owner incentives are suggested later in this chapter. Logistic implications of this management strategy include the increased need to monitor the level of herbivory at the site. If the population does become self-sustaining by producing viable seeds and in turn seedlings at the site, the seedlings will need extra protection from herbivorous

mammals, particularly livestock. As seen in Population C (Chapter 5), herbivory can be an important threat to population viability and recovery. This management strategy will however require less compliance monitoring by conservation authorities as no permits are required by the landowner. This is the management strategy currently experienced by Population A2 with a change in the land ownership of the property on which it occurs.

The second management (MS II) strategy involves the manipulation of adult sexually reproductive individuals in the population by removing male cones before pollen shed and "maturing" the cones in paper bags until all the pollen is released for collection and storage (landowner pers. comm.). The pollen is then used to artificially pollinate female cones in the population. The female cones are removed from the population once mature and ready to disintegrate. Seedlings are artificially propagated under nursery conditions and a percentage of the seedlings used for augmenting the existing population. The remaining artificially propagated seedlings are used in other restoration programmes and a percentage permitted for private sale by the landowner (see the *E. latifrons* BMP for a breakdown of the percentages for each category). This is currently the management scenario for the Population A1. The management strategy satisfies the need to maximise the seedling yield by artificial pollination in order to make plants available for augmentation and restoration programmes. This strategy also satisfies the need to provide the land owner with an incentive to protect their plants by allowing the sale of seedlings for his/her personal financial gain (identified as an important socio-economic criterion). There are logistic implications to this strategy in that strict permit conditions have to be adhered to, increasing the need for compliance monitoring by conservation authorities. The herbivory threat for this management strategy is reduced as older propagules are used for augmenting the population possibly increasing their resistance to herbivory and improving their chances of survival (see Chapter 5).

The third management strategy (MS III) is a mixed scenario between the two already mentioned. A portion of the male cones (identified as an important breeding site for pollinators) remain in the population and a "quota" of the pollen is harvested. This can be done by alternating cone harvesting between male plants from coning year to year. Artificial pollination can still occur and seeds harvested as long as this does not pose a threat to the pollinator population which need the male cones to complete their life cycle. This management strategy is a compromise between potential socio-

economic needs of the landowner/horticultural market and biological needs of the population. The biological criteria to create a conducive environment for pollinator recovery is met by this management scenario but seedling production is not maximised as it would be by the use of all the male cones for harvesting pollen. Threats to the population by herbivory would need to be controlled once/if the population becomes self-sustaining and compliance monitoring of permit conditions would still be a logistical caveat for this management option. A SWOT analysis (Strengths, Weaknesses, Opportunities, and Threats) of the different management strategies was compiled by the researcher (Table 6.2). Ideally, this would be performed by a panel of experts and stakeholders who can assess the management strategies from an unbiased perspective.

Table 6.2 SWOT analysis of the three proposed conservation management scenarios for *Encephalartos latifrons*, MS I, MS II and MS III

	MS I		MS II		MS III	
	Strengths	*Weakness*	*Strengths*	*Weakness*	*Strengths*	*Weakness*
Population level	- promotes a self-sustaining population - does not require intensive compliance monitoring of permit conditions - landowner incentives still apply (property relief/compensation) - decreased need for pest control - access to plants by researchers and conservation staff may become less restrictive	- long population recovery times are expected and population recovery is not guaranteed -fencing the population will be required to protect young seedlings that may germinate - fencing may increase biomass around the plants increasing the intensity of a fire at the site	- increase population size in the short term - fencing the population is not essential if older propagules are used for restoration/augmentation - involves a lucrative landowner incentive provided the landowner is keen on horticulture - may balance sex ratio by increase the number of individuals in the population	- may promote extinction of the local pollinator population - increases need for intensive pollinator restoration - increased need for pest control to increase seed viability; use of pesticides threaten existing/potential pollinator populations - intensive permit condition compliance monitoring is required by conservation authorities - increases the reliance of the population on artificial mechanisms for sexual reproduction - exposes the wild population to public knowledge potentially increasing the risk of poaching	- is a compromise strategy which includes biological and socio-economic benefits - a conducive environment is created for pollinator recovery - the landowner is able to artificially pollinate and harvest seed - population augmentation can be achieved at the same time as ensuring a self-sustaining population - the population has an increased chance as recovering its pollinator population - the population is not rendered completely dependent on artificial pollination should there be a change in land ownership - restoration of pollinator population may be more successful	- the need for compliance monitoring of permit conditions is the highest for this strategy - viable seed output may be reduced by the reduced amount of pollen available for artificially pollination - pest/insect control by the use of pesticides will need to be closely monitored
	Opportunities	*Threats*	*Opportunities*	*Threats*	*Opportunities*	*Threats*
Meta-population level	- inclusive biological monitoring with other populations - increase temporal scale of biological monitoring for the species - increase the number of self-sustaining populations	- slow down meta-population growth rate - reduce opportunities for augmentation and restoration of other populations - restrict meta-population connectivity	- provides opportunities to increase other population numbers and in turn, increase the growth rate of the meta-population	- depending on where the pollen is sourced, a threat to the meta-population may exist as a source of genetic pollution of populations. This management strategy is heavily reliant on the integrity of the landowner. - this management strategy creates expectations and sets a precedent for other landowners to profit from wild plants where the management solution may not be appropriate - highly dependent on landowners interest and skill in horticulture	- restoration of other populations is possible using propagules from this strategy - long term benefits of a potentially self-sustaining population increasing habitat connectivity across the distributional area of the species - potential model to be used for the management of other endangered cycad populations	- depending on where the pollen is sourced, a threat to the meta-population may exist as a source of genetic pollution of populations. This management strategy is heavily reliant on the integrity of the landowner.

Evaluation of management strategies

Hierarchy model for the decision

The overarching aim for the conservation of *E. latifrons* is to decrease the extinction risk of the species. This is in line with the aims of the BMP and PHVA (Daly et al. 2006; Department of Environmental Affairs 2011). The overall objective of the hierarchy model is to increase the persistence of the *in situ* Population A, by choosing the best management scenario according to what is currently known about the life history of the species and the threats that may be present at the site. This was done by the construction of a decision hierarchy, the first step in the AHP process (Figure 6.1).

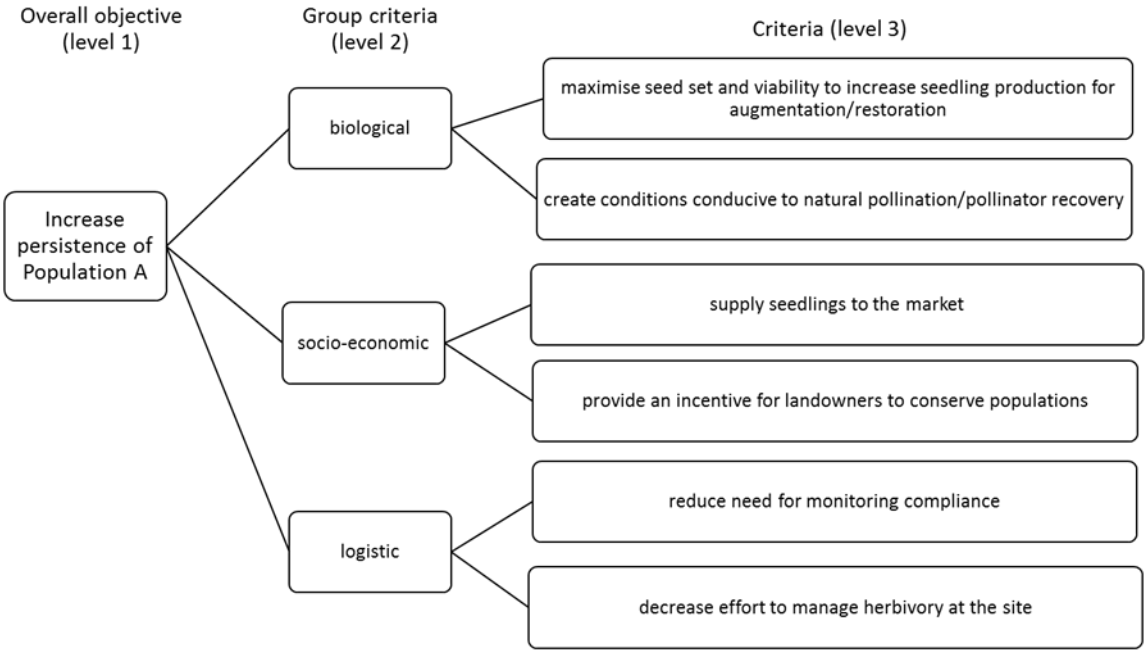


Figure 6.1 Structure of the decision tree (hierarchy) for *Encephalartos latifrons* developed by the researcher. Pairwise decisions are made at every level of the tree. The alternative management strategies are then compared under each criterion

The grouping criteria include biological, socio-economic and logistic factors that all influence the viability of Population A. The first biological criterion includes maximising seed viability (by artificial pollination) to increase the production of

artificially propagated seedlings for artificially increasing the number of individuals in Population A and other populations within the species distribution range. An increase in the number of individual plants at the site may decrease the influence of stochastic and deterministic forces on the population (Given 1994). There is also a greater chance that the sex ratio of the population may even out with the artificial increase in the number of plants restored to the population, sometimes seen in gynodioecious populations - see Nilsson and Agren (2006). The second and opposing biological criterion is to create conditions conducive for natural pollination. The idea that *E. latifrons* is incapable of recruitment under natural pollination originated as an assumption in the stakeholder workshop held for the original PHVA (Daly et al. 2006). This needs to be confirmed by testing the viability of seeds in the population under conditions of natural pollination e.g. by excluding any artificial manipulation and harvesting of male cones and by managing potential threats to seedling recruitment. Natural pollination in *E. latifrons* populations is possible in populations with critically low numbers where lack of seedling recruitment is likely from livestock herbivory at the site (see Population C – Chapter 5). Creating conditions for natural pollination and recruitment includes no manipulation of the population by not removing the male cones before pollen shed and in turn, and no artificial pollination of the female cone. This is an important consideration if the current/future pollinator populations are to remain viable increasing the chances that the population will become self-sustaining in the long term (Kearns et al. 1998).

There are many socio-economic factors that come into play regarding the conservation of *E. latifrons* and other cycad species around the world. One of the largest threats to cycad species globally is the illegal harvesting and trade of wild specimens (TRAFFIC 2003). This is also the case for *E. latifrons* where evidence of large-scale harvesting of wild *E. latifrons* plants dates back to the 1960's (Swart 2017). However, TRAFFIC (2003) reports that the bulk of recent trade in cycads is in artificially propagated specimens. Socio-economic factors included in the model therefore complement each other: in manipulating the plants by artificially pollinating the female cones and the artificial propagation of seedlings allows for a certain percentage of the seedlings to be sold to the open market. At the same time, this provides an incentive to the landowner to conserve populations on his/her private property. The PHVA identified that limited supply of *E. latifrons* plants stimulates high prices and illegal collecting (Daly et al. 2006). On the other hand, the sale of seedlings from artificially

propagated seedlings is not the only way to provide an incentive to conserve plants on private property. Not all landowners are keen horticulturalists. This was seen with the change in the conservation management of Population A2 where the landowners did not express an interest in propagating seedlings from the wild parental stock on their property but remain committed to *E. latifrons* conservation. The PHVA also identifies tax rebates (property rate relief) for landowners as a potential incentive. This is considered a viable incentive for landowners on realising conservation goals (Pence et al. 2003; Langpap 2006). Other incentives could include compensating the land owner for loss of productive land by protecting/fencing off the plants on his/her property. Incentives should always include a monitoring clause where the landowner undertakes to monitor the health of the population with the guidance of conservation/scientific authorities. An important consideration for any management strategy should include biological monitoring, threat status monitoring as well as monitoring the process of implementing interventions (Gibbs 2009).

An increase in the manipulation of populations comes with the added responsibility of government authorities to oversee that permit conditions are adhered to. The logistics around compliance monitoring are raised as an important consideration in the PHVA regarding lack of capacity/shortage of staff, change of staff/regular resignations and work overload of conservation authorities. This is a real concern where most of the activities undertaken by the landowner relies on his/her integrity. This is especially important regarding the possibility of genetic pollution, where land owners may find other sources of pollen to supplement their supply. Some permit conditions, such as prohibiting the mixing of pollen from other *E. latifrons* populations, are impossible to monitor and control. Other logistic considerations include efforts needed to manage herbivory at the site. This has not been a consideration for this Population A, but other sites such as the one with Population C have shown that herbivory can be an important threat to the re-establishment of seedlings (see Chapter 5). The protection of seedlings from herbivory becomes logistically more difficult the younger the plants used for augmentation or if natural recruitment becomes an important part of the management plan.

The criteria in Figure 6.1 are not exhaustive and are an example of how decision hierarchies for species such as *E. latifrons* can be constructed. The hierarchy in this example does not solely rely only on the biological information (or lack thereof) for the species concerned. It is however emphasised that the criteria should be developed as

part of a stakeholder workshop such as was held for the PHVA. The criteria may have to be revised along with the revision of the BMP and as more research information becomes available. Further motivation for the inclusion of certain criteria in the hierarchy is included in Table 6.3.

Table 6.3 Explanation of criteria included in the hierarchy model

Level 2 group criteria	Level 3 criteria	Motivation for inclusion	Indicator
1. Biological	maximise seed set and viability to increase seedling production for augmentation/restoration	With very few individuals remaining in the wild, the number of individuals can be improved by artificial pollination to increase the viability of seeds and in turn increase the number of available plants for restorative purposes. Increasing the numbers might also balance the sex ratio in the longer term and improve the likelihood of coning synchronicity (Daly et al. 2006).	Intrinsic population growth rate of 0.32 is expected for a healthy recovered population with an average of 2 female offspring per female during her lifetime (see Chapter 3).
	create conditions conducive to natural pollination/pollinator recovery	No definitive tests seed viability under natural conditions for Pop A has been done. Until this is confirmed through research, must manage the population for the maintenance of the potential pollinators. Other populations have shown that lack of seedling recruitment does not necessarily infer lack of natural pollination (see Chapter 4).	Evidence that key pollinators are present and the population is able to self-sustain through natural recruitment.
2. Socio-economic	supply seedlings to the market to reduce pressure on wild populations	Small scale trade in collectable species is likely to have an impact on rare species. Selective removal of individuals for the horticultural trade or parts of the plant such as bark harvesting for the indigenous medicinal trade is considered a major threat to cycad populations (Bamigboye et al., 2016; Cousins and Witkowski 2017; Donaldson 2008; Okubamichael et al. 2016; Williams et al. 2014) including *E. latifrons* populations.	The legal sale of seedlings decreases the demand for wild plants (Daly et al. 2006; Kay et al. 2011).
	provide an incentive for landowners to conserve populations	The PHVA for *E. latifrons* identified the need to provide landowners with incentives to protect wild populations on private land. Incentives include tax rebates or seedling propagation using wild plants as parental stock.	Landowners are more willing role-players in the conservation of plants on their properties and risk of poaching is decreased.
3. Logistic	reduce need for monitoring compliance	The PHVA workshop identified staff constraints within the government sector that make compliance monitoring logistically burdensome.	The level of compliance and monitoring by conservation authorities is reduced. Land owners take more ownership for monitoring plants on their properties and reporting findings to conservation authorities is improved.
	decrease effort to manage herbivory at the site	Seedlings in other populations are very vulnerable to herbivory (see Chapter 5). Some management alternatives might require the protection of seedlings if natural population recovery is to be enhanced.	Natural recruitment made possible by the protection of naturally germinated seedlings from herbivory. Decrease in the overall threat from herbivory.

Derive the weights by pairwise comparison

The next step in the AHP process is to derive relative priorities (weights) for the criteria. This is done by the pairwise comparison of all criteria using the comparison scale developed by (Saaty 2008). The three management strategies (MS I, II and III) at the lowest level of the hierarchy are evaluated against all third level criteria influencing the final decision made with respect to the best management scenario for the population given the primary goals and objectives. In this case, the relative importance of the criteria was judged by the researcher. What is important to one person (such as the researcher) may not be equally important to another person such as an *E. latifrons* landowner who may give more importance to other criteria. The landowners themselves may not agree on the relative importance of certain criteria creating stakeholder conflict. It is therefore important that a representative group of stakeholders are included in the process (Ishizaka and Labib 2011). The resulting comparison matrix (Table 6.4) will have the judgement values entered into the upper triangle of the matrix - either the actual value or the reciprocal value depending on which side of the decision the judgement was made – (see Mu and Pereyra-Rojas (2017) for an introduction of the AHP process and examples). The reciprocal values are calculated for the lower triangle as 1/ [the judgement value]. Averaging judgements and further statistical analysis would be necessary if stakeholder groups are included in the decision-making process.

The PriEsT (A Priority Estimation Tool) was chosen for the analysis (Siraj 2011; Siraj et al. 2015). The software is freely available on the internet (School of Computer Science, University of Manchester, UK; https://sourceforge.net/p/priority/wiki/Home/ downloaded on the 12/03/2018), is relatively easy to use and is a proven and efficient tool in natural resource management (Derak and Cortina 2014). The geometric mean (GM) or approximate method was chosen for the analysis. An evaluation of 18 different elicitation methods by Choo and Wedley (2004) recommended GM as one of the preferred methods to use due to its good performance on consistent and inconsistent matrices. In this example, the biological criteria were of foremost importance to the researcher scoring a 5 (strong importance) and a 6 (very strong importance) compared to socio-economic and logistic importance respectively.

Table 6.4 pairwise comparisons between all criteria and alternatives (management strategies) made by the researcher

Main criteria	1. Biological	2. Socio-economic	3. Logistic
1. Biological		5	6
2. Socio-economic	0.2		3
3. Logistic	0.17	0.33	

Pairwise comparisons of sub criteria		
sub-criteria (biological)	*a. max_seed*	*b. nat_pollination*
a. max_seed		0.17
b. nat_pollination	6.02	
sub-criteria (socio-economic)	*c. seedling_market*	*d. land_incentive*
c. seedling_market		0.25
d. land_incentive	4	
Sub-criteria (logistic)	*e. com_monitoring*	*f. manage_herb*
e. com_monitoring		1
f. manage_herb	1	

Pairwise comparisons of sub-criteria against each management strategy			
	Management strategy I	*Management strategy II*	*Management strategy III*
Management strategy I		a (0.125) b (9) c (0.125) d (0.111) e (8) f (0.143)	a (0.2) b (3) c (0.2) d (0.166) e (8) f (0.143)
Management strategy II	a (8) b (0.111) c (8) d (9.009) e (0.125) f (6.993)		a (3) b (0.166) c (4) d (4) e (1) f (1)
Management strategy III	a (5) b (0.333) c (5) d (6.024) e (0.125) f (6.993)	a (0.33) b (6.024) c (0.25) d (0.25) e (1) f (1)	

Model synthesis of calculated priorities and consistencies

The PriEsT program calculates the priority vectors as the relative weights among the comparisons. In this example, the calculated weight for the biological criterion was 0.717, followed by the socio-economic criterion of 0.195. The logistic group criterion

has a minimum calculated weight of 0.088. Group and sub criteria weights with calculated overall priorities for each management strategy are presented in Table 6.5. The overall results of the PVRM analysis indicates that MS I is the preferred management strategy (overall priority = 0.464) compared to MS II and MS III given the weight of all criteria from the pairwise judgements made by the researcher. Management strategies II and III are almost equally as preferable (overall priority of MS II = 0.271 and MS III = 0.265).

The PriEsT program also calculates a consistency ratio (CR) to determine the level of inconsistencies in the judgement matrix. A CR value of 0.10 or less is acceptable in an AHP analysis (Saaty 2012). The level of inconsistency in the decisions used in the AHP analysis for this study was acceptable according to the CR of the overall priorities (CR = 0.081) as well as for all the sub criteria (CR < 0.1). Other measurements provided by the PriEst software include an error indicator, a measure of the total deviation (TD) to estimate the performance of the prioritisation. The lower the TD value, the closer the weights ratio is to the comparisons (Siraj 2011). A measure of overall congruence (Θ) is also calculated using the PriEsT software as an additional measure of inconsistency (Siraj 2011) where the judgement for sub criteria d in this example is the most inconsistent (Θ = 0.984) while sub criteria a is considered the most consistent (Θ = 0.629).

Table 6.5 Calculated criteria and sub-criteria weights based on pairwise judgements. Overall priority (importance) of each management strategy is also shown

Criteria weights	**1. biological**		**2. socio-economic**		**3. logistic**		**overall priority**
	0.717		**0.195**		**0.088**		
Sub criteria weights	*a*	*b*	*c*	*d*	*e*	*f*	
	0,142	*0,853*	*0,200*	*0,800*	*0,500*	*0,500*	
MS I	0,067	0,663	0,064	0,056	0,800	0,067	0,464
MS II	0,661	0,058	0,699	0,701	0,100	0,467	0,271
MS III	0,272	0,279	0,237	0,243	0,100	0,467	0,265
TD	4,701	7,501	11,021	16,328	-	-	6,970
Θ	0,629	0,697	0,916	0,984	-	-	0,916

CR	0,038	0,047	0,081	0,094	-	-	0,081

Sensitivity analysis

Sensitivity or "what-if" analysis is used to determine how the decision outcome would change if the criteria weights had been different. Sensitivity analysis also tests the robustness of the decision and identifies which criteria influenced the original results. The PriEsT program allows for a variety of sensitivity analysis including probabilistic simulation and one-at-a-time sensitivity analysis (Leonelli 2012; Siraj et al. 2015).

Probabilistic Sensitivity Analysis

One option given by the probabilistic sensitivity analysis built into the PriEsT program is to randomly change weight values of any given parameter or a combination of parameters through the use of Monte-Carlo simulations (the default number of iterations is set to 10 000 in the program). The selected criteria weights are generated at random to determine how alternatives (management strategies) are ranked (prioritised) with this change. For example, a random change in the biological weighting results in MS II with the highest mean ranking out of the three alternatives, with the MS I and MS III strategies coming in second and third respectively. It is therefore possible for MS II to outrank MS I and II under certain conditions (Figure 6.2).

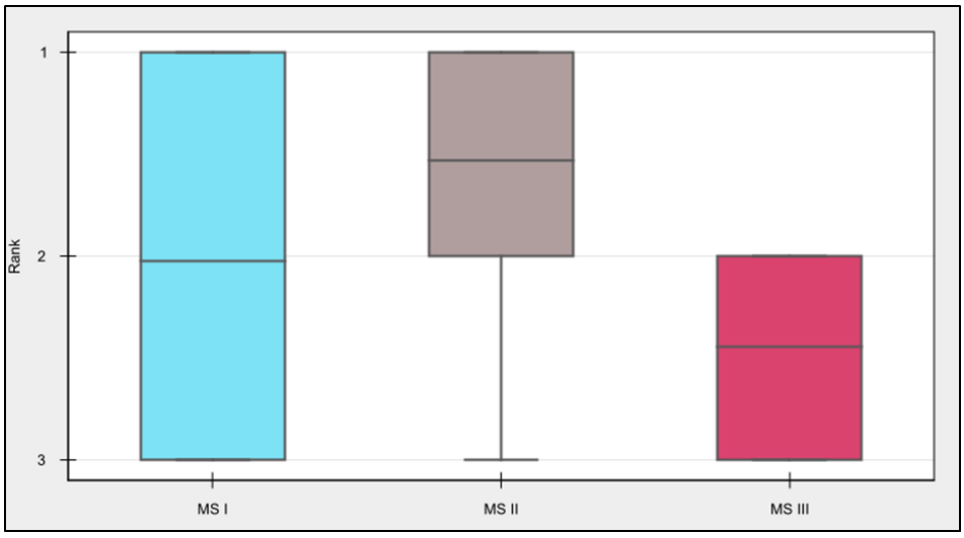


Figure 6.2 Box plot chart depicting the results of a probabilistic sensitivity analysis of management solutions with a random change in the overall biological criteria.

The grey mid-line corresponds to the mean ranking of alternatives, the box encloses 25% - 75% quartiles and the minimum and maximum ranks are the endpoints of the grey lines

One-at-a-time Sensitivity Analysis

One at a time SA is recommended when there is high confidence in the model judgement with low uncertainty in the criteria. This method works by changing the weight of one criterion (or management scenario depending on which part of the hierarchy is being analysed) and then recalculate the overall priority of the alternatives. This is done by making sure that all weights sum to 1, so when the weight of one criteria is changed, the other criteria weights change proportionately (Leonelli 2012). Figure 6.3 (a) shows how a change of weight in the biological criterion will affect the ranking of the three proposed management alternatives. Rank reversal between MS II and MS III occurs with a slight decrease in the biological weighting e.g. a biological weight of below 0.7 will increase the rank of MS II over MS III. MS II increases in a linear fashion with a decrease in the importance of the biological criterion. A reversal in rank between MS I and MS II occurs when the biological weight is decreased to below 0.5. Interestingly, MS III shows almost no movement with a change in the biological weight displaying considerable stability with a change in all criteria (Figure 6.3 a – b). Conversely, an increase in the importance of the socio-economic weighting will increase the overall priority of MS II. A reversal of ranks between MS I and MS II occurs with an increase of the socio-economic weight above 0.4 (Figure 6.3 b). A change in the logistic weighting had no impact on the management strategies not show here.

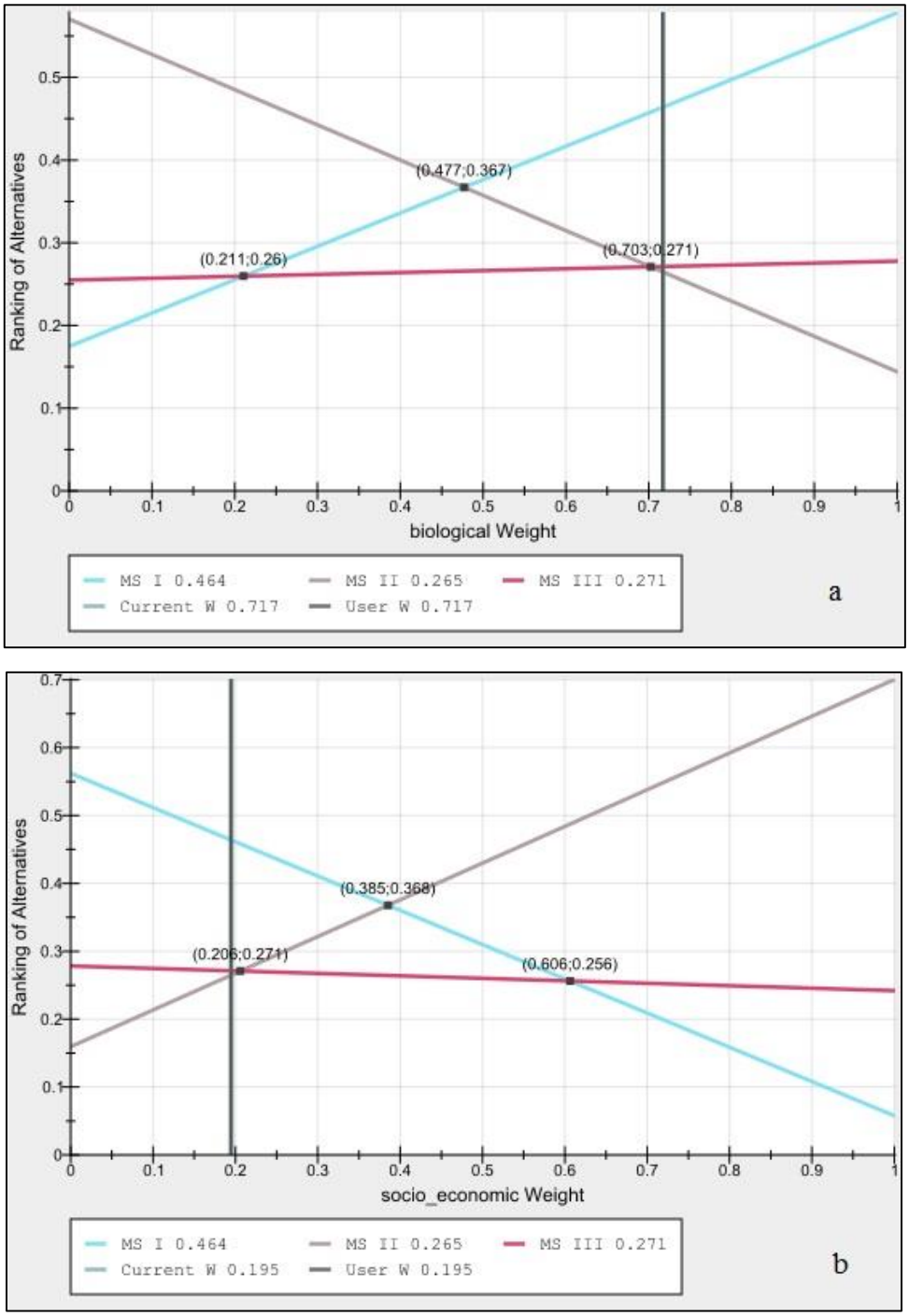
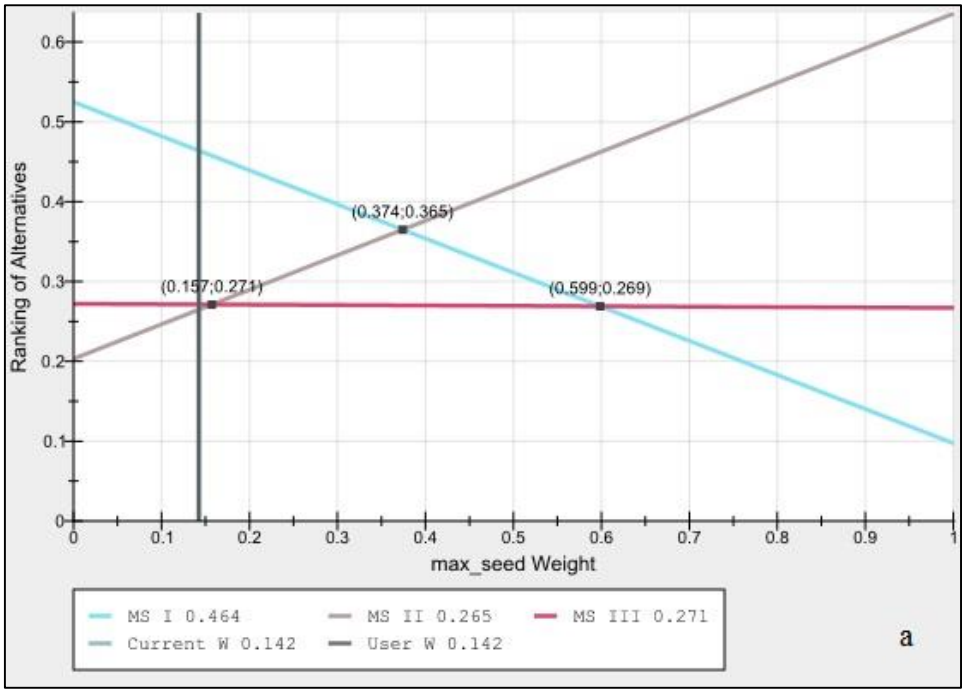


Figure 6.3 a, b One-at-a-time sensitivity analysis showing how a change in weight of the biological criteria (a) and socio-economic criteria (b) will affect the overall priorities of the three management strategies, MS I, II and III

In order to determine how a weight change in the two biological criteria will change the overall priority of management strategies, a one-at-a-time sensitivity analysis was calculated for a change in either of the biological criteria. Figures 6.4 (a) and (b) show how the ranking of alternatives will change when high importance is placed on maximising seed viability to increase seedling production (max_seed) Figure 6.4 (a). Alternatively, how the ranking of alternatives will change by creating an enabling environment for the recovery/restoration of pollinator populations (nat_pollination) in Figure 6.4 (b).



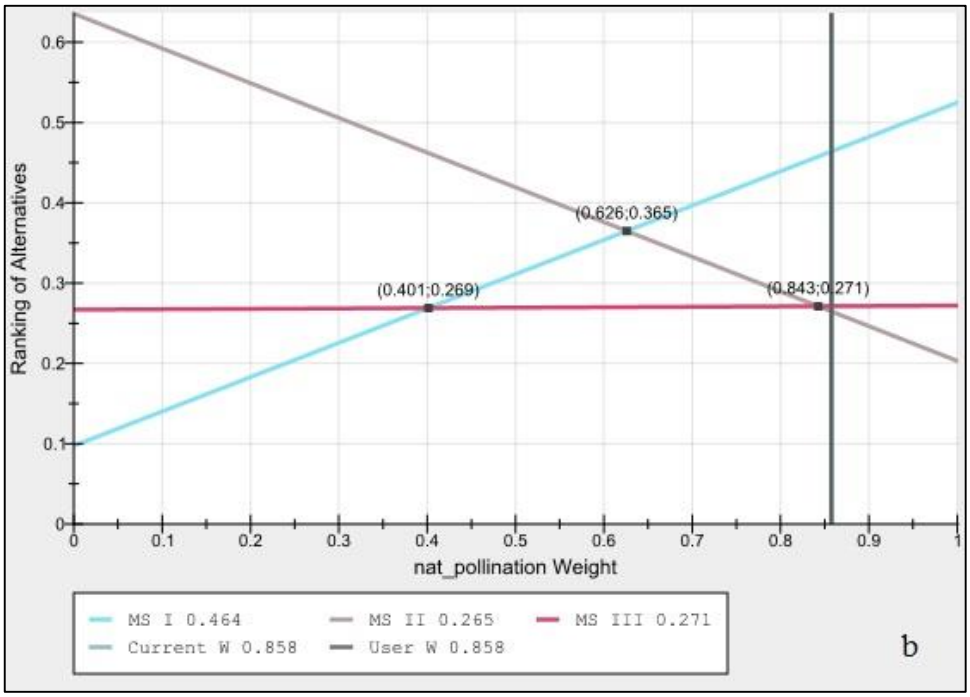


Figure 6.4 a, b One-at-a-time sensitivity analysis showing how a change in weight of the biological criteria max_seed (a) and biological criteria nat_pollination (b) will affect the overall priorities of the three management strategies, MS I, II and III

A slight change in the weight of max_seed sees a change in rank between MS II and MS III with a linear increase in MS II as the max_seed weight increases. A weight

change of seed_max to anything over 0.37 will result in MS II as the preferred management strategy with MS I decreasing linearly. Should the importance of max_seed increase to anything over 0.6 in weight, MS I becomes the least favourable management strategy. It is the converse for nat_pollination where a decrease in the weight favours MS II over MS I. MS III remains stable with a change in the weight of both criteria.

An example of using the sensitivity analysis is to determine how changing the criteria would change how the management strategies are ranked is illustrated below. For this example, the idea that tax rebates/compensation of productive land used for conservation offer workable solutions in providing the landowner with an incentive to conserve the wild plants on his property (the weighting of land incentive therefore remains unchanged). The weights of the following criteria are however set to change randomly as they become less important when not used as a landowner incentive: max_seed, seedling_market and com_monitoring. The simulation ranks MS I as the preferred option. MS II becomes the least preferred option in this scenario (Figure 6.5).

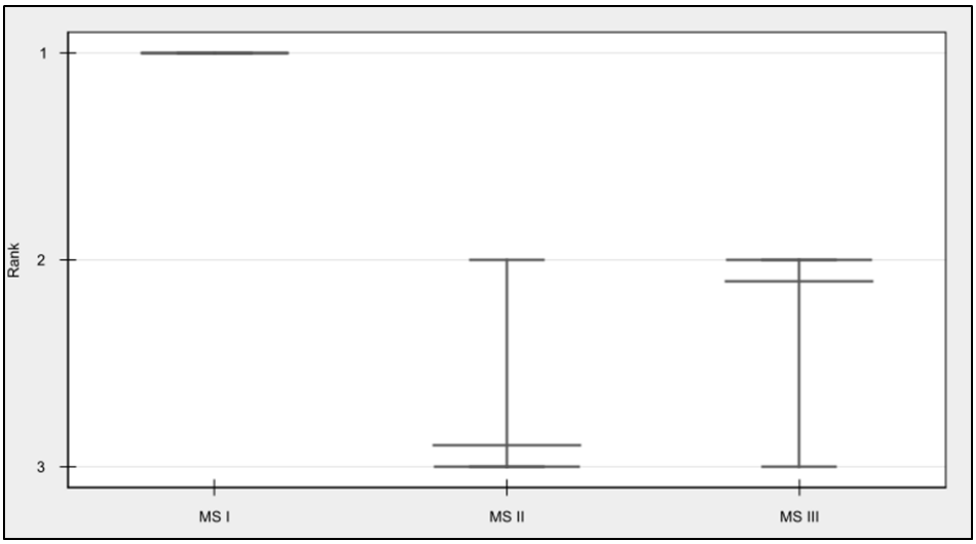


Figure 6.5 Probability sensitivity analyses for a random weight change in the max_seed, seedling_market and com_monitoring criteria.

Discussion

It must be emphasised again that this chapter does not intend to replace a stakeholder workshop to determine the best possible management solution for one *E. latifrons* population. This method has been applied to one site using one perspective in order to provide general guidance on how future stakeholder workshops may be conducted in order to revise the outdated PHVA and as a precuror the revision of the BMP for *E. latifrons*. The idea is not to use the information from this chapter in order to make policy decisions based on the results of the model, but to rather highlight alternative options to how the PHVA was previously conducted where a formal PVA was not possible. The assumption is that this chapter may provide some insight into how the information future stakeholder workshops for *E. latifrons* and other endangered cycad species may be conducted and analysed with minimal bias.

The results of the PVRM indicate that MS I is the best strategy for enhancing the viability of Population A based on the hierarchy model developed by the researcher and the pairwise judgements made for the criteria. The researcher placed emphasis on the biological criteria, particularly the need to create an enabling environment for the persistence of the pollinator population and in turn, to create the conditions that will enable a self-sustaining population in the future. This requires minimal compliance monitoring by conservation authorities but may include controlling potential threats (such as herbivory) to protect seedlings that may germinate. The time taken for a population to recover from poaching/intensive management is uncertain; as is the health status of the pollinator population, so MS I is possibly a solution where results may only be realised in the long-term. MS I does not favour the socio-economic criteria that may be important to certain role-players in the conservation of *E. latifrons* The results of the PVRM further indicate that MS II and MS III are close second alternatives to MS I with MS II slightly favoured. MS II strongly favours the socio-economic criteria in the model hierarchy whereas MS III is more of a hybrid strategy between MS I and MS II placing importance on both biological and socio-economic criteria.

The sensitivity analysis indicates that when the weight value of the biological criteria is randomly simulated, the MS II strategy is preferred. This shows that a change in weighting of the biological criteria can demote MS I in the rankings. A closer look at a change in the weight of the biological criteria using one-at-a-time sensitivity analysis confirms that MS II will outperform MS I with a decrease in the biological

criteria weighting. MS III remains stable with a change in the biological weighting and does not outrank MS I or II at any point.

Sensitivity analysis for the biological criteria was further decomposed and analysed by the third level criteria max_seed and nat_pollination. Both criteria are biologically important. Maximising the seed output of the population through artificial pollination and propagation of seedlings will make plants available for augmentation programmes increasing the size of the population. This may eventually even out the currently male-biased sex ratio of the population (Nilsson and Agren 2001). MS II is the preferred management strategy to satisfy this criterion but does not include a longer-term strategy to ensure that the population is self-sustaining by providing an environment for pollinator recovery. MS I is favoured when the nat_pollination criteria weighting increases above 0.626 where a self-pollinating population is likely in the longer term compared with MS II.

Both MS I and MS II have inherent risks associated with them (Table 6.2). MS II may disrupt any pollinator mutualisms that may still exist in the population, rendering the population dependent on artificial pollination or requiring intensive pollinator restoration of the population at a later stage. Global trends indicate that certain pollinator species may be difficult to restore – owing to their complex life cycles or recovery from local extinction may be slow (Menz et al. 2011). Menz et al. (2011) suggests that captive breeding and reintroduction programmes may offer solutions to pollinator recovery but restoration becomes more of a challenge for pollinators that have highly specific ecological requirement. In addition, MS II is highly dependent on market forces and landowners interest in horticulture. MS I requires a complete resting phase for the population where plant and pollinator population recovery may be slow or non-existent in the short-term (or the risk that the population remains functionally extinct in the long term). Although this strategy aims to ensure population self-sufficiency in the longer term, it does not guard against the threat of extinction, characteristic of small isolated populations (Schemske et al. 1994; Matthies et al. 2004).

MS III outranks either MS I or MS II at various points in the sensitivity analysis for a change in weight of both biological criteria. It is however never the preferred alternative over MS I and MS II together at any one time. The stability of this management strategy against fluctuating weighting of most criteria is interesting and possibly hints at the idea that this is the best management strategy in the face of uncertainty. MS III also comes with less risk as it provides an environment beneficial

to pollinator recovery as well as ensures that population numbers can be increased satisfying both biological criteria. The biggest downfall of this management strategy is the need for intensive compliance monitoring to ensure strict permit conditions are adhered to. It is impossible to monitor compliance to all permit conditions for example: ensuring that pollen from other sources is not used to limit the threat of genetic contamination. Adhering to the permit conditions ultimately will rely on the integrity of the landowner.

The PVRM process should include multi-stakeholder judgements and a final decision for the management of *E. latifrons*, ideally workshopped under the guidance of the *Encephalartos latifrons* forum (ELF). The AHP process is suitable for this application, and recommended prior to the revision of the Biodiversity Management Plan for the species where scientific information is limited and uncertainty is high. The PVRM can include a PVA analysis once this information becomes available for the species. In this way, it may be possible to include quantitative information into the decision criteria. The AHP decision protocol has room become more structured and may be combined with the use of programs such as RAMAS GIS or Integrated Projection Modelling more appropriate for modelling the population dynamics of long-lived perennial plant species (compared to the VORTEX system used by the CBSG). The AHP process is also highly flexible and may be combined with commonly used methods such as the Strengths, Weaknesses, Opportunities and Threats (SWOT) analysis (A'WOT method described by Kajanus et al. (2004) and Kajanus et al. (2012). The CBSG philosophical approach is supported by the use of the AHP process in that it allows a mixed source of information (PVA quantitative information as well as political/financial/logistic information) similar in the way the PHVA was originally developed for *E. latifrons*. Moore et al. (2011) pointed out that one of the biggest threats to the conservation of threatened species can come from bureaucratic barriers such as seen in the conservation of Mead's Milkwood. Moore et al. (2011) also noted that management performance is improved by an adaptive management approach when uncertainty is reduced by an increase in information through species monitoring and research. It is important to state that although any conservation plan should be adaptive and subject to change, some management decisions such as legalising the manipulation and artificial pollination of wild populations are difficult to reverse (if found that this has become a threat to the population). In this way, non-traditional methods may in themselves become a threat to the species persistence (Marler et al. 2017). Runge

(2011) advocated the idea that conservation decisions made today should also take into account the future course of decision making. This is important as the current condition of a population with all the management interventions and environmental stochasticity in between, will ultimately foretell the future persistence of a population.

References

Ainsworth C (2000) Boys and girls come out to play: the molecular biology of dioecious plants. Annals of Botany 86:211–221

Álvarez-Yépiz JC, Búrquez A, Dovčiak M (2014) Ontogenetic shifts in plant-plant interactions in a rare cycad within angiosperm communities. Oecologia 175:725–735

Ananda J, Herath G (2009) A critical review of multi-criteria decision making methods with special reference to forest management and planning. Ecological Economics 68:2535–2548

Basson M (1991) Eerste verslag wat die bron en status van die *Encephalartos* spesies in die Trappe's Valley area in die Oos-Kaap aandui met spesiale verwysing na die *Encephalartos latifrons*. Grahamstown, South Africa

Campbell BM (1986) Montane plant communities of Fynbos Biome. Vegetatio 66:3–16

Canessa S. (2015) Decision analysis for threatened species management across the captive-wild spectrum. Unpublished PhD thesis. The University of Melbourne

Canessa S, Guillera-Arroita G, Lahoz-Monfort JJ, Southwell DM, Armstrong DP, Chades I, Lacy RC, Converse SJ (2015) When do we need more data? A primer on calculating the value of information for applied ecologists. Methods in Ecology and Evolution 6:1219–1228

CBSG (2010) Population and Habitat Viability Assessment (PHVA) workshop process reference packet (www.cbsg.org)

Choo EU, Wedley WC (2004) A revised framework for deriving preference values from pairwise comparison matrices. Computers and Operational Research 31:893–908

Cousins SR, Witkowski ETF (2017) African Cycad Ecology, Ethnobotany and Conservation: A Synthesis. The Botanical Review 83:152–194

Cowling RM (1983) Phytochorology and vegetation history in the south-eastern Cape, South Africa. Journal of Biogeography 10:393–419

Da Silva J, Donaldson JS, Reeves G, Hedderson TA (2012) Population genetics and conservation of critically small cycad populations: a case study of the Albany Cycad, *Encephalartos latifrons* (Lehmann) Biological Journal of the Linnean Society 105:293–308

Daly B, Donaldson JS, Friedmann Y, Hahndiek Q, King N, Newton D, Southwood A (2006) Population and habitat viability assessment for the Albany Cycad (*Encephalartos latifrons*). Conservation Breeding Specialist Group (SSC / IUCN) / CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg

DEA (2014). National strategy and action plan for the management of cycads. Pretoria, South Africa

Department of Environmental Affairs (2011) Biodiversity Management Plan for Albany Cycad, *Encephalartos latifrons*. National Environmental Management: Biodiversity Act (10/2004): South African Government Gazette No. 34388

Derak M & Cortina J (2014) Multi-criteria participative evaluation of Pinus halepensis plantations in a semiarid area of southeast Spain. Ecological Indicators 43:56–68

Dhar A, Ruprecht H, Vacik H (2008) Population viability risk management (PVRM) for *in situ* management of endangered tree species — A case study on a *Taxus baccata* L. population. Forest Ecology and Management 255:2835–2845

Di Minin E & Moilanen A (2012) Empirical evidence for reduced protection levels across biodiversity features from target-based conservation planning. Biological Conservation 153:187–191

Donaldson J (2003) Cycads: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK

Forsyth GG, Le Maitre DC, Farrell PJO, van Wilgen BW (2012) The prioritisation of invasive alien plant control projects using a multi-criteria decision model informed by stakeholder input and spatial data. Journal of Environmental Management 103:51–57

Freeman DC, Doust JL, El-Keblawy A, Migilia KJ, McArthur ED (1997) Sexual specialisation and inbreeding avoidance in the evolution of dioecy. The Botanical Review 63:65–92

Garcia MB (2003) Demographic viability of a relict population of the Critically Endangered plant *Borderea chouardii*. Conservation Biology 17:1672–1680

Gibbs JP (2009) Monitoring for adaptive management in conservation biology. Lessons in Conservation: 2:5–18

Given DR (1994) Principles and Practice of Plant Conservation. Timber Press, Inc., Portland, Oregon

Guo D, Desmet PG, Powrie LW (2017) Impact of the future changing climate on the southern Africa biomes, and the importance of geology. Journal of Geoscience and Environment Protection 5:1–9

Hilfiker K, Gugerli F, Schutz J-P, Rotach P, Holderegger R (2004) Low RAPD variation and female-biased sex ratio indicate genetic drift in small populations of the dioecious conifer Taxus baccata in Switzerland. Conservation Genetics 5:357–365

Ishizaka A, Labib A (2011) Review of the main developments in the analytic hierarchy process. Expert Systems with Applications 38:14336–14345

Kajanus M, Kangas J, Kurttila M (2004) The use of value focused thinking and the A'WOT hybrid method in tourism management. Tourism Management 25:499–506

Kajanus M, Leskinen P, Kurttila M, Kangas J (2012) Forest Policy and Economics Making use of MCDS methods in SWOT analysis — lessons learnt in strategic natural resources management. Forest Policy and Economics 20:1–9

Kangas J, Kangas A (2005) Multiple criteria decision support in forest management — the approach, methods applied, and experiences gained. Forest Ecology and Management 207:133–143

Kay J ,Strader AA, Murphy V, Nghiem-Phu L, Calonje M and Griffith MP (2011) Palma Corcho: a case study in botanic garden conservation horticulture and economics. Public Horticulture 21(4): 474 - 481

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29:83–112

Kraaij T, Wilgen BW Van, Van Wilgen BW (2014) Drivers, ecology, and management of fire in fynbos. Pages 47–72 in Allsop N, Colville JF and Verboom GA (editors). Fynbos: ecology, evolution and conservation of a megadiverse Region. Oxford University Press

Kukrety S, Jose S, Alavalapati JRR (2013) Exploring stakeholders' perceptions with analytic hierarchy process- A case study of red sanders (*Pterocarpus santalinus* L.) restoration in India. Restoration Ecology 21:777–784

Lacy RC, Pollak JP (2014) Vortex: A stochastic simulation of the extinction process. Version 10.0. Chicago Zoological Society, Brookfield, Illinois, USA

Langpap C (2006) Conservation of endangered species: can incentives work for private landowners? Ecological Economics 57:558–572

Lavergne S, Thuiller W, Molina J, Debussche M (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. Journal of Basic Microbiology 32:799–811

Lefkovitch LP (1965) The study of population growth in organisms grouped by stages. Biometrics 21:1–18

Leonelli RCB (2012) Enhancing a decision support tool with sensitivity analysis. Unpublished MSc thesis. University of Manchester

Marler TE, Lindström AJ (2015) Carbohydrates, pollinators, and cycads. Communicative & Integrative Biology 8:6–9

Marler TE, Lindström AJ (2017) First, do no harm. Communicative & Integrative Biology 10: e1393593
Matthies D, Bräuer I, Maibom W, Tscharntke T (2004) Population size and the risk of extinction: empirical evidence from rare plants. Oikos 105:481–488

Menz MHM, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science 16:4–12

Monks L, Coates D, Bell T, Bowles M (2012) Determining success criteria for long-lived plants (pp 189-208) in Maschinski J and K. E. Haskins KE (editors). Plant reintroduction in a changing climate: promises and perils. Island Press

Moore CT, Fonnesbeck CJ, Shea K, Lah KJ, McKenzie PM, Ball LC, Runge MC, Alexander HM (2011) An adaptive decision framework for the conservation of a threatened plant. Journal of Fish and Wildlife Management 2:247–261

Mu E, Pereyra-Rojas M (2017) Practical decision making using super decisions v3: an introduction to the Analytical Hierarchy Process. Springer

Nilsson E, Agren J (2006) Population size, female fecundity, and sex ratio variation in gynodioecious Plantago maritima. Journal of Evolutionary Biology 19:825–833

Noel F, Maurice S, Mignot A, Glemin S, Carbonell D, Justy F, Guyot I, Olivieri I, Petit C (2010) Interaction of climate, demography and genetics: a ten-year study of *Brassica insularis*, a narrow endemic Mediterranean species. Conservation Genetics 11:509–526

Norstog KJ, Fawcett PKS (1989) Insect-cycad symbiosis and its relation to the pollination of *Zamia-furfuracea* (Zamiaceae) by *Rhopalotria mollis* (Curculionidae). American Journal of Botany 76:1380–1394

Pence GQK, Botha MA, Turpie JK (2003) Evaluating combinations of on-and off-reserve conservation strategies for the Agulhas Plain, South Africa: a financial perspective. Biological Conservation 112:253–273

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1–9

Raimondo DC (2015) South African strategy for plant conservation. South African National Biodiversity Institute & The Botanical Society of South Africa

Raimondo DC, Donaldson JS (2003) Responses of cycads with different life histories to the impact of plant collecting: Simulation models to determine important life history stages and population recovery times. Biological Conservation 111:345–358

Ramanathan R (2001) A note on the use of the analytic hierarchy process for environmental impact assessment. Journal of Environmental Management 63:27–35

Razgour O, Hanmer J, Jones G (2011) Using multi-scale modelling to predict habitat suitability for species of conservation concern: The grey long-eared bat as a case study. Biological Conservation 144:2922–2930

Rebelo AG, Boucher C, Helme N, Mucina L, Rutherford MC (2006) Fynbos Biome (pp 53 – 219) in Mucina L and Rutherford MC (editors). The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute., Pretoria, South Africa

Regan HM, Ben-haim Y, Langford B, Wilson WG, Lundberg P, Andelman SJ, Burgman MA (2005) Robust decision-making under severe uncertainty for conservation management. Ecological Applications 15:1471–1477

Roura-Pascual N, Richardson DM, Krug RM, Brown A, Chapman RA, Forsyth GG, Le Maitre DC, Robertson MP, Stafford L, van Wilgen BW, Wannenburgh A, Wessels N (2009) Ecology and management of alien plant invasions in South African fynbos: accommodating key complexities in objective decision making. Biological Conservation 142:1595–1604

Runge MC (2011) Adaptive management for threatened and endangered species. Journal of Fish and Wildlife Management 2:220–233

Saaty TL (2008) Decision making with the analytic hierarchy process. Int. J. Services Sciences 1(1):83-98

Schaub M, Gimenez O, Sierro A, Arlettaz R (2007) Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. Conservation Biology 21:945–955

Schemske DW, Husband BC, Ruckelshaus MH, Goodwillie C, Parker IM, Bishop JG (1994) Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606

Segura M, Ray D, Maroto C (2014) Decision support systems for forest management: A comparative analysis and assessment. Computers and Electronics in Agriculture 101:55–67

Siraj S (2011) Preference elicitation from pairwise comparisons in multi-criteria decision making. Unpublished MSc thesis. University of Manchester

Siraj S, Mikhailov L, Keane JA (2015) PriEsT: an interactive decision support tool to estimate priorities from pairwise comparison judgments. International Transactions in Operational Research 22:217–235

Stott I, Townley S, Carslake D, Hodgson DJ (2010) On reducibility and ergodicity of population projection matrix models. Methods in Ecology and Evolution 1:242–252

Swart C (2017) The globetrotting Albany Cycad. Veld and Flora (103)2: 79-80

Tinch R, Balian E, Carss D, Ezzine de Blas D, Geamana NA, Heink U, Keune H, Nesshöver C, Niemelä J, Sarkki S, Thibon M, Timaeus J, Vadineanu A, van den Hove S, Watt A, Waylen KA, Wittmer H, Young JC (2018) Science-policy interfaces for biodiversity: dynamic learning environments for successful impact. Biodivers Conserv 27: 1679 - 1702

TRAFFIC (2003) Review of Significant Trade Cycads. PC14 Doc. 9.2.2 Annex 1. Pp 3 – 44
Vice A (1995) *Encephalartos altensteinii*: A massive rape and recovery. Encephalartos 1:15–19

Vovides AP, Ogata N, Sosa V, Peña-García E (1997) Pollination of endangered Cuban cycad *Microcycas calocoma* (Miq.) ADC. Botanical Journal of the Linnean Society 125:201–210

Young JA, Manen FT Van, Thatcher CA (2011) Geographic profiling to assess the risk of rare plant poaching in natural areas. Environmental Management 48:577–587

Zuidema PA, Jongejans E, Chien PD, During HJ, Schieving F (2010) Integral projection models for trees: A new parameterization method and a validation of model output. Journal of Ecology 98:345–355

CHAPTER 7
Conclusion and further research

Extinction debt and cycads

The slow burning fuse of plant extinction is how Cronk (2016) described long extinction lag times experienced by long-lived plants, such as cycads, sometimes measured in many centuries. There is an advantage to these long lag times to extinction experienced by cycad taxa and other long-lived woody plant species. Conservation intervention is more possible when there is a larger window period in which to take action (Essl et al. 2015). It is vital that conservation action is taken during the window period before the extinction process is complete, but at the same time, the cautionary conservation approach should be applied to ensure that conservation action does not inadvertently speed up the lag time to extinction. Cronk (2016) identified two types of conservation intervention and the effect on extinction debt in long-lived plant species. Type I conservation reduces extinction debt and prevents extinction; Type II conservation extends the lag time and delays extinction. I add a third type: Type III conservation which speeds up the lag time and shortens time to extinction. An example of this is seen in Guam where numerous individuals of Endangered *Cycas micronesica* trees were uprooted from a construction site. The rescue project was considered to be an additional threat to the already highly threatened native Guam *C. micronesica* sub-populations, in that genetic pollution is now considered a major emerging threat that may result in once resilient populations succumbing to genetic pollution (Marler and Lindström 2017). Type I conservation interventions are the ultimate goal in reducing cycad extinctions and biodiversity loss across the globe, yet few examples in the published literature exist where extinction of a cycad species was successfully halted through conservation intervention during this critical window period. There is good news however for other long-lived species such as the dioecious conifer *Taxus baccata* frequently mentioned in earlier chapters of this thesis. Also known as the English Yew, *T. baccata* is currently listed as Least Concern under the IUCN Red List Version 3.1 with increasing populations (Farjon 2013). The species has made a remarkable comeback with a current population trend as increasing due to dedicated yew conservation societies specifically targeting the conservation of adult trees and

exploiting cultivated rather than wild populations for chemical compounds found within the species used to fight cancer (Farjon 2013; IV International Yew Workshop 2014). This Type I conservation intervention is considered a successful example of yaking advantage of the prolonged window period before extinction to take to bring the species back from the brink of extinction. Unfortunately, the same cannot be said for cycad conservation in Africa or elsewhere in the world where 73% of IUCN listed cycad species are declining and threatened with extinction (http://www.iucnredlist.org/ accessed 20/08/2018).

It is important to understand the scale of extinction time lags by assimilating historical data on threats to species with present-day data on species states and trends (Essl et al. 2015). Historical information reveals when the first disturbances to *E. latifrons* and most likely other threatened Eastern Cape Cycads in South Africa may have begun in earnest. Prior the late 17th century, the area of the Eastern Cape which forms the natural distribution range for *E. latifrons* and other cycads such as *E. caffer*, *E. trispinosus,* and *E. altensteinnii* was inhabited mostly by the Gonqua agropastoralists. They were a mixed Khoi and Xhosa group who kept mostly sheep and cattle and small-scale cereal pastures (Hall 1986).. It was in 1820, that the British Government undertook to colonise the Eastern Cape in one of the most ambitious state-aided schemes. Brunger (2003) reports that 3500 British people in over 800 families immigrated into the Eastern Cape persuaded (after the expansion of the Cape Colony from Cape Town during the 17th and 18th centuries) by offers of free land. Initially, farming had not been very successful in some areas, as the Albany District (the area surrounding Grahamstown) was not suited to arable cultivation and lack of local knowledge of local environmental conditions and which crops to grow made farming difficult (Brunger 2003). This changed in about 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) with the price of land substantially increasing due to “improvements” made by clearing bush and planting exotic trees (Wallace 1896). Bathurst, another important area within the *E. latifrons* distribution range was settled at the same time as Grahamstown, by about 700 British immigrants (Wallace 1896) and was more suitable to crop farming. By 1896, many well cultivated farms were established between Bathurst and Grahamstown including bamboo, pineapple and plantain (Wallace 1986). The areas north of Grahamstown were considered excellent for ostriches, sheep and cattle according to Wallace (1986).

Pineapple farming took off in the south eastern distribution area of the *E. latifrons* distribution range between 1938 and 1953 (Department van Landbou, 1957) and in 1953, 180 000 000 pineapple plants were planted in the main pineapple growing area of the Eastern Cape, including a large part of the natural distribution range for *E. latifrons* (Figure 7.1).

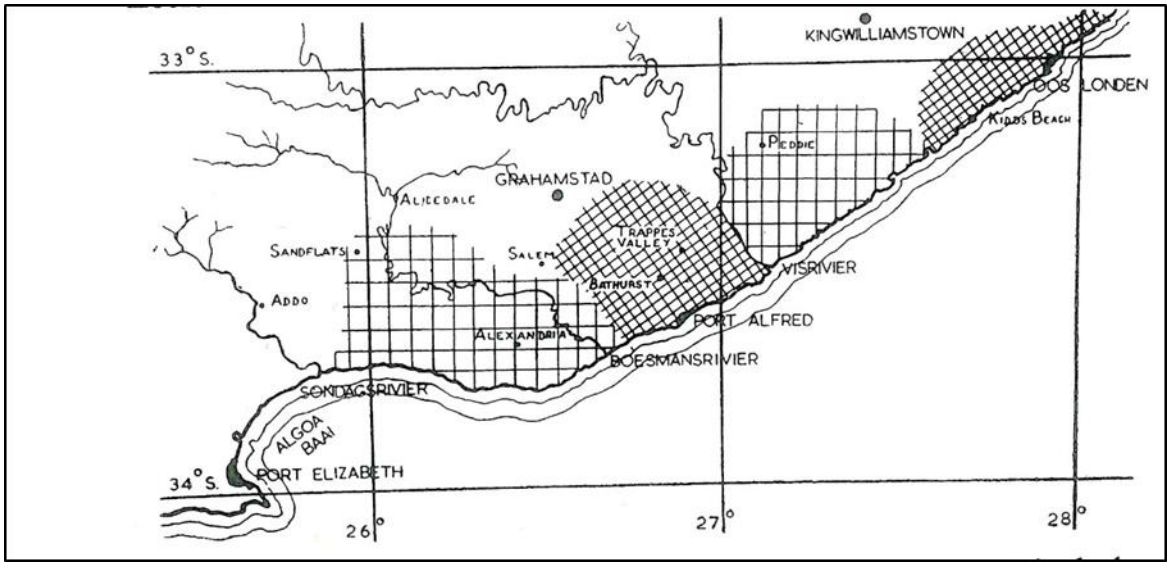


Figure 7.1 Map showing pineapple growing area in the Eastern Cape in 1957. Dark shading indicates the older already established pineapple growing area while the lighter shading indicates the newly established areas (Dept. van Landbou 1957).

Pineapple farming was particularly environmentally destructive in that up until 1957, farmers would plough new land rather than re-use old fields to plant. The Department of Land at the time, indicated in their report that by 1957, areas of pristine land started becoming less available and farmers needed other methods to plant pineapples using lands previously ploughed with the addition of fertilizer (Dept. van Landbou 1957).

Historical notes on commerce, industries, and resources in the Cape Colony by Somerset Payne (1910) mention activities on specific farms, some of them know to be important historical localities for *E. latifrons*. For example, the Trappes Valley Farm spanning just over 850 hectares, 161 hectares of which were under dry cultivation and a considerable portion of the property devoted to growing crops for food with over 150 ostriches and a herd of 100 cattle. The report mentions that the property was purchased in 1892 but no steps had been taken to cultivate it until 1910/1911. Other important farms where *E. latifrons* populatons were known to exist include Coombs Vale and

Claypits (Dixon pers. com) purchased by WR Dixon in 1887. Somerset Payne (1910) noted that in 1887, when the farm was purchased, most of it was still covered by dense bush which was largely removed by 1911 with just over 200 hectares brought under cultivation. The farm also had 300 herd of cattle and 1000 fruit trees planted on it at the time. Atherstone Farm closer to Grahamstown, and approximately five kilometres from a property with an existing *E. latifrons* population is situated in the northern distribution range for *E. latifrons* is also mentioned in the report and gives an indication of what activities were occurring in the area and surrounding farms at the time. Somerset Payne (1910) indicates that the farm was used for grazing with just over three hectares of Paspalum grass planted (an exotic weed grass which was doing well and spreading for miles along the river bank). Thousands of forest trees were planted on Atherstone Farm farm including exotic *Pinus* and *Acacia* and by 1910, the landowner intended on planting vast areas every year. In addition to the cultivation of orange and apple trees, the farm also had 500 Merino sheep. This area southwest of Grahamstown, in an extension of the Highlands Range towards Howieson's Poort is considered a core area of suitable habitat for *E. latifrons* (Chapter 2), and the legacy of exotic tree planting still exists today with the hills and ranges are infested with alien trees (Swart, 2008).

Interest in cycads as horticultural plants in the Eastern Cape started in the late 1960's (Swart 2017) where a *E. latifrons* collector sold over 70, mostly mature plants, from his once larger collection in an inspection report dated 1974 (permit records held at DEDEA). Further reports of plants being stolen from the natural distribution range surfaced in court proceedings and inspection reports between 1980 and 1993 (mentioned in previous chapters). This is likely to have had a major effect on the persistence of populations at the time, causing the species to move along the extinction trajectory. A summary of the historical environmental impacts and where *E. latifrons* is currently on the extinction trajectory is illustrated in Figure 7.2.

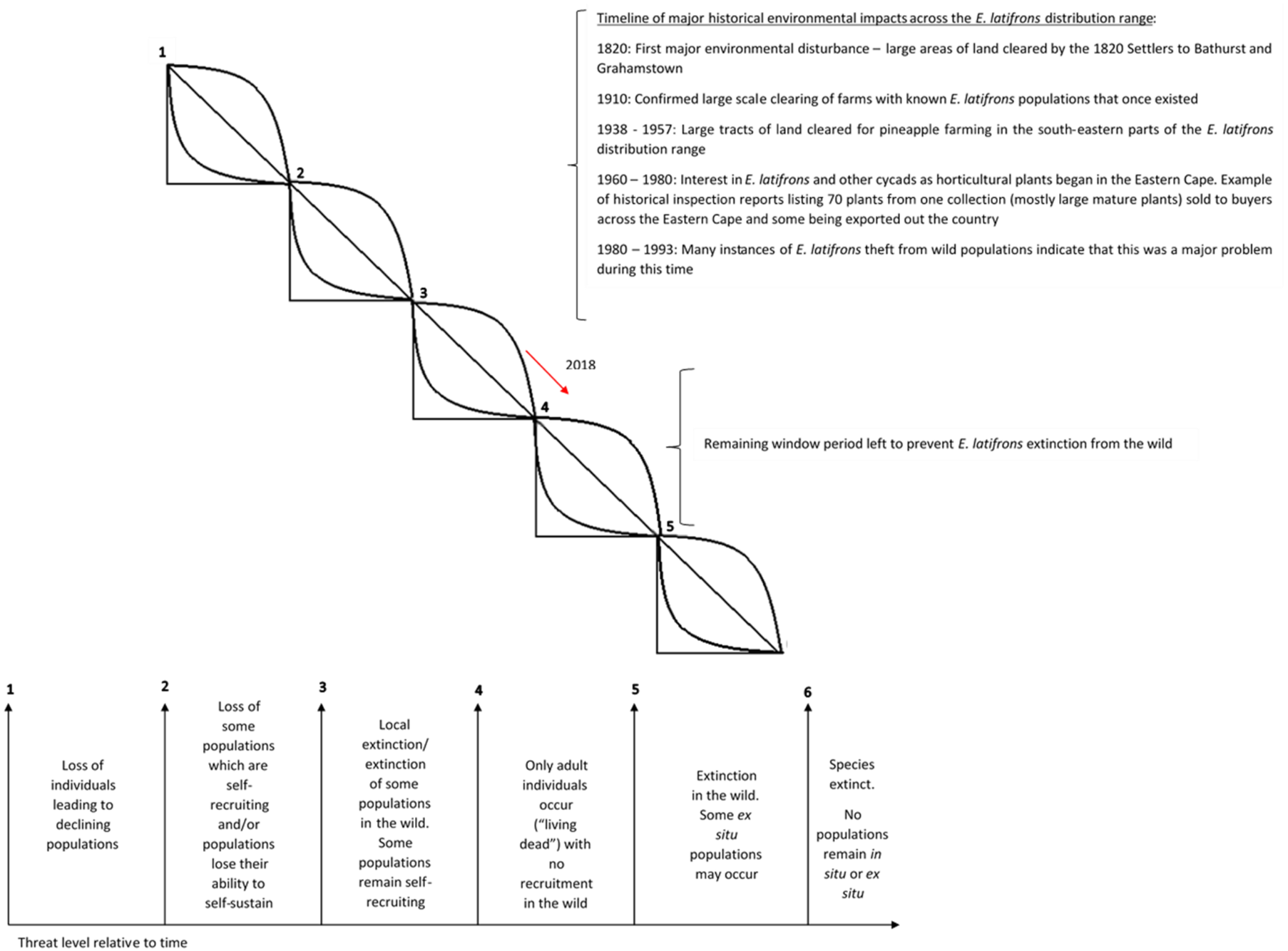


Figure 7.2 Diagram illustrating how historical disturbances may have influenced the persistence of *Encephalartos latifrons* populations and caused the species to move along the extinction trajectory. The status of the species is currently between threshold three and four likely to breach threshold four in the near future.

Key Biodiversity Areas for cycads

The window period remaining to save *E. latifrons* from extinction is diminishing (Figure 7.2). Modelling a suitable habitat for *E. latifrons* reveals that there are large conservation gaps where critical *E. latifrons* habitats are not formally protected or included in conservation planning areas such as the National Protected Area Expansion Strategy or Critical Biodiversity Areas (see Chapter 2). There are however global initiatives that may be a useful in filling these conservation gaps (Eken et al. 2004), specifically for CR and EN cycad species in Africa and worldwide. This includes Alliance for Zero Extinction Sites, a subset of the IUCN Key Biodiversity Area (www.zeroextinction.org; IUCN 2016). These global initiatives are useful in that they provide a standardised method to locate and promote sites that make substantial contributions to the persistence of global biodiversity. They also contribute to meeting Aichi Targets (Convention on Biological Diversity 2011) and national targets such as those defined in South Africa's 2nd National Biodiversity Strategy and Action Plan 2015 – 2025 (Government of South Africa 2015). The KBA and AZE criteria were assessed against information from this thesis to evaluate the suitability of the area which includes Population B (the last known remaining self-sustaining population of *E. latifrons*) to be included as an AZE and KBA site (Table 7.1).

Table 7.1 KBA and AZE assessment for site containing *Encephalartos latifrons* Population B

Key Biodiversity Area (IUCN 2016)	Site containing Population B	*Alliance for Zero Extinction*	Site containing population B
IV. A1. Threatened species	CR (Donaldson 2010)	*Endangerment* *Site must contain at least one Endangered (EN) or Critically Endangered (CR) species, as assessed on the IUCN Red List.*	CR (Donaldson 2010)
a. ≥ 0.5% of the global population size and ≥ 5 reproductive units of a CR or EN species	57% of the global population size and at least 5 reproductive units (9 females; 5	*Irreplaceability* *The sole area where an EN or CR species occurs, contains the*	This site contains the only known self-sustaining population of *E. latifrons* where

	males; 7 unknown adult/mature individuals).	*overwhelmingly significant known resident population (>95%) of the EN or CR species.*	natural recruitment is occurring.
b. Effectively the entire global population size of a CR or EN species	The only known self-sustaining and functional *E. latifrons* population. Although other sites hold *E. latifrons* populations, they are considered functionally extinct.	<u>*Discreteness*</u> *The area must have a definable boundary within which the character of habitats, biological communities, and/or management issues have more in common with each other than they do with those in adjacent areas.*	The site is 1335 hectares of semi-protected state land and is currently used for recreational purposes. All individuals in the population fall within a defined boundary which also forms part of a conservancy with neighbouring properties.

In terms of the criteria set out by the IUCN and AZE, the site containing *E. latifrons* Population B qualifies to be listed under both initiatives. The listing of *E. latifrons* will add another cycad trigger species to the 10 already qualified and proposed cycad trigger species in South Africa: https://globally-threatened-bird-forums.birdlife.org/2017/07/cycads-2017-aze-update-consultation/ (accessed 23/08/2018). The listing of qualifying cycads with international initiatives such as KBA and AZE should align with national policies and initiatives such as SANBSAP, SASPC and the National Strategy and Action Plan for the Management of Cycads (NSAPMC) which will in turn contribute to achieving global Aichi Targets, specifically target 11 and 12. This may also provide the last remaining option to take definitive action against further losses and to prevent species moving further along the extinction trajectory during this critical window period before extinction.

Further research

This is the first in-depth study of the biology, reproductive ecology, restoration and distribution of the Critically Endangered cycad, *Encephalartos latifrons*. This thesis provides a framework to guide future studies of *E. latifrons* and gives some direction to conservation authorities regarding the conservation of the species now and in the future.

Species distribution modelling in Chapter 2 is a useful tool to assess and prioritise conservation areas for *E. latifrons*, as well as to assist conservation decision-makers regarding translocation and restoration programmes for the species. Finer-scale modelling is however needed for *E. latifrons*, especially in areas where suitable habitat becomes patchy towards the coast. Finer scale (e.g. 30 m resolution) modelling would need to include soils, fire (regime and extent), higher resolution climate and geological data. Breiner et al. (2015) have suggested that combining a number of small models (referred to as ESMs - ensembles of small models), rather than the standard SDM approach outlined in Chapter 2, may result in improved and more accurate predictions for very rare species such as *E. latifrons*. In this way, model overfitting is avoided by reducing the number of predictor variables when running the model. Nevertheless, SDMs for rare and endangered species are useful for predicting habitat suitability at most scales and have become an important global conservation tool for such species (Gogol-Prokurat 2011; Kamino et al. 2012; Sousa-Silva et al. 2014; McCune 2016; Rovzar et al. 2016; Villero et al. 2016). Research reveals that range-restricted rare species may be more vulnerable to the effects of climate change compared to species with more widespread distributions (Casazza et al. 2014). Modelling future suitable habitat areas under climate change is therefore important for *E. latifrons*, particularly to identify areas that may act as refugia for the species (Porfirio et al. 2014; Keppel et al. 2015; Pacifici et al. 2015; Jones et al. 2016; Guo et al. 2017).

In the past, general information on the population structure, survival, fire response and reproductive ecology of *E. latifrons* was limited. This was largely owing to the fact that *E. latifrons* has critically small population sizes, the secrecy around the location of the existing populations and permits/red tape involved in undertaking research on the species. It was very fortunate that the researcher with the help of her field work assistant ‘discovered’ an existing, healthy, naturally recruiting population. The population was known to only a few recreational users in the area and the plants

are relatively well-hidden and out of site. A five-year census of the population gave some useful insight into the structure of a successful *E. latifrons* population including: its ability to respond to frequent fires, the existence of male cone fauna/potential pollinators, and ability to naturally recruit seedlings. This life history information is a prerequisite to undertaking a detail population viability assessment (PVA) for the species. PVA's for long-lived perennial species are not common (Monks et al. 2012) and require long-term census data to accurately understand how environmental and management drivers influence population persistence (Jolls et al. 2015). Fundamental assumptions of the projection matrix are that they are irreducible, i.e. there are transitions between all stages in the life cycle (Stott et al. 2010). This is problematic for long-lived species such as *E. latifrons* where transitions between life history stages (e.g. an immature plant becoming sexually reproductive for the first time thus moving into the adult category) will not be realised over a 5-year study period. An alternative to matrix models, Integral Projection Models or IPMs, offer a solution to this problem when modelling the population dynamics of long-lived plants (Zuidema et al. 2010). Chapter 3 includes a framework upon which a PVA can be done at a later stage once more census and growth data has been collected. Results from the life-table suggest that at least one population is stable and increasing under current environmental conditions, albeit in an area experiencing high fire frequencies. The ongoing annual monitoring and collection of census data for this population is recommended so that enough information is acquired in order to model population dynamics of the species. Information from this chapter can also inform non-detriment finding for *E. latifrons* and possibly identify generalisations for making NDFs that apply across a group of cycads with a similar life-history and habitat requirements to *E. latifrons* (Smith et al. 2011).

Surprising insights into the reproductive ecology of *E. latifrons* is revealed in Chapter 4. Firstly, preliminary samples of male cone fauna suggest that *E. latifrons* male cones are host to a diverse ensemble of weevils including a new undocumented species in Population B. Further research is needed to determine the role these weevils play in the natural pollination of *E. latifrons* and to what degree of host specificity plays a role in pollination (Downie et al. 2008; Da Silva et al. 2012; Brookes et al. 2015). Furthermore, critically small populations (2 individuals, male and female) are capable of pollinating under natural conditions to produce viable seedlings as seen in Population C. Pollination under natural conditions for other populations such as Population A

needs to be prioritised as a research objective. The assumption that *E. latifrons* populations such as Population A are not capable of natural pollination has not yet been tested. It is important that Population A2, now in a resting phase, is monitored continuously for signs of recovery and possible natural recruitment; and that seed viability tests are done as soon as the female plants cone. It is recommended that seed viability testing not be confined to one coning season to come to conclusions regarding the self-recruiting ability of a population. Seed viability testing in Population B was unsuccessful in that none of the seeds sampled germinated. Population B is however very successful at self-recruitment with seedlings making up 55% of the population (see Chapter 3). In this case, the timing of a fire may play a role in limiting seed development if the cone is burnt causing the abortion of seeds. The role fire plays in the malformation of seeds and restricting recruitment needs further investigation (Liddle 2004; Treurnicht et al. 2016).

Chapter 5 gives interesting insight into the often overlooked role livestock herbivory and trampling may play in restricting seedling recruitment and hampering restoration efforts in *E. latifrons* populations. Hall and Walter (2014) refer to ecologically 'naive' livestock who target the toxic fleshy fruit or new soft leaves of cycads with harmful consequences. This was the case for young seedlings (mostly less than a year old) used to augment Population C. Seedling deaths were primarily caused by uprooting which coincided with images of livestock herds grazing the area caught on camera traps. Grazing livestock can cause seedling deaths either by directly feeding on the leaves and uprooting the young plant, or overgrazing the area around the site so that no nurse plants are available to facilitate seedling germinating (Castro et al. 2004; Smit et al. 2005; Padilla et al. 2006; Álvarez-Yépiz et al. 2014; Al-Namazi et al. 2017). The potential influence of livestock disturbance around populations needs further exploration, particularly for sites such as Population A1 and any other sites were livestock are active in the area. If restoration/augmentation of populations is to be done using young seedlings, considerations regarding how the seedlings are to be protected from livestock needs to be investigated. The use of viable seeds for restoration/augmentation is a viable alternative and could potentially negate the need for elaborately designed cages to protect seedlings if seeds are sown in areas (such between rocks) where grazing livestock cannot reach, protecting the plants in the early developmental phases until the leaves become less palatable.

The Biodiversity Management Plan for *E. latifrons* (Department of Environmental Affairs 2011) is due for an amendment 5 years after its implementation. Chapter 6 suggests a PVRM approach as a revision of the PHVA before the amendment of the BMP. The PVRM is population and property specific, in the same way Habitat Conservation Plans (HCPs) are developed for specific areas (where the geographic boundaries of the target area are clearly established) under the U.S. Endangered Species Act of 1973. Developing a conservation plan to be area and landowner specific makes sense in that land use, land owner profiles (including aspects such as commitment to conservation/interest in horticulture), land management scenarios and threats to populations differ between properties and landowner/management styles as described in Chapter 6. The current BMP for *E. latifrons* is too broad in the sense that it supports a single management style across all populations which is not necessarily applicable to all populations and/or landowners. At the same time, the BMP is too prescriptive in that it names individuals responsible for actions under the operational goals described. In this case, individuals responsible have changed positions/moved to other employment etc. over the 5 years of the implementation of the BMP. Ideally, the PVRM would be applicable to a specific population of endangered species (Dhar et al. 2008) and in some cases, a sub-population if it occurs on separate properties as is the case for *E. latifrons* Population A1 and A2. The use of the PVRM approach is all-encompassing in that it can include the results of a PVA but is not dependent on it if this is not available for the species. The PVRM approach also takes into account factors that the traditional PVA approach neglects such as socio-economic, political and logistic influences that may restrict the effective conservation of the species. The PVRM approach does not prescribe a single management strategy for the species as a whole, but includes a review of alternative management strategies with the ultimate goal to increase the persistence of the population under scrutiny. A further comparison between the HCP approach and the BMP for *E. latifrons* relates to monitoring. Under the HCP approach, there are three types of monitoring (compliance, effectiveness, and effects) where the requirement is that the permit-holder is responsible for ensuring that all the required monitoring occurs. Monitoring reports are reviewed and the permit-holder is notified if any further action is required (U.S. Fish & Wildlife Service 2011). The BMP for *E. latifrons* identifies the provincial authorities to undertake compliance monitoring and to initiate the implementation of a monitoring programme (Department of Environmental Affairs 2011). Lack of capacity, staff turnover and other logistic and/or trust issues related to

the monitoring of highly valuable species on private land has been stressed in both the PHVA and BMP. To date, the monitoring of *E. latifrons* populations by conservation authorities on private land has not been successful. This is due to a number of issues, but primarily, there is still an element of distrust and a long history of disputes between certain landowners and conservation authorities. The situation is made worse by a change in staff where previous strong relationships between landowners and conservation authorities are not guaranteed in the longer term. It would be more effective if monitoring, particularly biological monitoring, is the responsibility of the private landowner as with the HCP approach and according to the requirements set out in permit conditions. The debate whether conservation plans for endangered species on private land do more harm than good is still ongoing (Langpap & Kerkvliet 2012). There is often a substantial time-lag from the when a conservation decision is made to any evidence of the effect a decision has on biodiversity (Tinch et al. 2018) and only time will tell how past decisions will influence the future persistence of *E. latifrons.*

Cycads have captured the world's attention in many ways as one of the most threatened group of organisms on the planet (Hoffmann et al. 2016). Extinction causing mechanisms such as habitat destruction are often compounded by the targeted harvesting of valuable species such as *E. latifrons*. Their slow life histories and often rare status make them further vulnerable to extinction increasing their lag time to extinction. The advantage however is that there is a larger window period between extinction causing events and final extinction which allows for conservation action to take place. Historical information may prove very valuable in order to understand the scale of time lags as well as to supplement often limited information inherent for rare and endangered cycad species. Historical data can be integrated with contemporary data to make informed conservation decisions for cycads. Modern-day techniques such as computer modelling can greatly assist decision makers and conservation authorities make informed decisions to improve global cycad conservation. International initiatives such as AZE and KBA are important mechanisms to further the conservation of CR and EN cycad species, especially when such initiatives are aligned with national and local policies in order to achieve national and international conservation targets. There are currently 70 AZE cycad trigger species (proposed and qualified) worldwide, 18 of which are African species (six qualifying South African species and 3 proposed species) which is a positive step towards making a difference to global cycad conservation.

References

Al-Namazi AA, El-Bana MI, Bonser SP (2017) Competition and facilitation structure plant communities under nurse tree canopies in extremely stressful environments. Ecology and Evolution 7:2747–2755

Álvarez-Yépiz JC, Búrquez A, Dovčiak M (2014) Ontogenetic shifts in plant-plant interactions in a rare cycad within angiosperm communities. Oecologia 175:725–735

Breiner FT, Guisan A, Bergamini A, Nobis MP (2015) Overcoming limitations of modelling rare species by using ensembles of small models. Methods in Ecology and Evolution 6:1210–1218

Brookes DR, Hereward JP, Terry LI, Walter GH (2015) Evolutionary dynamics of a cycad obligate pollination mutualism – pattern and process in extant Macrozamia cycads and their specialist thrips pollinators. Molecular Phylogenetics and Evolution 93:83–93

Brunger AG (2003) The geographical context of planned group settlement in Cape Colony: The 1820s British emigrants. J. Hist. Geogr. 29: 51–72

Bush A, Mokany K, Catullo R, Hoffmann A, Kellermann V, Sgrò C, McEvey S, Ferrier S (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters 19:1468–1478

Casazza G, Giordani P, Benesperi R (2014) Climate change hastens the urgency of conservation for range-restricted plant species in the central-northern Mediterranean region. Biological Conservation 179:129–138

Castro J, Zamora R, Hódar JA, Gómez JM, Gómez-Aparicio L (2004) Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. Restoration Ecology 12:352–358

Convention on Biological Diversity (2011) Conference of the Parties Decision X/2: Strategic Plan for biodiversity 2011-2020. https://www.cbd.int/decision/cop/?id=12268. Accessed 16 Aug 2018

Cousins SR, Witkowski ETF (2017) African cycad ecology, ethnobotany and conservation: a synthesis. The Botanical Review 83:152–194

Da Silva J, Donaldson JS, Reeves G, Hedderson TA (2012) Population genetics and conservation of critically small cycad populations: a case study of the Albany Cycad, Encephalartos latifrons (Lehmann). Biological Journal of the Linnean Society 105:293–308

Department of Environmental Affairs (2011) Biodiversity Management Plan for Albany Cycad, Encephalartos latifrons. Pages 1–48. National Environmental Management: Biodiversity Act (10/2004): South African Government Gazette No. 34388

Department van Landbou (1957) Hulpboek vir boere in Suid-Afrika. Deel II. Akkerbou en Tuinbou. Die Staatsdrukker, Pretoria, South Africa

Dhar A, Ruprecht H, Vacik H (2008) Population viability risk management (PVRM) for *in situ* management of endangered tree species — a case study on a Taxus baccata L. population. Forest Ecology and Management 255:2835–2845

Donaldson JS (2010) Encephalartos latifrons. The IUCN Red List of Threatened Species 2010: e.T41892A10571584. http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T41892A10571584.en. Downloaded on 23 August 2018

Downie DA, Donaldson JS, Oberprieler RG (2008) Molecular systematics and evolution in an African cycad-weevil interaction: Amorphocerini (Coleoptera: Curculionidae: Molytinae) weevils on Encephalartos. Molecular Phylogenetics and Evolution 47:102–116

Eken G, Bennun L, Brooks TM, Darwall W, Fishpool DC, Foster M, Knox D, Langhammer P, Matiku P, Radford E, Salaman P, Sechrest WES, Smith ML, Tordoff A (2004) Key Biodiversity Areas as site conservation targets. Bioscience 54: 1110–1118

Essl F, Dullinger S, Rabitsch W, Hulme PE, Pyšek P, Wilson JRU, Richardson DM (2015) Delayed biodiversity change: no time to waste. Trends in Ecology and Evolution. 30(7): 375-378

Evans T, Diamond SE, Kelly MW (2015) Mechanistic species distribution modelling as a link between physiology and conservation. Conservation Physiology 3:1–22

Farjon A (2013) Taxus baccata (errata version published in 2017). The IUCN Red List of Threatened Species 2013: e.T42546A117052436. http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T42546A2986660.en. Downloaded on 23 August 2018.

Genovart M (2009) Natural hybridization and conservation. Biodiversity and Conservation 18:1435–1439

Gogol-Prokurat M (2011) Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. Ecological applications 21:33–47

Government of South Africa (2015) National Biodiversity Strategy and Action Plan 2015 – 2025. Department of Environmental Affairs, Pretoria

Guo D, Desmet PG, Powrie LW (2017) Impact of the future changing climate on the Southern Africa biomes, and the importance of geology. Journal of Geoscience and Environment Protection 5:1–9

Hall SL (1986) Pastoral adaptations and forager reactions in the Eastern Cape. South African Archaeol. Soc. Goodwin Ser. 5: 42–49

Hoffmann M, Hilton-taylor C, Angulo A, Böhm M, Brooks, TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Katariya V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vie J-C, Aguiar JM, Allen DJ, Allen GR and Amori G (2010) The impact of conservation on the status of the world's vertebrates. Sci New Ser 330:1503–1509

IUCN (2016) A global standard for the identification of Key Biodiversity Areas: version 1.0. Gland, Switzerland: IUCN

Jolls CL, Marik JE, Hamzé SI, Havens K (2015) Population viability analysis and the effects of light availability and litter on populations of Cirsium pitcheri, a rare, monocarpic perennial of Great Lakes shorelines. Biological Conservation 187:82–90

Jones KR, Watson JEM, Possingham HP, Klein CJ (2016) Incorporating climate change into spatial conservation prioritisation: a review. Biological Conservation 194:121–130

Kamino LHY, de Siqueira MF, Sánchez-Tapia A, Stehmann JR (2012) Reassessment of the extinction risk of endemic species in the neotropics: how can modelling tools help us? Brazilian Journal of Nature Conservation 10:191–198

Keppel G, Mokany K, Wardell-Johnson GW, Phillips BL, Welbergen JA, Reside AE (2015) The capacity of refugia for conservation planning under climate change. Frontiers in Ecology and the Environment 13:106–112

Langpap C, Kerkvliet J (2012) Endangered species conservation on private land: assessing the effectiveness of habitat conservation plans. Journal of Environmental Economics and Management 64:1–15

Liddle DT (2004) The ecology of Cycas armstrongii and management of fire in Australia's tropical savannas. PhD thesis. Charles Darwin University, Australia, Darwin

Marler TE and Lindstrom AJ (2017) First do no harm. Communicative and Integrative Biology, 10:5-6, e1393593

McCune JL (2016) Species distribution models predict rare species occurrences despite significant effects of landscape context. Journal of Applied Ecology 53: 1871–1879

Monks L, Coates D, Bell T, Bowles M (2012) Determining success criteria for long-lived plants. Pg 189–208 in J. Maschinski and K. E. Haskins (editors) Plant reintroduction in a changing climate: promises and perils. Island Press

Pacifici M, Foden WB, Visconti P, Watson JEM, Butchart SHM, Kovacs KM, Scheffers BR, Hole DG, Martin TG, Resit Akçakaya H, Corlett RT, Huntley B, Bickford D, Carr JA, Hoffmann AA, Midgley GF, Pearce-Kelly P, Pearson RG, Williams SE, Willis SG, Young B and Rondinini C (2015) Assessing species vulnerability to climate change. Nature Climate Change 5:215–225

Padilla FM, Pugnaire FI, Frontiers S, May N, Padilla FM and Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4:196–202

Porfirio LL, Harris RMB, Lefroy EC, Hugh S, Gould SF, Lee G, Bindoff NL and Mackey B (2014) Improving the use of species distribution models in conservation planning and management under climate change. PLoS ONE 9: e113749

Rovzar C, Gillespie TW, Kawelo K (2016) Landscape to site variations in species distribution models for endangered plants. Forest Ecology and Management 369:20–28

Smit C, Béguin D, Buttler A, Müller-Schärer H (2005) Safe sites for tree regeneration in wooded pastures: a case of associational resistance? Journal of Vegetation Science 16:209–214

Smith MJ, Benitez-Diaz H, Clemente-Munoz MA, Donaldson J, Hutton JM, McGough HN, Medellin RA, Morgan DHW, O'Criodain C, Oldfield TEE, Schippmann U, Williams RJ (2011) Assessing the impacts of international trade on CITES-listed species: current practices and opportunities for scientific research. Biol. Conserv. 144: 82–91

Somerset Payne FRGS (Ed) (1910-1911) Cape Colony (Cape Province): its history, commerce, industries and resources. The foreign and colonial compiling and publishing co. London & Union of South Africa. JC Juta and Co

Sousa-Silva R, Alves P, Honrado J, Lomba A (2014) Improving the assessment and reporting on rare and endangered species through species distribution models. Global Ecology and Conservation 2:226–237

Stott I, Townley S, Carslake D, Hodgson DJ (2010) On reducibility and ergodicity of population projection matrix models. Methods in Ecology and Evolution 1:242–252

Swart C (2008) Life history, population dynamics and conservation status of Oldenburgia grandis (Asteraceae), and endemic of the Eastern Cape of South Africa. MSc thesis, Rhodes University

Swart C (2017) The globetrotting Albany Cycad. Veld Flora 103: 79–80

Tinch R, Bugter R, Blicharska M, Harrison P, Haslett J, Jokinen P, Mathieu L, Primmer E (2018) Arguments for biodiversity conservation: factors influencing their observed effectiveness in European case studies. Biodivers Conserv 27: 1763-1788

Treurnicht M, Pagel J, Esler KJ, Schutte-Vlok A, Nottebrock H, Kraaij T, Rebelo AG, Schurr FM (2016) Environmental drivers of demographic variation across the global geographical range of 26 plant species. Journal of Ecology 104:331–342

U.S. Fish & Wildlife Service (2011) Habitat conservation plans under the Endangered Species Act. Available from http://www.fws.gov/endangered/what- we-do/hcp-overview.html (accessed April 25, 2018)

Villero D, Pla M, Camps D, Ruiz-Olmo J, Brotons L (2016) Integrating species distribution modelling into decision-making to inform conservation actions. Biodiversity and Conservation 26:251–271

Vovides AP (1990) Spatial distribution, survival, and fecundity of Dioon edule (Zamiaceae) in a tropical deciduous forest in Veracruz, Mexico, with notes on its habitat. American Journal of Botany 77:1532–1543

Wallace R (1896) Farming industries of the Cape Colony. Juta and Co., Cape Town, Port Elizabeth and Johannesburg

Zuidema PA, Jongejans E, Chien PD, During HJ, Schieving F (2010) Integral projection models for trees: a new parameterization method and a validation of model output. Journal of Ecology 98:345–355