LIFE HISTORY TRAITS OF SOUTH AFRICAN *ENCEPHALARTOS* SPP. (ZAMIACEAE) AND THEIR IMPLICATIONS FOR UNDERSTANDING POPULATION STRUCTURE, RESPONSES TO THREATS AND EFFECTIVE CONSERVATION ACTION

Kim Martina Konings

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Supervisors:
Prof John Sydney Donaldson (South African National Biodiversity Institute)
Prof Michael Timm Hoffman (Plant Conservation Unit, University of Cape Town)

DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own

Kim M. Konings.   February 2016

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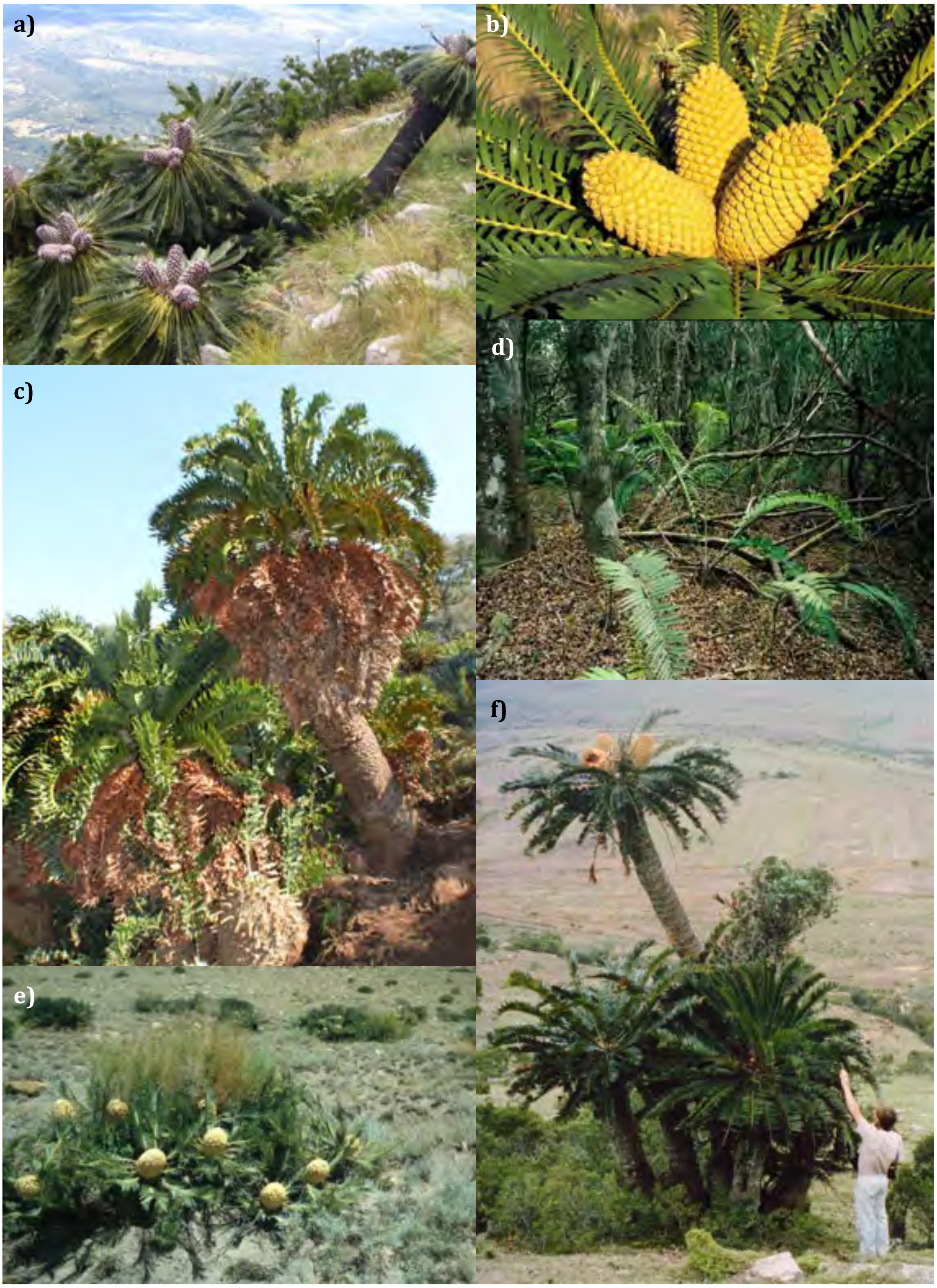

Life forms within the genus *Encephalartos*. **a)** *E. laevifolius* **b)** female cones of *E. senticosus* **c)** *E. latifrons* **d)** *E. villosus* **e)** *E. cycadifolius* **f)** *E. altensteinii*.
Photos taken by John S. Donaldson.

ABSTRACT

Understanding life history traits and how they influence population-level processes under different conditions have been important areas of study in evolution and ecology. One application in ecology has been to determine whether there are general responses that apply to species with similar life history traits, which could provide a predictive understanding of species with shared traits rather than having to adopt a species-specific approach to management. In this study, an analysis of life history traits was applied to cycads, the oldest living seeds plants which are at risk of extinction due to vulnerability to illegal wild harvesting and habitat loss. The study focused on South African cycad species within the genus *Encephalartos*, as well as two species from Swaziland. The first objective was to identify groups of species with similar life histories and to assess whether these groups are aligned with phylogenetic relationships or an association with particular environments. The second objective was to determine whether species with shared suites of life history traits exhibited a similar population stage structure.

Hierarchical cluster analysis and Principal Component Analysis (PCA) were used to identify groups based on key life history traits, namely, cone number and coning interval, number of seeds produced, number of stems, stem height and plant habit. Four life history groups emerged, these were: Group 1 with single-stemmed, subterranean species such as *E. villosus*; Group 2 generally characterised by medium-height species with many stems such as *E. lehmannii*; Group 3 with the tallest species which generally produce the most cones at the most frequent interval such as *E. natalensis*; and Group 4 with dwarf-arborescent, multi-stemmed species such as *E. horridus.* The groups were not found to correspond with the most recent phylogeny for *Encephalartos* and thus phylogenetic constraints were excluded. An analysis of environmental variables for 193 populations of species in all groups, including maximum and minimum temperatures, mean annual precipitation, moisture index, rainfall co-efficient of variation and fire return frequency, showed that the means per group were not significantly different from each other for most of the variables. However, it was evident that the variable ranges showed clear trends with biological significance. These tended towards more stable, less variable environments with more predictable rainfall for Group 1 species, and less

stable, more variable environments with less predictable rainfall for species within Group 4. Groups 2 and 3 showed a large range and overlap in environmental associations with no consistent patterns.

Population structure is valuable for determining whether recruitment in a population is adequate for species survival. Static life tables and Chi-Squared analyses were used to test differences in the population structure and survivorship patterns of species between and within the life history groups. If particular demographic patterns were shown to be emergent properties of certain suites of life history traits, autecological studies may be avoided for predictive-ecological conservation frameworks. The results showed that species in Group 1 had populations with a high proportion of juveniles and fewer reproductive adults, indicating high recruitment as well as high juvenile mortality. In contrast, species in Group 4 had populations with a high proportion of adults and fewer juveniles indicating low recruitment and high juvenile mortality with primary investment into adult plant persistence through vegetative suckering. Group 2 consisted mostly of rare species with very small populations and high proportions of adult plants showing evidence of episodic recruitment events. Species in Group 3 showed a similar trend towards intermittent recruitment with adult persistence, however, no explicit population structure emerged. This led to the conclusion that Groups 1 and 4 are relatively consistent and predictable, however, Groups 2 and 3 would better benefit from an autecological approach to management. This study was helpful to assemble life history data for South African *Encephalartos*, as well as environmental parameters for each species. Ultimately, it has shown that primary investment into seeds versus persistence, or a combination thereof, can influence population structure.

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CHAPTER 1: INTRODUCTION

1.1 GENERAL BACKGROUND AND CONTEXT OF STUDY

Understanding the evolution of life history traits and their implications for ecological processes and community structure is a pervasive theme in evolutionary biology and ecology (Kleyer *et al*., 2008; Díaz *et al*., 2013; Hille & Cooper, 2015). Evolutionary biologists have focused on why and how certain life history traits have evolved and whether these traits are constant within a species or if there is phenotypic plasticity between individuals or populations (Nylin & Gotthard, 1998; Cressler *et al*., 2010; Cochrane *et al.,* 2015). Ecologists and population biologists have been interested in how particular life history traits influence the population dynamics of species and the way they respond to ecological processes, such as competition, or environmental influences like frost, drought or rainfall variability (Franco & Silvertown, 1996; Forbis & Doak, 2004). A good example is the classification of species as either r- or K- selected depending on their reproductive rate and longevity (MacArthur & Wilson, 1967), but there are numerous other examples such as the division between resprouter and reseeder life histories in fynbos species (Bond & Midgley, 2001) and bet-hedging theory (Stearns, 2000).

One of the reasons for trying to understand life histories is to determine whether there are general responses that apply to species with similar traits. This allows ecologists to gain a more predictive understanding of a large number of species rather than having to follow a purely autecological approach (Lavorel *et al*., 1997; Kahmen *et al*, 2002). These patterns can provide a theoretical basis for ecology (Leishman & Westoby, 1992). This is particularly relevant for the conservation of diverse groups such as plants, where it is not possible to undertake detailed species-specific studies in order to manage them effectively.

In this study, life history analysis was applied to cycads, a monophyletic group of gymnosperm plants that evolved in the Carboniferous or early Permian about 280 million years ago (Donaldson *et al*., 2003; Walters *et al*., 2004). Cycads are the oldest living group of seed plants with ca. 320 species. They are distributed globally across tropical and subtropical regions and are one of the most threatened groups of organisms on earth (Hoffmann *et al*., 2010). About 62 % of the world's cycads are listed as threatened on the IUCN Red List, emphasizing an urgent need for conservation action (IUCN, 2010a). To know which management interventions are likely to make a difference we need to understand how different cycad species respond to threats. One of the challenges is that it is simply not possible to undertake detailed population studies for such a large number of species and to develop species-specific interventions. This study seeks to determine whether shared life history traits in South African cycads result in a predictable population structure and responses to particular environments which would provide for more general approaches to cycad conservation.

1.2 OVERVIEW OF CYCADS

There are three families of cycads: Cycadaceae, Stangeriaceae and Zamiaceae, collectively made up of 10 genera. Cycadaceae contains one genus, *Cycas* Linnaeus, of which most species are found in the Old World countries that border the coastlines of the Pacific or Indian Ocean. Stangeriaceae contains two genera, *Stangeria* T. Moore, found only in Africa, and *Bowenia* Hooker ex Hooker *filius*, found only in Australia. Zamiaceae is the largest family containing the Australian genera, *Lepidozamia* Regel and *Macrozamia* Miquel, as well as, *Microcycas* (Miquel)A. de Candolle, which is endemic to Cuba; the New World genera, *Ceratozamia* Brongniart, *Zamia* and *Dioon* Lindley; and lastly, the African genus, *Encephalartos* Lehmann which is endemic to Africa (Donaldson *et al*., 2003; Walters *et al*., 2004).

Despite the widespread distribution of these taxa, most cycad species have very small and isolated populations (Raimondo & Donaldson, 2003; Golding & Hurter, 2003). Due to their dioecious biology and their slow growth rate (Barkhuizen, 1975), they are left at a predisposed risk of extinction in the face of a number of threats. The most important threats to cycad populations are human induced and include the degradation and destruction of their natural habitat and illegal wild harvesting for the horticultural and traditional medicine (muthi) trade (Osborne, 1995; Donaldson, 2003a; Golding & Hurter, 2003; Cousins *et al*., 2012; Cousins *et al*., 2013; Williams *et al*., 2014). The removal of adult plants and seedlings from the wild, stochastic events such as fire, and loss of habitat can be detrimental to the persistence or recovery of a cycad population and can result in reproductive failure and subsequent extinction of the species. This reproductive failure normally results from low seed fertility due to 1) larger dispersal distances between male and female plants causing pollen limitation, 2) a skewed sex ratio, or 3) local pollinator extinction (Donaldson, 2003b). These threats highlight the importance of proper species management at a local, national and global scale.

1.3 THE SOUTH AFRICAN SPECIES OF ENCEPHALARTOS

Encephalartos comprises 66 species which occur primarily from the eastern side of Southern Africa to Sudan, extending through the Democratic Republic of Congo and Angola, as well as through Nigeria, Benin and Ghana in the west (Donaldson, 2003b). South Africa is regarded as a hotspot for cycad diversity and threat (Donaldson 2003b), containing more than half of Africa's *Encephalartos* species (Retief *et al.*, 2014) with a greater proportion (29 %) of these listed as Critically Endangered (CR) than anywhere else in the world (IUCN 2010a). A CR-rating by the IUCN is the category for the highest risk of extinction for wild species (IUCN 2010b). The genus occurs naturally along the South African coast from the Eastern Cape to KwaZulu-Natal as well as into the Mpumalanga and Limpopo provinces (Cousins *et al.*, 2012). Thirty-seven *Encephalartos* species occur in South Africa, of which 29 are endemic (Donaldson, 2008; Cousins *et al.*, 2013). Seventy-eight percent of South African cycads have an IUCN rating of "Threatened", "Endangered" or "Critically Endangered" (VU. EN or CR) (Retief et al., 2014) and three species (*E. brevifoliolatus*, *E. woodii* and *E. nubimontanus*) are already extinct in the wild (IUCN, 2010b).

The illegal wild harvesting of South African cycads has escalated since the 1990's (Retief *et al.*, 2014). Currently, all *Encephalartos* species are listed on Appendix I of CITES (the Convention on International Trade in Endangered Species of Wild Flora and Fauna) which prohibits the international trade of wild-harvested specimens (Donaldson, 2003b). There is a growing pressure to reverse the impacts of illegal harvesting and trade, and implement conservation actions. The South African government has recently published biodiversity management plans which include recovery targets. There is an urgent need for increased scientific knowledge of cycad ecology on which to base conservation actions to ensure the implementation of realistic and effective strategies.

Access to sound ecological data on each species would be ideal but this is not possible for several reasons. First, several species have declined to critically low numbers making it difficult, if not impossible, to understand their population processes. Second, with current resources, it would take too long to study all the species in order to take action in time to limit their decline. Analysing cycad life history traits, therefore, potentially provides a way to generate meaningful information without detailed studies of all species. If each cycad species has a unique suite of traits, resulting in idiosyncratic behaviour, then autecological studies will be needed, focusing on priority species. However, if cycad species share particular combinations of life history traits, these traits may influence their dynamics and result in similar responses to threats as well as to conservation interventions. It may therefore be possible to identify life history groupings with inherent emergent properties, and to use these to develop more generic management responses for each major group.

1.4 PROJECT AIMS

There are two essential questions relating to *Encephalartos* for this study (i) Are there consistent species-wide attributes that are repeated in different species which can be used as a basis for grouping species? (ii) Do these life history attributes have emergent properties such that species that share the same attributes respond similarly to environmental conditions and disturbance?

The practical implications of this study is that if it is possible to group cycads into a small number of life history types, a framework could be developed for conservation action that could be applied to all cycads in the country as an alternative to individual species-specific approaches.

1.5 PROJECT OBJECTIVES

(1) To determine the life history trait information available for the South African and Swaziland *Encephalartos* species and construct a species X trait matrix for further analyses.

(2) To use quantitative clustering tools, ordination methods and supporting multivariate analyses to identify groups (response types) of South African *Encephalartos* species based on the their life history traits.

(3) To evaluate whether the resultant groups are phylogenetically constrained, and establish which life history traits are represented across the phylogeny

(4) To assess whether the key life history traits are associated with particular environmental attributes.

(5) To analyze the population structure of different cycad species to determine whether the observed patterns are an emergent property of the life history type (group) which would allow for predictive power in cycad conservation and management.

CHAPTER 2: LIFE HISTORY TRAITS AS A BASIS FOR GROUPING CYCADS SPECIES

2.1: INTRODUCTION

2.1.1 LIFE HISTORY TRAITS IN CONTEXT

A species-specific approach to conservation has several limitations, especially when there are time and resource constraints. Consequently, both conservation and ecological studies have advocated the inclusion of life history information to understand ecological responses to particular conditions (Shaffer, 1981; Menges, 1986; Shemske *et al.*, 1994; Donaldson, 1995; Raimondo & Donaldson 2003). The IUCN Red List is the most comprehensive global inventory for the conservation assessment and status of most studied species. The criteria for undertaking the assessment and evaluating plant extinction risk, incorporate a description of life history traits, including a measure of recruitment levels in the population (Keith,1998). This illustrates the importance of these traits when evaluating species' survival, growth and reproduction.

Life history-based approaches have also been used in conservation and ecological research to determine plant responses to disturbance (Lavorel *et al.*, 1997; Kühner & Kleyer, 2008), climate change (Franks & Weis, 2008) and ecological restoration (Pywell *et al.*, 2003). They are equally valuable in the creation of vegetation, community and landscape models, as well as the assessment of meta population dynamics and trait-environment relationships (Weiher *et al.*, 1999). Most relevant to this study is the usefulness of life history traits to identify groups or response types which portray similar patterns and can potentially be used to predict responses to environmental change or disturbance (Weiher *et al.*, 1999; Kolb & Diekmann, 2005; Kleyer *et al.*, 2008).

2.1.2 BACKGROUND TO LIFE HISTORY THEORY

Life history theory is strongly tied in with evolutionary theory and how traits influence reproductive success and continuation into further generations (Stearns, 1992). Life history theory extends the predictions that can be made from genetics to considering the whole organism's traits and how they relate to fitness (Stearns, 1992; Stearns, 2000). It involves selectionist and developmental components in which the species' phenotype is expected to ensure reproductive success, although this may be physiologically constrained to only express certain genetic variation (Stearns, 2000). It is generally accepted that both intrinsic and extrinsic factors influence life history traits (Stearns, 2000;). Extrinsic factors involve ecological impacts while intrinsic factors involve the tradeoffs between traits as well as inherent genetic limitations (Fréville *et al*., 2007). Therefore, to understand life history evolution we should understand the influence of the environment on survival and reproduction at different ages, sizes and stages of an organism as well as the connection and variation between traits.

Life history traits are characteristics of a species that provide insight into the allocation of energy towards reproduction versus somatic activities (Trendall, 1982). They are phenotypic properties and reflect the range of adaptive strategies used for optimal survival and reproductive success within an organism's life cycle in response to the environment (Flatt & Heyland, 2011). The goal of life history studies is to understand the variation in species and populations within different environments. An analysis of life histories examines how fitness is maximized through variations and interactions in growth, maturation, reproduction and survival (Stearns, 1992). Genetic, developmental, physiological and phylogenetic limitations often restrict the expression of alternative life history traits. Therefore, phenotypic variation, which can be explained by identifying trade-offs versus constraints, is central to life history studies (Braendle *et al*., 2011). Predicting which combinations of traits will present themselves in specific circumstances is a key outcome of life history studies (Stearns, 1976).

Classical life history traits include the size of individuals at birth, length of life, age and the size of reproductive investment, as well as the mortality schedule. They also include growth patterns and the size of mature adults, as well as the number, size and sex ratio of offspring (Stearns, 1992; Roff, 2001). More recently, any phenotypic characters that influence reproduction and survival have been referred to as life history traits (Braendle *et al*., 2011). Very importantly, when determining fitness, life history evolution considers the interaction of a suite of traits rather than single traits in isolation (Roff, 2001).

Classical life history theory is based on optimization models where the fitness of a phenotype is measured by the population's growth (Roff, 1992; Stearns, 1992). Certain inherent costs are associated with maturation at different ages and sizes. The optimum age and size at maturity exists when the positive differences are the largest. Early maturation allows for a shorter generation time and therefore a shorter period of exposure to mortality before the first reproductive event. Alternatively, a later maturation allows for more time for growth, leading to higher quality offspring (higher per-time-unit survival) and a larger body size with its associated higher fecundity (Stearns, 1992; Stearns, 2000).

A popular example of an optimization curve in life history evolution is illustrated by Stearns and Crandell (1981). The main feature of the optimality model incorporates the costs and benefits of trait variation represented by a curve relating trait contribution to fitness. The optimum fitness profile can be found at the peak of the curve where fitness is maximized. A more robust prediction is made when the peak is sharp and naturally buffers for unaccounted effects. However, regardless of the peak inclination , optimality models suggest that traits involved in tradeoffs maximize fitness at intermediate values. This highlights the importance of the relationship and interactions of these traits with the other traits building up the organism which in turn is undergoing selection pressures from interacting with the external environment.

Reaction norms are the assortment of phenotypes that can be expressed in an organism across a variety of environmental conditions. There are a number of potential optimal reaction norms, one of the simplest ones proposes young maturation and a larger body-size in good conditions and older maturation with a smaller body-size in poor conditions (Stearns & Koella, 1986). Environments that strongly influence reproduction have a strong influence on shaping the reaction curve (Houston & McNamara, 1992; Kawecki & Stearns, 1993).

Reproduction comes with costs such as parent mortality or decreased future reproductive events. The question intrinsic to life-history theory is: What is the best way to spread out reproduction in a lifetime to minimize costs and maximize reproductive success? Reproductive Effort Models attempt to answer this question by generating the optimal strategy. A classic result of an age-specific Reproductive Effort Model would state that if mortality increases in a specific age class, then the optimal reproductive effort will increase before that age and decrease thereafter (Michod, 1979).

Alternatively, optimal reproductive effort will increase in earlier life if mortality increases in all the age classes (Charlesworth, 1980) or if adult mortality increases (Roff, 1981). The use of life history theory, with its associated models, is still relevant today forming the foundation for many life history studies (Ozinga *et al*., 2007; Burton *et al*., 2010; Cressler *et al.,* 2010; Altwegg *et al*., 2015; Kleyer & Minden, 2015; Norghauer & Newbery, 2015).

When the value of adults is high and juveniles low, life expectancy is expected to be longer. Selection pressures that lead to longer life expectancies are: having less adult mortality and variation in adult mortality rates between reproduction events, as well as having more juvenile mortality and variation in juvenile mortality between reproductive events (Harcombe, 1987). Investment will shift to the age class that is less exposed to risk. These evolutionary strategies are important for understanding the persistence of species in a diversity of ecological systems.

2.1.3 LIFE HISTORY THEORY IN ECOLOGY

Understanding the factors affecting the survival and reproduction of different life stages and ages, as well as the connection between traits and the constraints on trait variation, has implications for understanding ecological responses (González-Astorga *et al*., 2006; Kühner & Kleyer, 2008). There are some good examples of ecological life history responses based around fire-prone ecosystems such as savanna (Watkinson & Powell, 1997), fynbos (Altwegg *et al.*, 2015), grassland (Kahmen *et al*., 2002) and chaparral (Pratt *et al.*, 2007) or coniferous forests (Bond & Keeley, 2005). Fire in an ecosystem has resulted in a number of adaptive responses and fitness trade-offs in plant life history strategies (Altwegg *et al*., 2015). These fitness trade-offs aren't well understood (Roff & Fairbairn, 2007), but provide a good opportunity for study, especially where different life history strategies coexist.

Fire adaptations in plants involve a trade-off between persistence and reproduction. Persistence involves life history strategies geared towards fire survival such as the ability to resprout, whereas a reproductive life history strategy could allow for fire mortality, but select for fire-stimulated dispersal (serotiny) and rapid growth to a reproductive age (reseeders). Intermediate life history forms where different individuals within a species display different strategies are rare (Schutte *et al*., 1995).

Reseeders or non-sprouters (Bond & Midgley 1995; Schutte *et al*. 1995; Pratt *et al*. 2012) can be defined as plants with a life history strategy in which all adults die in the case of a fire and regeneration occurs after the fire through seeds. Conversely, resprouters, also known as facultative seeders (Keeley *et al*., 2012), will survive fire and resprout afterwards through buds or tubers, with fire additionally stimulating seedling production in some species. The two strategies differ according to their allocation of resources to either fast growth or protective tissues. Both strategies hold certain advantages and disadvantages. Ecologically, reseeders require a more predictable rainfall with favourable environmental conditions that can facilitate seedling establishment (Keeley *et al*., 2012) as well as time for the seeds to germinate and establish. Resprouters can use their underground resources to immediately recolonize the newly-opened spaces. In terms of investment, reseeders have a much lower cost without the need for carbon-rich storage and defence structures (Pausas *et al*. 2004; Pratt *et al*. 2012). It is clear from a discussion of these two life history strategies that understanding the life histories of plants helps us to understand ecological responses and can aid in ecological predictions.

Another life history scheme with evolutionary and ecological implications is that of r- and K- selection (MacArthur & Wilson, 1967). This is one of the most well-known theories in ecology, from which several variations have arisen (Taylor *et al*., 1990; Franco & Silvertown, 1996). The theory provides a microevolutionary approach to the regulation of populations (Stearns, 1992). It predicts that density-independent conditions give rise to short-lived species with very high reproductive output (r-selected) and conversely, density-dependent conditions give rise to long-lived species with a low reproductive output (K-selected) (Gadgil & Solbrig, 1972; Stearns, 1992). There have been many criticisms of the r-K dichotomy (Stearns, 1977; Stearns, 1992) as well as defenders of the idea (Boyce, 1984). However, despite the lack of concurrence of the validity of this specific theory, it highlights the advantage of having a framework on which to understand patterns and processes in ecological systems.

2.1.4 FACTORS AFFECTING LIFE HISTORY TRAITS

A key question involving the study of life history traits is why different species develop different characteristics? Limits set by ancestral phylogenetic character states on the range of life history traits that can be expressed, are referred to as phylogenetic constraints (Price, 1994). Not all life history strategies are phylogenetically constrained and some plant species, such as in the genus *Leucadendron*, have shown evidence of multiple transitions between life history strategies within their phylogeny (Barker *et al.*, 2004). It is not known exactly how these switches occur (Linder, 2003). When carrying out life history analysis, it is valuable to determine the variability of traits or life history groups in relation to their phylogenetic history.

There is debate about whether the phenotypic expression of a single genotype over varying environments is due to a summation of selection pressures on the species. Some phenotypes are known to be robust and relatively invariant despite environmental variation, while others appear relatively plastic (Nylin & Gotthard, 1998). Phenotypic plasticity is mostly ignored in studies of global change despite numerous species being able to adjust their functional phenotypic expression in reaction to spatial and temporal heterogeneity (Anderson & Gezon, 2015). Evolutionary trajectories and species distribution patterns are strongly influenced by climate (Stearns, 1992). Similarly, plant functional traits have a strong influence on plant ecological processes and will vary in response to climatic heterogeneity (Anderson & Gezon, 2015). Heat, cold and drought are the most significant abiotic stresses on plants and different species are differently-adapted for their diverse environments (Bita & Gerats, 2013). Therefore it is useful to investigate if there is selection for certain life history traits in certain environments.

2.1.5 OVERVIEW OF FUNCTIONAL RESPONSE TYPES AND CYCAD APPLICATIONS

In ecological studies, it is recognized that identifying “functional types” for terrestrial plant species, rather than taxonomic groupings, can be effective in answering ecological questions (Cornelissen *et al.*, 2003). Consequently, these response types can be used to predict ecosystem responses to environmental changes including disturbance, habitat degradation (Cornelissen *et al.,* 2003) and climate change (Leishman & Westoby, 1992).

Plant functional groups are defined as groups of species that share similar responses to environmental factors due to a shared set of traits and organismal-level functioning (Cornelissen *et al.*, 2003; Lavorel *et al.*, 1999).

Although cycads are a relatively small and monophyletic group, and all are long-lived species, their life-span, growth form, cone structures and general reproductive biology vary considerably among species (Raimondo & Donaldson, 2003; Griffith *et al*. 2015). For example, South African *Encephalartos* species range from being relatively small with subterranean stems (eg. *E. villosus*, *E. caffer*) to large trees with stems greater than 6 m in length (eg. *E. transvenosus, E. natalensis*). Cycads also occupy a very diverse range of habitats varying from forest understory and thicket vegetation types, to grassland and savannah (Golding & Hurter, 2003). South African *Encephalartos* are representative of the range of life history types found throughout the genus in Africa. If it is possible to group cycads into a small number of life history types, a framework can be provided for conservation actions that can be applied to all cycads as an alternative to individual species-specific approaches.

Donaldson (1995) hypothesized that South African cycads could be grouped according to their life history traits and proposed four possible groups based on the tendency towards reproduction or persistence. The four groups comprised one group with a strong dependence on reproduction, a second group with highly persistent stems and lower reproduction, and two intermediate groups. This hypothesis has never been formally tested, nor has there been a rigorous analysis of how cycad species may fit into different groups or the ecological responses of species in different groups. Even so, Raimondo and Donaldson (2003) partly tested the application of the concept by investigating the effect of different harvesting scenarios on population growth in two species from contrasting life history groups via simulation models. One species with traits favouring reproduction and another with traits for persistence. Despite their different life histories, harvesting adult plants in both species had a strong negative effect on their population growth, whilst seed harvesting had minimal impact. Apparently large differences in life history traits did not seem to affect the immediate impacts of harvesting but did have a significant effect on recovery periods. The question posed by the study was whether these responses would be similar in other species that shared particular life history traits.

To test whether any life history response groups are phylogenetically constrained, or whether some or all of the cycad life history traits are evolutionary labile requires an understanding of the phylogeny of *Encephalartos.* A tentative taxonomic grouping, based on morphological and geographical features, was developed for *Encephalartos* by Vorster (2004). He explicitly stated that the groups should not be considered phylogenetic, because they were not identified using any phylogenetic methods and were based predominantly on the morphological characters and species distributions. This classification therefore cannot be used to test for phylogenetic constraints because it is not independent of the data used to identify life history groups. For a reliable phylogenetic approach, Vorster (2004) recommended the combined use of a range of traits including pollen and vegetative morphology, the morphology of the reproductive structures, leaflet anatomy, plant chemical characteristics, associations with organisms such as insects, Cyanophyta and mycorrhizae, geographical evidence and reproductive isolation, and molecular evidence including DNA analysis, chromosome morphology and number as well as Isoenzymes. This kind of comprehensive approach has yet to happen for *Encephalartos,* however, cycad phylogenies have increasingly relied on combined data (Brenner *et al,* 2003) and some phylogenies for *Encephalartos* have started to combine DNA methods with morphological characters (Chaiprasongsuk *et al*., 2007). Treutlein *et al* (2005) provided a phylogeny based on morphological and DNA data and Yessoufou *et al* (2013) proposed a phylogeny based on several DNA markers. These provide a basis for at least a tentative analysis of phylogenetic constraints.

The primary aim of this study was to determine whether it is possible to derive groups from among the South African species of *Encephalartos* based on statistical analysis of a set of easily measurable key life history traits. In addition, the study set out to determine whether these groups were (i) phylogenetically constrained or (ii) associated with particular environmental variables.

The hypotheses I tested in this chapter were:

1. That at least three groups of *Encephalartos* can be identified based on key traits such as cone number, coning behaviour, and stem size and stem number;
2. That ecologically-defined groups will not correspond closely to phylogenetic groups, indicating an absence of phylogenetic constraints on the development of different life history traits;
3. That ecologically-defined groups will be associated with particular environmental variables due to selection for particular traits in these environments

2.2 METHODS

2.2.1 COMPILING THE SPECIES TRAIT MATRIX

A suite of traits for each South African *Encephalartos* species, as well as two Swaziland species (*E. aplanatus* and *E. umbeluziensis*) was compiled into a species x trait matrix using several literature databases and consultation with experts (see Appendix 1 for trait references). *Encephalartos brevifoliolatus*, *E. relictus* (Swaziland) and *E. woodii* were not included as they are extinct in the wild and there is no life history information available for female plants. Traits associated with survival and longevity included those that are indicative of resource allocation towards tissue production as well as cone and leaf protection. Traits associated with reproduction included those that indicate the resources allocated towards reproductive events.

Cycad stems are simple in comparison with flowering plants, but the size of their stems can be a good indication of their stored resources and overall growth rate (Norstog & Nicholls, 1997). Stem size and leaf production can have important effects on overall fitness through fecundity and survival (Ornduff, 1991a). The production of multiple stems versus single stems can also indicate relative investment in persistent stems. In contrast, cone size, cone number, seeds per cone and frequency of coning provide information on investment in reproduction. In many species of *Macrozamia*, there is evidence that fire plays a role in triggering mast seeding events, although the exact mechanism is not fully known (Asmussen, 2009). Most species of *Encephalartos* show some degree of synchronous coning, however only *E. cycadifolius* displays evidence of fire-induced coning (Donaldson, 2008) and thus due to a lack of information, coning cues could not be used as a trait. It should be noted that ovules in *Encephalartos* reach their full size before pollination and it is not possible to distinguish whether a seed is a true fertilized ovule (true seed) or an unfertilized ovule. Therefore these structures have been collectively termed omnules for *Encephalartos*, *Macrozamia* and *Lepidozamia* species (Grobbelaar, 1995). For this thesis, any reference to cycad seeds is therefore a reference to omnules.

The following traits were considered:

1. Traits associated with survival and longevity
    a. stem height and diameter
    b. growth form (acaulescent or arborescent; branching, suckering)
    c. leaflets lobed or with spines (potentially deterring herbivores)
    d. leaf colour (associated with the presence or absence of a protective wax coating on the leaf surface protecting against transpiration(Grobbelaar, 2004)
2. Traits associated with reproduction
    a. cones (shape, number, size and diameter)
    b. coning frequency
    c. average number of seeds per female cone
    d. seed size (shape, length, width)
    e. Sclerotesta (shape, length, diameter)
    f. Female sporophyll face height and length (seed protection)

A number of descriptive principal component analyses were carried out in PC-ORD (McCune & Mefford, 2011) to narrow down the most important suite of traits and to eliminate the noise in the data

The final datasheet for analysis consisted of only those traits which were considered to have the most important influence on the life history of *Encephalartos.* These were traits that could be measured across all species and which provided a means to demarcate like and unlike species based solely on regeneration, reproduction and persistence attributes rather than taxonomic attributes which reflect evolutionary relatedness. These traits consisted of:

1. The typical number of female cones (numerical discrete data type)
2. Average number of seeds produced over ten years (numerical discrete data type)

    Calculated as:

    $[(average\ \#\ of\ seeds\ per\ cone) \times (average\ \#\ of\ cones\ per\ stem) \times (average\ \#\ of\ reproductive\ stems)] \times \left({}^{10}/_{coning\ interval}\right)$

3. Coning interval in years (numerical discrete data type)
4. Maximum stem height (cm) (numerical continuous data type)
5. Stem number (categorical nominal data type)
    - Single stem
    - Few stems
    - Multiple stems
6. Habit (categorical nominal data type)
    - Subterranean
    - Erect
    - Dwarf erect (stems are short and more or less the same size)

A certain amount of variation exists within each species for each trait. Using average and maximum recorded values as well as typical values according to experts served to account for some of that variation, however,within-species variation should be considered when interpreting the groups.

2.2.2 STATISTICAL ANALYSES OF TRAIT MATRIX TO FIND GROUPS

Unless specified otherwise, all analyses were done using R software (R Core Team, 2014).

2.2.2.1 MULTIVARIATE NORMALITY ASSESSMENT AND OUTLIER ANALYSIS

An outlier analysis and assessment of multivariate normality were done using the package MVN (Korkmaz *et al*., 2014). Data were not multivariate normal according to Mardia's Multivariate Normality Test (Mardia, 1974). When excluding the eight outliers (*E. cupidus, E. cycadifolius, E. horridus, E. trispinosus, E. latifrons, E. lehmannii, E. laevifolius, E. transvenosus*), the data were Multivariate normal. Multivariate normality is not essential for the analyses providing the results will not be used to create models or perform direct *post hoc* tests and are rather exploratory (Jackson, 1991). However, multivariate normality enables a more robust interpretation of Principal Component Analysis (PCA) (Jackson, 1991) and it was therefore considered more valuable to conduct the PCA excluding the outliers.

2.2.2.2 CLUSTER ANALYSIS

A hierarchical agglomerative cluster analysis of the trait matrix, including and excluding outliers, was performed using the package "Cluster" (Maechler *et al*., 2015). The function "daisy" was used to handle the mix-mode data, specifying the use of Gower's coefficient as a distance measure for generating the dissimilarity matrix (Gower, 1971). The use of the Gower coefficient within this function implies that a standardization is applied to the data, hence the use of the raw data values despite different measurement scales. The categorical variables were coded as n-1 binary variables to avoid multicollinearity.

Three different linkage methods (Wards Minimum Variance, Complete Linkage (furthest neighbour) and Average Linkage (UPGMA)) were performed to define clusters and compare results between methods. This is a standard procedure used to assess the reliability of the clustering, and not all results need be represented if all methods agree (Yim & Ramdeen, 2015). Wards method and Average Linkage are recommended by Milligan & Cooper (1988) and Ferreira & Hitchcock (2009) and are presented here (See Appendix 2 for Single Linkage method).

2.2.2.3 PRINCIPAL COMPONENT ANALYSIS

For comparison and further visualization, a Principal Component Analysis (PCA) was undertaken using the package "PCAMixdata" by Chavent *et al*. (2014). Outlier species were excluded. Although, Principal Component Analysis (PCA) should only be performed on numerical continuous data types and a Multiple Correspondence Analysis (MCA) can only be performed on categorical data types (Chavent *et al*., 2014), PCAMixdata was developed specifically to combine these multivariate techniques to handle mix-mode data. The method is based on Generalized Singular Value Decomposition (GSVD). The GSVD technique implements all linear multivariate techniques (Abdi, 2007) and is superior to other mix-mode, data-handling packages available (Chavent *et al*., 2014). For the mathematical justification of PCAMixData, see Chavent *et al*. (2014).

To account for the variables having measurements on different scales, the numerical data was Z-score standardized using Microsoft Excel (2007) to have equal means and standard deviations. The categorical variables were left as categories and not bins (binary). A PCA was performed on the trait matrix using the package "PCAMixData" (Chavent *et al*., 2014) and excluding the outliers mentioned in section 2.2.2.1.

2.2.2.4 ASSESSING PHYLOGENETIC SIGNAL OF DERIVED GROUPS

The genetic relationship to species' traits values is referred to as the phylogenetic signal (Revell *et al*., 2008). This can be quantitatively measured using Pagel's lambda (λ) (Pagel, 1999) or the K-statistic (Blomberg *et al*., 2003). Pagels λ works as a scaling parameter of the correlations between species compared to the correlation under expected Brownian motion. The K-statistic calculates a scaled ratio of the among species variance over the variance of the contrasts.

Typically these statistics are used to trace the origin of particular traits and to determine historical character states. The objective of this study was to simply determine whether life history types could be mapped onto a phylogeny to determine whether they are constrained to particular clades.

To assess whether the derived groups have a phylogenetic signal, the most recent phylogeny for *Encephalartos*, by Yessoufou *et al*. (2014) was used to construct relationships using Mesquite Software (Maddison & Maddison, 2015). The groups were then added as a character into the software and overlaid onto the phylogeny, each group represented by a different colour. The result was assessed visually.

2.2.2.5 ASSESSING THE ASSOCIATION OF LIFE HISTORY TRAITS WITH ENVIRONMENTAL VARIABLES

Distribution records were obtained for 193 *Encephalartos* populations. This included representatives of all South African species. The Climatic (Bioclim) information was downloaded from the CliMond archive (Kriticos *et al.,* 2012) for each site. The variables chosen were:

1. BIO05 (maximum temperature of the warmest week (°C)) (Hutchinson *et al*., 2009).
2. BIO06 (minimum temperature of the coldest week (°C)) (Hutchinson *et al*., 2009).
3. BIO28 (annual mean moisture index) (Hutchinson *et al*., 2009).
4. Mean annual precipitation (mm) (Dent *et al*., 1989).
5. Rainfall Co-efficient of Variation (%) (Schulze, 1979;1983).

The moisture index represents the relative wetness or dryness of an area. It is calculated as the ratio of time-averaged precipitation to time-averaged moisture demand (Thornthwaite, 1984). Variables of maximum and minimum temperature, as well as the moisture index and precipitation measurements, signify important abiotic stresses such as heat, cold and drought. The rainfall coefficient of variation may indicate how variable rainfall is and thus how stable the moisture regime is in which the population occurs.

Additionally, the vegetation types were extracted manually for each coordinate (SANBI, 2009) and the associated fire return frequency (in years) was derived from Forsyth *et al.* (2010). Fire has been determined as an important factor in a number of cycad species where it may stimulate cone-production, influence recruitment and reduce competition (Ornduff, 1991a, b; Watkinson & Powell, 1997; Pérez-Farrera *et al*., 2006) or kill off seeds and plants when fire frequency or intensity changes (Liddle, 2009).

A box plot was made for each climatic variable, using the package "ggplot2" (Wickham, 2009), to show the quartiles, as well as the true mean for each cycad group derived from the previous results. Separate one-way ANOVAs were performed in Statistica 12 (Statsoft, Inc., 2014) to assess for differences among the four groups for each climatic variable. After the ANOVA analysis, the residuals were checked for normality via a QQ plot and Levines test was performed per variable to test for equal variances. This was to ensure that the data met the assumptions of normality and equal variances for ANOVA. If the data met the assumptions and a significant difference was present, Tukey's post hoc test was performed to identify the different groups. If the data did not meet the assumptions for ANOVA, a non-parametric Kruskal-Wallis test was performed.

2.3 RESULTS

2.3.1 IDENTIFYING GROUPS BASED ON LIFE HISTORY TRAITS

Several distinct groups could be derived from the cluster analyses and the PCA (Table 3). Both the cluster analysis methods derived four defendable groups with large enough dissimilarity distances between them relative to the within group dissimilarity distances (Figures 2 and 3). The first and second principal components of the PCA accounted for 81.35 % of the variation between the species (Table 2) and the plot of dimension 1 and dimension 2 separated the 30 species (these excluded the outliers) into three groups (Figure 1a) that corresponded with the cluster analyses (Figures 2 and 3). Group 1 species, which included *E. villosus*, were widely separated from the other species in the PCA (Figure 1a), but were tightly clustered together. All the species in Group 1 were negatively correlated with Dimension 1, whereas the rest of the species were positively correlated with Dimension 1 (Table 1). Dimension 1 was positively correlated with all the variables and 80 % of the variance was explained by the number of stems, stem height and habit (Figure 1b). Group 1 comprised species with a single, subterranean stem and typically a single female cone. This group was also well resolved in the cluster analysis, with less than 0.1 units of dissimilarity between the species within the group and nearly the maximum of 1.5 units of dissimilarity with the species in separate groups (for Ward's method) (Figure 2). Similarly, the Average Linkage method indicated less than 0.03 units of dissimilarity among Group 1 species, and 0.55 units of dissimilarity between this group and the remaining species, out of a total of 0.6 units of dissimilarity (Figure 3).

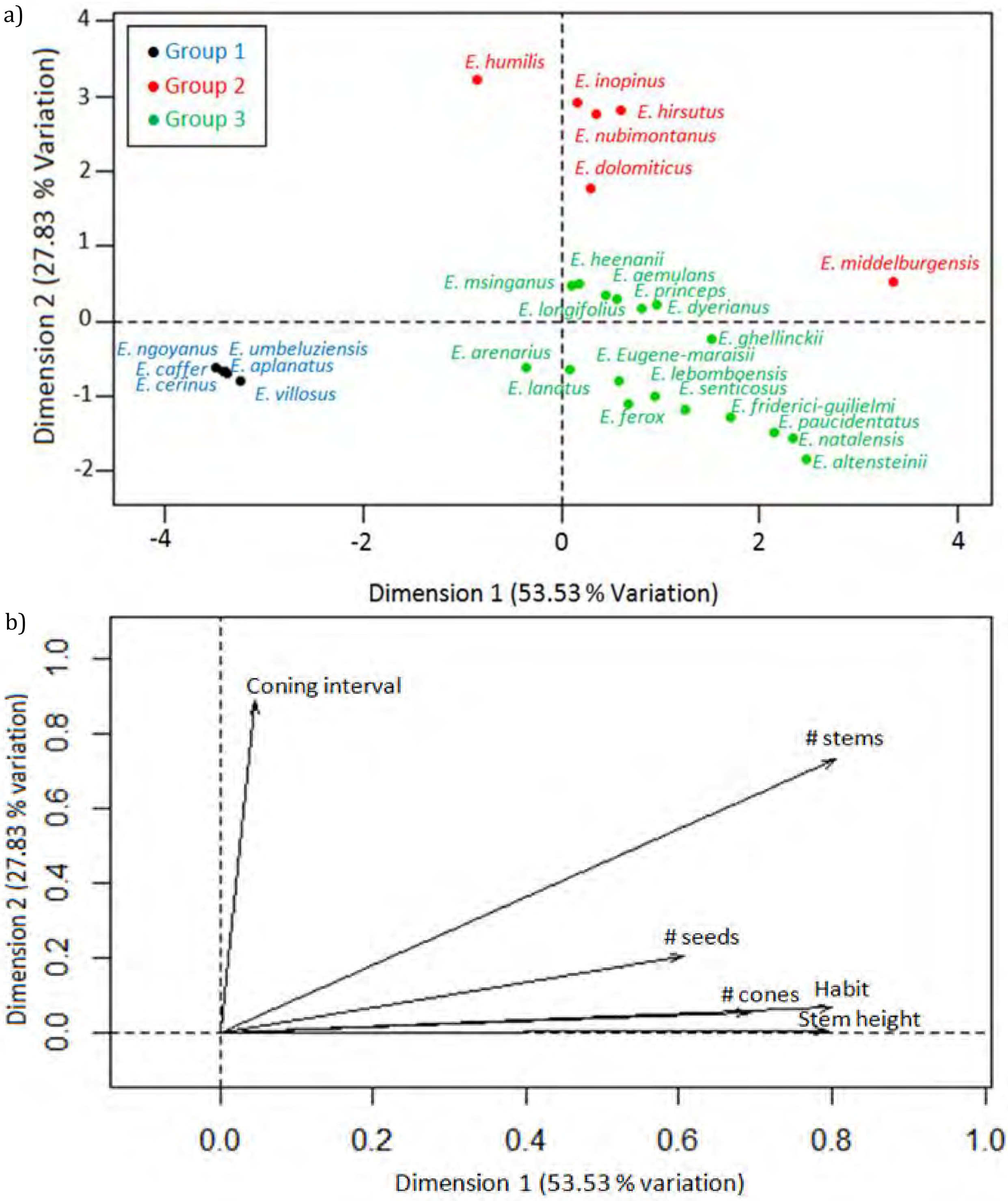

***Figure 1*: a).** A plot of Dimensions 1 and 2 (Principal Components 1 and 2) for 35 South African and two Swaziland *Encephalartos* species based on their key life history traits. The outliers identified by the multivariate outlier analysis were excluded in the PCA. **b)** A plot of the squared loadings (correlations) for Dimensions 1 and 2 indicating the proportion of variance of the variables that is explained by the dimensions.

Table 1: The coordinates for a PCA representing 35 South African and two Swaziland *Encephalartos* species analysed according to their key life history traits. Dim represents the Dimension, with each value indicating the strength of the correlation between the species and that dimension, as well as whether the correlation is positive or negative (-).

Species	**Dim 1**	**Dim 2**	**Dim 3**	**Dim 4**	**Dim 5**
E. aemulans	0.55481268	0.2813046	-0.88836174	0.28019618	0.563604070
E. altensteinii	2.47938188	-1.8367089	0.79900342	-0.13506166	-0.675224475
E. aplanatus	-3.36930350	-0.7111755	0.58497539	0.11695404	0.018432180
E. arenarius	-0.35372920	-0.6300650	-1.24913920	-0.76360903	-1.051470564
E. caffer	-3.40350574	-0.6836212	0.55485731	0.13193190	0.063954803
E. cerinus	-3.41034618	-0.6781104	0.54883369	0.13492747	0.073059327
E. dolomiticus	0.28629727	1.7634810	0.63769920	-0.94071083	-0.003449098
E. dyerianus	0.95773213	0.2045398	-0.64263794	0.57616179	0.907730038
E. eugene-maraisii	0.58943024	-0.8070498	-0.60805782	-0.51908056	0.577432153
E. ferox	0.66851867	-1.1158677	-0.39028823	-1.29297010	0.089733828
E. friderici-guilielmi	1.70893079	-1.2949751	0.20897154	0.31092655	-0.720727945
E. ghellinckii	1.52671203	-0.2483733	-0.06351501	-0.20669179	1.146371625
E. heenani	0.18638331	0.4936845	-1.20246416	0.46196339	0.428527629
E. hirsutus	0.60353951	2.8134689	0.51911355	0.44373440	-0.103163910
E. humilis	-0.86169492	3.2204445	-0.38511454	-0.69725648	-0.347195163
E. inopinus	0.16162950	2.9216457	0.23905513	0.16484355	-0.395394087
E. lanatus	0.09074451	-0.6531329	-0.93811226	0.77310815	-0.360769530
E. lebomboensis	0.94661994	-1.0185852	-0.42098199	0.10460278	-0.766448384
E. longifolius	0.45654113	0.3550014	-1.05298454	0.85691695	-0.301542619
E. middelburgensis	3.35261346	0.5323616	2.79244928	0.07854799	0.317360076
E. msinganus	0.09499210	0.4828745	-1.27261010	0.52240992	-0.075282061
E. natalensis	2.33807245	-1.5594647	0.57581786	0.41965737	-0.232188665
E. ngoyanus	-3.49243156	-0.6119800	0.47655029	0.17087434	0.182313623
E. nubimontanus	0.35018217	2.7724790	0.44413537	-0.18457034	-0.148382336
E. paucidentatus	2.14920485	-1.4917449	0.41983538	0.52279081	-0.606258879
E. princeps	0.80573173	0.1581208	-0.75582355	0.68357478	-0.140859703
E. senticosus	1.25861561	-1.1855005	-0.15657441	-0.05245096	-0.556259615
E. umbeluziensis	-3.42402708	-0.6670886	0.14091862	0.53678646	0.091268377
E. villosus	-3.25164779	-0.8059624	0.68858160	0.06543020	-0.138165645

Table 2: The eigenvalues representing the dimensions of a PCA representing 35 South African and two Swaziland *Encephalartos* species analyzed according to their key life history traits. The cumulative column indicates the percentage variation represented dimension.

Dimension	**Eigenvalue**	**Proportion**	**Cumulative (%)**
1	3.747	53.526	53.526
2	1.948	27.826	81.351
3	0.728	10.405	91.757
4	0.261	3.734	95.490
5	0.245	3.501	98.992
6	0.071	1.008	100.000

A second group, including *E. horridus,* was also well resolved in the cluster analyses with relatively little separation between the species in the group (Figures 2 and 3). Each species comprising this group was identified as an outlier in the multivariate outlier analysis making them distinct from the rest of the species. The cluster analysis using Ward's method showed less than 0.1 units of dissimilarity among species within the group and 1.0 units of dissimilarity between this group and the next Group's partition (Figure 2). The Average Linkage method indicated similar results, with 0.09 units of dissimilarity among species within the group and the maximum of 0.6 units of dissimilarity between the group and the rest of the species (Figure 3). This group comprised species with multiple dwarf stems and typically a single cone on each stem. This group was referred to as Group 4 due to the contrast of life history traits from the species in Group 1. It is easier to refer to the groups if the group number has a logical spectrum.

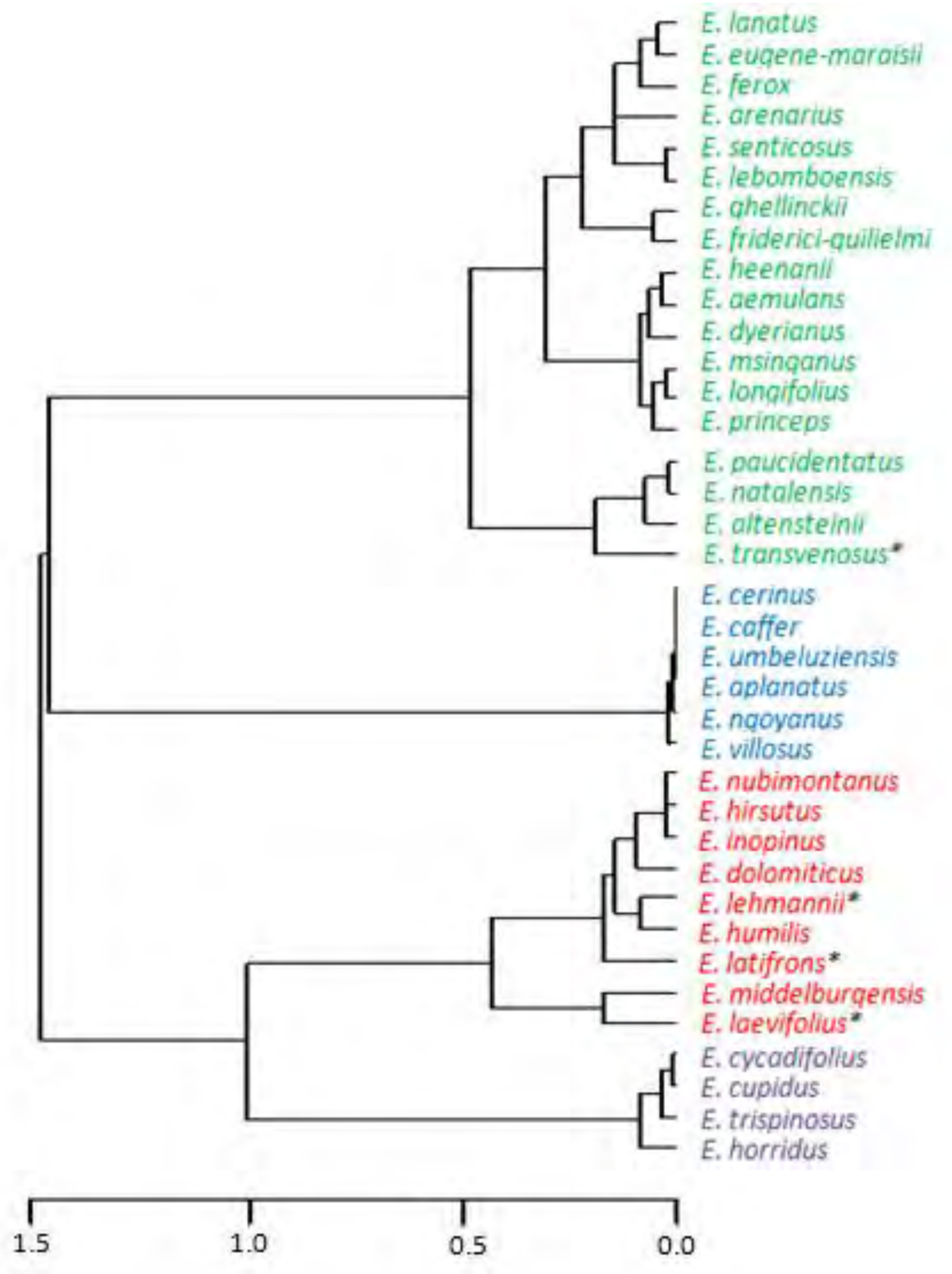

Figure 1: Horizontal dendrogram produced by a cluster analysis using Ward's linkage method showing 35 South African and two Swaziland *Encephalartos* species hierarchically arranged in fewer clusters as the amount of dissimilarity permitted within each cluster increases, based on key life history traits. At 0.5 units of dissimilarity, there are four clusters, each represented by a different colour. Group 1 = blue; Group 2 = red; Group 3 = green and Group 4 = purple. Outliers identified by the multivariate outlier analysis are indicated by an asterisk (*).

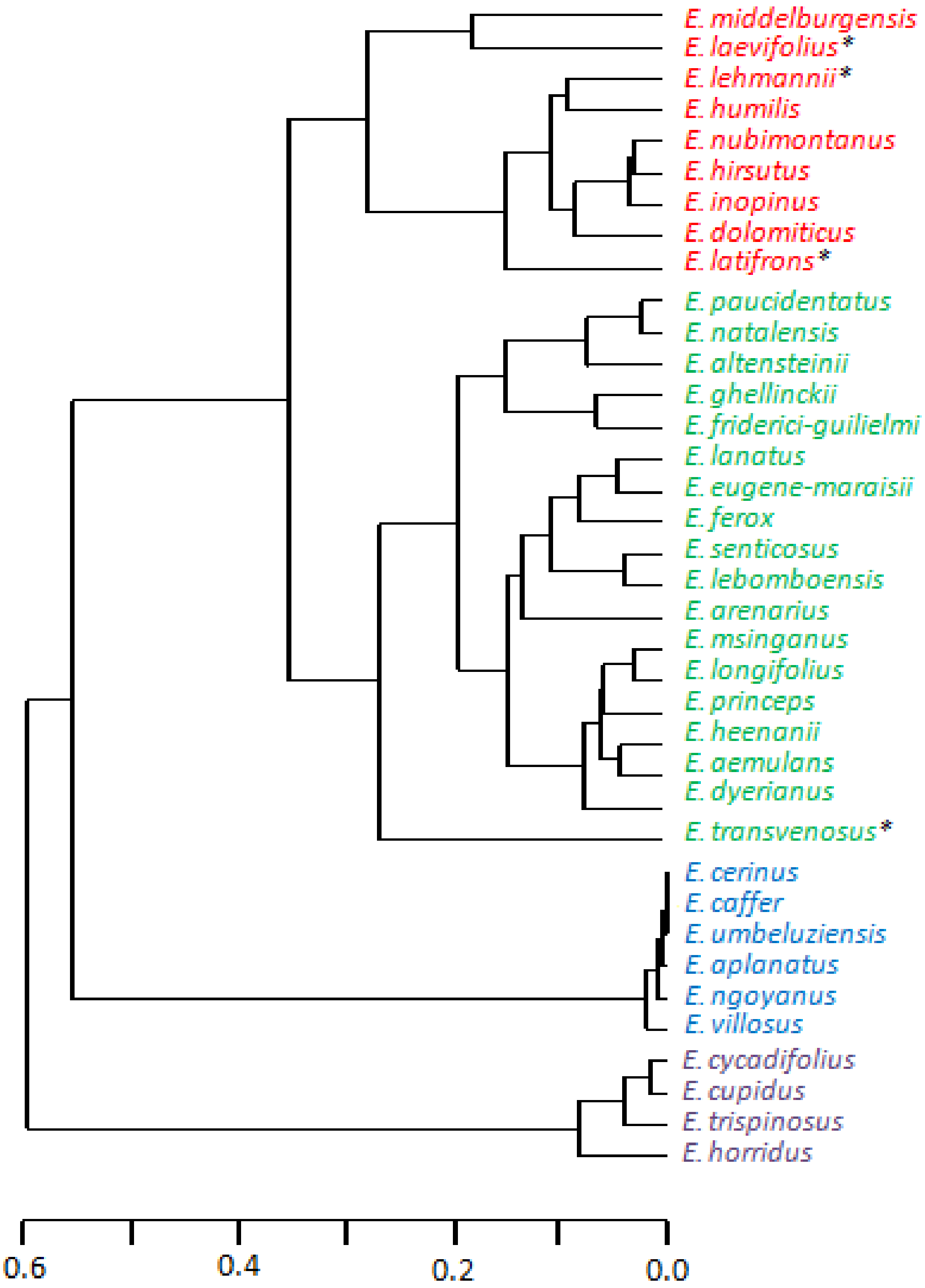

Figure 2: Horizontal dendrogram produced by a cluster analysis using Average (UPGMA) linkage method showing 35 South African and two Swaziland *Encephalartos* species hierarchically arranged in fewer clusters as the amount of dissimilarity permitted within each cluster increases based on key life history traits. At 0.3 units of dissimilarity, there are four clusters, each represented by a different colour. Group 1 = blue; Group 2 = red; Group 3 = green and Group 4 = purple. Outliers identified by the multivariate outlier analysis are indicated by an asterisk (*).

At least two additional groups can be identified by the cluster analyses and PCA. What is referred to as Group 2 includes *E. inopinus*, and was separated from the next group, Group 3, by 0.5 units of dissimilarity according to Ward's method, out of a total of 1.6 units of dissimilarity (Figure 2). However, the Average Linkage method separated these two groups by only 0.1 units of dissimilarity out of a total of 0.6 units of dissimilarity (Figure 3). The distinction between Group 2 and 3 was not as persuasive as between Groups 1 and 4 due to a shorter dissimilarity distance between them in comparison with the dissimilarity distances isolating Group 1 and 4. However, the PCA supported the separation of species in Groups 2 and 3 with the exception of *E. middelburgensis* which was spaced relatively far away from all the species (Figure 1a). Similarly, the cluster analyses indicated that *E. laevifolius* and *E. middelburgensis* could be considered together either as a distinct subgroup within Group 2 or a group of their own. *Encephalartos laevifolius* was identified as an outlier from the multivariate outlier analysis and both species separated out from the rest of Group 2 by more units of dissimilarity than between the rest of the species within Group 2 (Figure 2 and 3). The multivariate outlier analysis also identified *E. latifrons* and *E. lehmannii* as outliers, although the cluster dissimilarity distances between those species and the rest of the group did not indicate group exclusion (Figure 2 and 3). The species placed in Group 2 had many arborescent stems and produced 1 -4 cones.

Group 3, including E. *friderici-guilielmi*, was the largest group. Three subgroups were evident from the cluster analyses: a) *E. altensteinii, E. natalensis, E. paucidentatus*; b) *E. princeps, E. longifolius, E. msinganus, E. dyerianus, E. aemulans, E. heenanii* and c) *E. lebomboensis, E. senticosus, E. arenarius, E. ferox, E. eugene-maraisii, E. lanatus* (Figures 2 and 3). However, the distances of dissimilarity between these subgroups were not sufficient to independently isolate them as individual groups. Additionally, *E. friderici-guilielmi* and *E. ghellinckii* were not consistently placed, with Ward's method placing them either as an isolated subgroup or nearest to subgroup c) (Figure 2), and the Average Linkage method placing them as an isolated subgroup or nearest to subgroup a) (Figure 3). The Average Linkage cluster analysis also identified *E. transvenosus* as an outlier in the group (Figure 3), which was consistent with the multivariate outlier analysis, however Ward's method included this species in subgroup (a) (Figure 2). The species in Group 3 had a few tall stems and produced 2 – 4 cones.

Table 3: The proposed core life history type groups of South African and Swaziland *Encephalartos* species based on their key life history traits and derived from a Principal Components Analysis and hierarchical agglomerative cluster analysis using both Ward's and Average (UPGMA) linkage methods. The asterisk (*) indicate an outlier according to the multivariate outlier analysis with superscript letters indicating potential subgroups within group 3.

Group 1	**Group 2**	**Group 3**	**Group 4**
E. villosus	*E. dolomiticus*	*E. altensteinii*^{a}	*E. cycadifolius*
E. umbeluziensis	*E. hirsutus*	*E. natalensis*^{a}	*E. cupidus*
E. aplanatus	*E. inopinus*	*E. paucidentatus*^{a}	*E. horridus*
E. caffer	*E. latifrons**	*E. friderici-guilielmi*	*E. trispinosus*
E. cerinus	*E. lehmanni**	*E. ghellinckii*	
E. ngoyanus	*E. nubimontanus*	*E. dyerianus*^{b}	
	E. humilis	*E. longifolius*^{b}	
	*E. laevifolius**	*E. msinganus*^{b}	
	E. middelburgensis	*E. princeps*^{b}	
		E. aemulans^{b}	
		E. heenanii^{b}	
		E. arenarius^{c}	
		E. lebomboensis^{c}	
		E. senticosus^{c}	
		E. ferox^{c}	
		E. eugene-maraisii^{c}	
		E. lanatus^{c}	
		*E. transvenosus**	

2.3.2 PHYLOGENETIC SIGNAL

Several life history groups were represented across the phylogeny with only single-stemmed species (Group 1) forming a coherent phylogenetic group that was isolated within a single clade (Figure 3). All other life history groups occurred in multiple clades which suggests a repeated rearrangement of traits as different species evolved. As a result, the data did not support the hypothesis that life history groups are phylogenetically constrained indicating that the key life history traits are evolutionary labile.

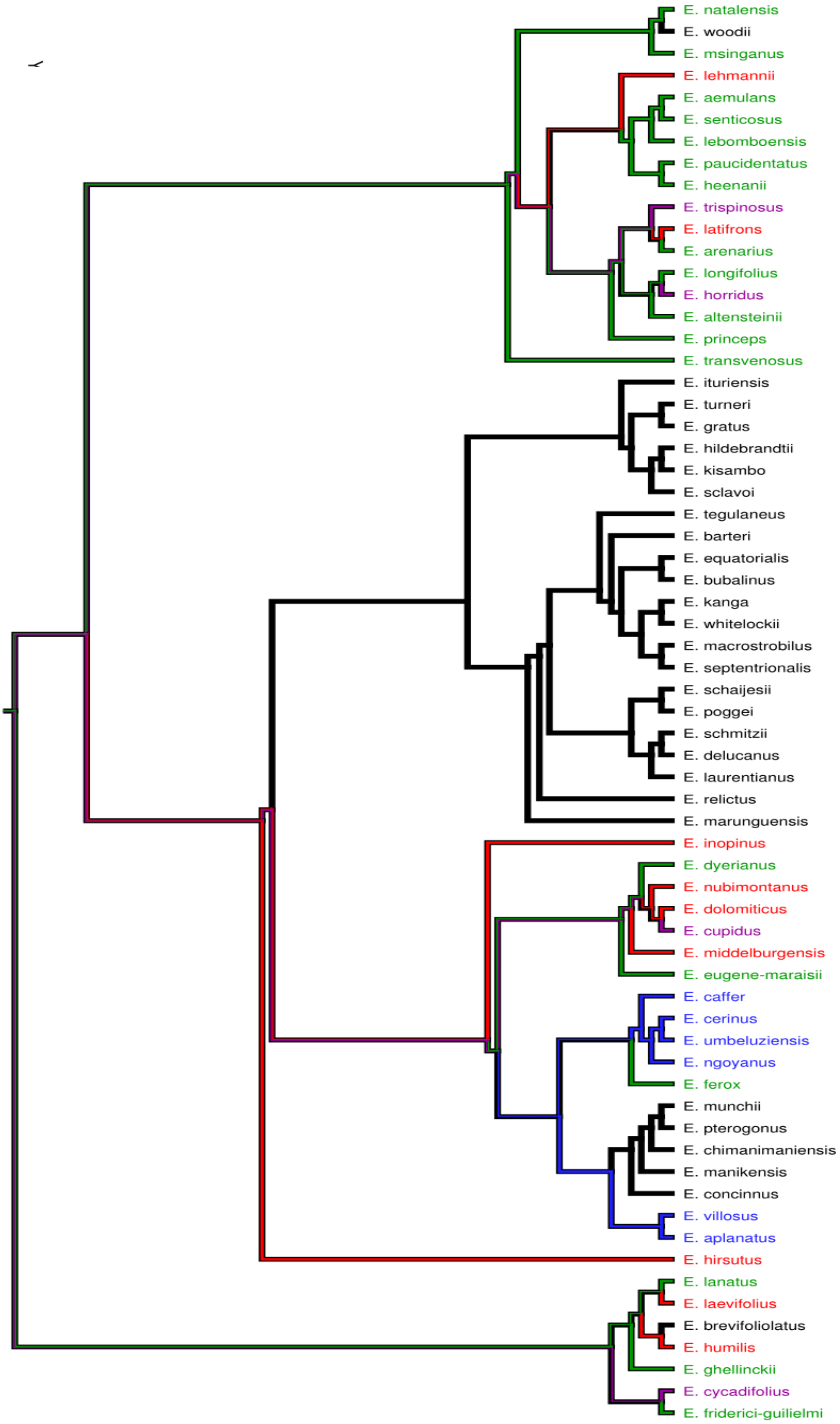

Figure 3: The phylogeny of *Encephalartos* species after Yessoufou *et al.* (2014) with the derived functional response groups of South African and Swaziland species indicated by different colours. Group 1 = blue; Group 2 = red; Group 3 = green and Group 4 = purple.

2.3.3 ASSOCIATION WITH ENVIRONMENTAL VARIABLES

An analysis of habitat attributes for species in each response group showed a number of consistent patterns within groups. Species belonging to Group 1 occurred within a narrower range of maximum temperatures compared to species in Groups 2 and 3 (Figure 4A), as well as within a narrower range of minimum temperatures compared to species in all the other groups (Figure 4B). However, these differences were not statistically different (ANOVA (maximum temperature), [F(3,31) = 0.620, p = 0.607]; ANOVA (minimum temperature), [F(3,31) = 1.046, p = 0.386];) due to the large range of temperatures over which the other species occur. Similarly, species in Group 4 were confined to habitats within a narrow band of mean annual precipitation and moisture index (Figure 4 C&D). These habitats had a significantly lower mean annual precipitation (MAP) and moisture index (MI) than other groups (ANOVA (MI), [F(3,31) = 3.186, *p = 0.0374*]; Kruskal Wallis (MAP), [χ^2(3)=8.557, *p = 0.036*]). Post hoc comparisons indicated that the difference was between Group 4 and Group 3 for both variables ((MI) Tukey-Kramer test, *p = 0.0419*; (MAP) multiple comparisons,[H(3) = 11.902, *p = 0.008*]). Habitats for species in Group 4 also had a significantly higher coefficient of variation in annual rainfall [ANOVA, F(3,31) = 5.606, *p = 0.003*] (Figure 4E) than species in Group 3 (Tukey-Kramer test, *p = 0.003827*) (Figure 4E). The fire return interval was variable across all groups with Groups 1 and 2 showing no species with intermediate fire return frequencies and the majority of species in Group 3 having a short fire return interval of 1-4 years (Figure 5). These results support the hypothesis that different life history traits are associated with particular environmental attributes.

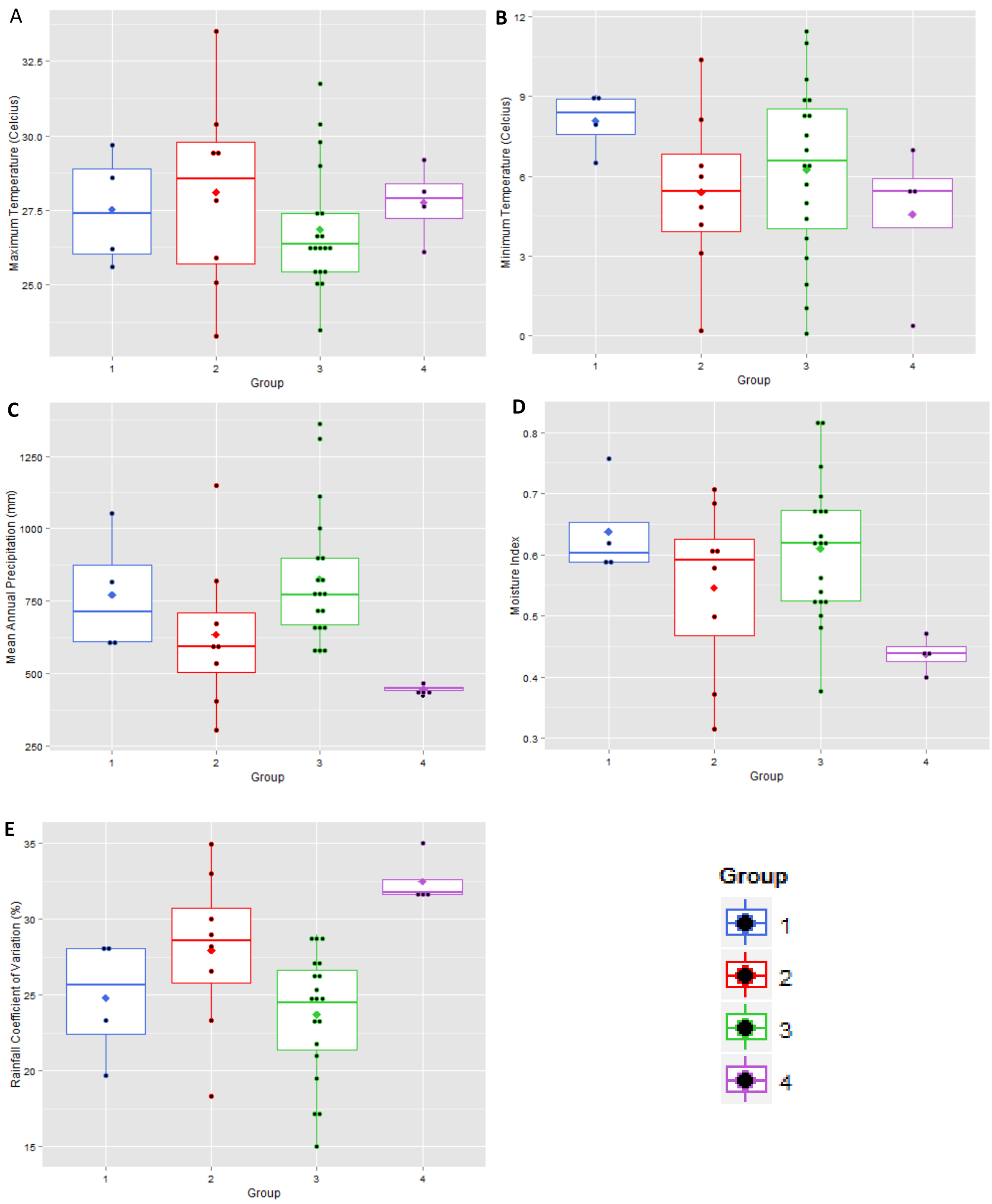

Figure 4: Boxplots showing the climatic differences between life history groups of South African *Encephalartos* species. Each plot shows the four quartiles within a group. The diamond (♦) represents the true mean. Each point (•) represents one of the species within the group. Graphs represent: (A) the Maximum temperatures within each group; (B) the minimum temperatures within each group; (C) the Mean Annual Precipitation within each group; (D) the Moisture index within each group and (E) the coefficient of variation of annual rainfall in each group

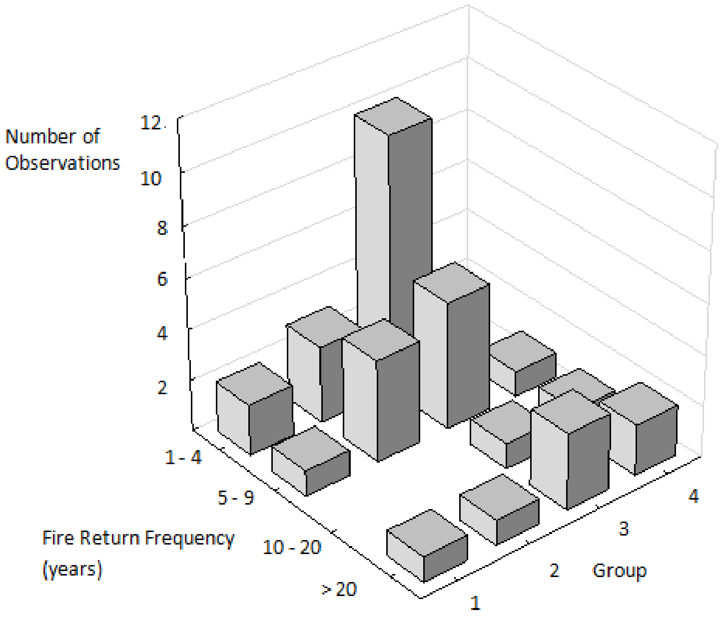

Figure 5: Fire return frequency (in years) for South African *Encephalartos* species grouped according to their key life history traits.

2.4 DISCUSSION

2.4.1 OVERVIEW

The underlying rationale for this analysis is the hypothesis that the classification of plant species into response types is a useful framework for assessing plant species' responses to environmental change, both natural and human-induced, as well as for understanding the mechanisms behind these responses (Lavorel *et al*., 1997; Kolb & Diekmann, 2005). Life history trait approaches have been used to assess species' reactions to disturbance (Lavorel *et al*., 1997), climate change (Diaz & Cabido, 1997), restoration (Pywell *et al*., 2003), habitat fragmentation (Kolb & Diekmann, 2005) and distribution patterns (Eriksson & Jakobsson, 1998). In the same way, approaches are needed to reduce the complexity of individual species into a smaller number of common and recurrent patterns (Kolb & Diekmann, 2005).

The primary aim of this chapter was to determine whether it was possible to identify life history types of South African *Encephalartos* species based on their life history traits. A second aim was to evaluate whether the resultant groups reflected their evolutionary history (i.e. were phylogenetically constrained). A third aim was to determine how closely each of the life history types was associated with a number of key environmental variables most likely to influence their long-term survival. The results confirmed that it is possible to identify at least four groups within South African species of *Encephalartos* based on easily measured life history attributes. Some of the analyses indicated that additional subgroups may be substantiated. The results also supported the hypothesis that ecological response groups are not strongly linked to phylogenetic groups. This implies that certain attributes are evolutionarily labile, such as the number of cones, and brings into question why certain traits occur together. Finally, the hypothesis that life history groupings will correspond with certain environmental variables was partially supported. These components of the results are discussed further below.

2.4.2 GROUP DISTINCTION

Response groups based on key life history traits were identified for South African *Encephalartos* species using a number of statistical measures. Four core groups can be identified (Table 3) with a number of subgroups possible. Groups 1 and 4 are clear and coherent, each consisting of species with notable within-group similarity and clear differentiation from species in other groups. Group 1contains six species, including *E. villosus*, and consists of single-stemmed, subterranean species which produce single cones at the shortest coning interval of between one and three years. In contrast, Group 4 contains four species, including *E. cycadifolius*, and has multiple, dwarf arborescent stems that form large clusters. Furthermore, Group 4 species typically produce one cone at the longest coning interval of between six and eight years. Group 1 and 4 are consistent with two of Donaldson's (1995) preliminary groupings, Type 4 (Reproducers) and Type 1 (persisters) respectively. Species within these two groups can easily be identified on the basis of their habit and the number of stems without the need for extensive evaluation.

The distinction between the species forming Groups 2 and 3 are less obvious, but the division between these Groups is statistically justified based on a sufficient dissimilarity distance within the cluster analyses and support from the PCA. Species within both groups are tall with several to multiple stems. The distinction between these groups is likely due to species within Group 2 being slightly shorter, having more stems and less cone and seed production than the majority of species in Group 3. This could suggest less recruitment in Group 2 species which would link this Group to the Type 2 persister/reproducers proposed by Donaldson (1995).

A number of subgroups and outlier species are evident within Groups 2 and 3. These cannot be considered as standalone groups because the cluster distances between the subgroups are not sufficient to warrant independence. However, it is useful to consider the largest group in more manageable subunits as well as highlight species that will need individual consideration in predictive models and management frameworks. It should also be noted that some of the life history traits used to classify the species, such as the number of seeds produced every ten years and the coning interval, are not straightforward measurements. Due to the rarity, slow growth and infrequent, often unpredictable coning behaviour of most cycad species (Grobbelaar, 2004), these measurements may have errors which contribute to the disparity within and between species of Groups 2 and 3.

Group 3 is the largest derived group consisting of 18 species. Both cluster analyses recognize three subgroups within this group (Table 3). A possible reason for the separation is that subgroup a) contains the tallest species and subgroup b) contains species which produce relatively fewer seeds than subgroup c). Two species, namely, *E. friderici-guilielmi* and *E. ghellinckii*, do not correspond to one subgroup and should be considered separately. *Encephalartos transvenosus* is the tallest species, reaching up to 12 meters in height, whereas the next tallest species include *E. paucidentatus* and *E. natalensis* which reach a comparatively low height of 6 meters. This indicates why *E. transvenosus* was identified as an outlier and additionally explains why this species was placed into subgroup a) with the tallest species according to the average linkage method. Even so, I would suggest that *E. transvenosus* is considered individually.

Similarly in Group 2, there is evidence that *E. laevifolius* and *E. middelburgensis* are dissimilar to the rest of the species in Group 2. These species were likely placed into Group 2 due to their number of stems and placed as outliers because they produce more cones, and therefore also more seeds, than the other species in Group 2. It is also important to highlight that all the members of Group 2 are very threatened species (IUCN, 2010a) due to historically small populations as well as the impact of illegal collection and habitat loss (Golding & Hurter, 2003; da Silva *et al*., 2012). *Encephalartos* *hirsutus* has only one plant left in the wild (Government Gazette, 2013) and *E. inopinus* is recently thought to be extinct in the wild (Government Gazette, 2013). This implies that documented life history attribute parameters may not create an accurate profile of the species owing to the lack of sufficient and reliable field measurements for enough plants, and for plants in healthy, natural populations. Group 2 also includes all the detected outliers apart from *E. transvenosus*. This should be considered before regarding Group 2 as coherent for predictive and managerial frameworks.

2.4.3 PHYLOGENETIC SIGNAL IN THE LIFE HISTORY TYPES

An important consideration when deriving groups of species based on similar traits is the phylogenetic relationships between those species. Evolutionary relationships can indicate which traits evolve at multiple points in evolutionary history (i.e. are evolutionary labile) and which traits have a single origin. The results show that the derived groups are not phylogenetically constrained. All the species in Group 1 have a common ancestor, confining all the South African subterranean, single stemmed species to one clade. However, this clade also includes species from Mozambique and Zimbabwe, such as *E. munchii* and *E. concinnus* respectively, which were not included in this analysis, as well as *E. ferox*. Contrary to the life history of Group 1 species, some of these species are arborescent indicating that having multiple stems is an evolutionary labile trait, whilst having single stems may not be. *Encephalartos ferox* is also arborescent and can be considered a morphologically and environmentally distinct species and often an anomaly in phylogenetic studies (Rousseau *et al*., 2015). This species is found growing on stabilized sand dunes close to the beach in Mozambique and KwaZulu Natal and produces a vibrant salmon-orange cone (Grobbelaar, 2004).

It is evident that species of Group 2, 3 and 4 are completely spread out over the whole phylogeny. A small but distinct clade represented on the phylogeny (*E. lanatus, E. laevifolius, E. humilis, E. ghellinckii, E. cycadifolius* and *E. friderici-guilielmi*) contains life history types from Groups 2, 3 and 4. All these species occur in grasslands at cool and high elevations with snow or frost and share attributes of narrow leaflets and hairy cones (Vorster, 2004). This highlights that different life history properties can emerge even when species evolve under apparently similar environmental conditions from a common ancestor.

2.4.4 ASSOCIATION OF GROUPS WITH THE ENVIRONMENT

In present-day landscapes, the changes in species abundance and occurrence require an understanding of plant-environment relationships (Kolb & Diekmann, 2005). An obvious consequence of grouping species based on their life history attributes involves an investigation into the key drivers which influence their development. The environment plays a significant role in shaping plant communities through the ecological responses of associated species. Such responses in turn are influenced by the species' life history attributes (Lavorel & Garnier, 2002). It is interesting, therefore, to investigate how different life history groups within the South African and Swaziland cycads are associated with the main environmental variables over their range, particularly since *Encephalartos* has the largest diversity of life history strategies (Raimondo & Donaldson, 2003). In other words, how tightly coupled are life history strategies in *Encephalartos* with the environment and is it possible that different temperature, rainfall or fire regimes favour one life history strategy over another?

Small energy reserves associated with small, single stems (Group 1) and frequent coning would suggest a life history type that has high reproduction and rapid transition to a reproductive adult stage. This can be likened to r-selected (Stearns, 1977) or obligate reseeding (Altwegg *et al.,* 2015) species. Plants that cone less and invest more in stems and suckering (Group 4) are expected to have a greater investment in the persistence of individuals which is similar to the expectations for K-selected (Stearns, 1977) or resprouting (Altwegg *et al.,* 2015) species. It is necessary to test the population stage structure of these species' populations to see what survivorship pattern is expressed for each species and group and deduce if a survivorship framework exists for cycad life history groupings.

If the prediction of high reproduction via seeds is true for species with small energy reserves, we would expect Group 1 species to evolve under stable conditions that consistently favour seedling survival such as high mean annual precipitation and a low coefficient of variation for annual rainfall. This is based on the fact that increased availability of water in the form of rainfall favours seed germination and seedling establishment (López-Gallego, 2014). Moreover, the degree of inter-annual variation in rainfall indicates the consistency and predictability of precipitation in an area (Chandler & Wheater, 2002). Less variation indicates a more stable and predictable rainfall regime with higher and more consistent water availability. In stable, predictable environments that favour seed germination and seedling establishment, a high moisture index where rainfall demands are met, would be expected. Group 1 species do not have resource-requiring insurance in the form of vegetative backup should seed desiccation or seedling mortality occur from frost or heat stress (Pérez-Harguindeguy *et al*., 2013). Therefore, it is expected that Group 1 species would also occur within a relatively narrow temperature range.

The results show that there were no significant differences between the climatic means of Group 1 with any of the other groups. This is likely due to the fact that Groups 2 and 3 contain more species and have a wider range of patterns which overlap with the patterns represented by Group 1. The ANOVAs do not account for the smaller range of the species in Group 1. Additionally, the climatic variables were only tested for the South African species and Group 1 contains both of the Swaziland species, *E. umbeluziensis* and *E. aplanatus*. Therefore, the sample size was quite small with only four species accounted for. So despite no significance, trends were observed that supported the predictions for species with high reproduction via seeds. The habitats of Group 1 species had the highest average minimum temperature suggesting slightly less extreme environments without snow or frost. As predicted, they also had the highest moisture index, a very narrow range of maximum temperatures, a generally high mean annual precipitation, as well as a low rainfall coefficient of variation.

In contrast with Group 1, Group 4 species show a substantial investment in vegetative structures with less emphasis on reproduction via seeds. We would expect species in Group 4 to occur in areas with a high rainfall coefficient of variation and low mean annual precipitation. Species under these conditions are expected to rarely produce cones and seeds, waiting instead for rare favourable conditions for seedling establishment (Stöcklin & Bäumler, 1996). These species would invest in adult survival and persistence due to the high degree of environmental variability where they occur. This is in agreement with Bond (1989) who stated that species with a lower competitive ability are often found in less hospitable habitats as they usually have a higher tolerance to wind, drought and frost. This is especially true of gymnosperms which are poor seedling and juvenile competitors yet superior adult competitors. The moisture index and mean annual precipitation were generally lower for species in Group 4 and were significantly lower than species in Group 3. The variation in annual rainfall was significantly higher in Group 4 species than Group 3. The climatic ranges were very small for this group and correspond with conditions of variable and low rainfall. This group had the highest average rainfall variation and the lowest average rainfall and moisture index. This implies a less stable and more extreme environment where conditions for recruitment are less suitable.

The contrasting climatic trends of Group 1 and Group 4 raises questions about why species in these groups only produce one cone each despite the ability to produce multiple cones being an evolutionary labile trait. Group 1 species appear to allocate few resources to vegetative structures and therefore cannot store reserves in anticipation of a future reproductive event. Considering their more stable environments, which suggest that conditions are usually good for germination and growth, they should cone as soon as they have sufficient resources to do so. In *Encephalartos,* which typically have large cones (Goode, 2001), this may result in consistent production of a single cone. In contrast, species in Group 4 appear to allocate most of their resources to vegetative growth in the form of multiple stems. The more variable and extreme environments in which they occur suggests that seed production and recruitment are more high risk investments that take place sporadically. The presence of multiple dwarf stems suggests that they produce many terminal points for producing a single cone when suitable conditions do occur. Species in Group 2 and 3 have a very large range for each climatic variable which generally overlap with the other groups, so no explicit pattern can be deduced from the results for these two groups. They appear to be more flexible in terms of their investment in cones versus vegetative growth.

In addition to the climatic variables, the fire return frequency was assessed between Groups. Fire is considered an important factor in a number of cycad species where it is thought to stimulate cone-production (Ornduff, 1991a). Therefore fire could result in higher recruitment as well as high mortality of seedlings that are not yet established and able to withstand being burnt (Watkinson & Powell, 1997; Pérez-Farrera *et al*., 2006). The results show that all the groups contain species which inhabit fire-prone environments but the same groups can also contain species where fire is a rare occurrence. For example, several Group 1 species (e.g. *E. aplanatus, E. umbeluziensis, E. villosus*) inhabit forest areas or woodlands where fires are rare (Forsyth *et al.,* 2010). The rest of the Group 1 species inhabit areas with a relatively short fire return frequency of 1 – 9 years in savanna and grassland areas. Similarly, several species making up Group 4 occur in environments with fire return frequencies between 10 and over 20 years, but two occur in thicket vegetation with little or no fire (*E. horridus* and *E. trispinosus*).

Species in Groups 2 and 3 occur across the savanna, thicket, grassland, forest and Nama Karoo biomes. No pattern in terms of fire return intervals was observed. The species placed in the clade by Yessoufou et al (2014), containing *E. friderici-guilielmi, E. lanatus, E. humilis, E. laevifolius, E. ghellinckii,* and *E. cycadifolius*, all occur in high altitude grasslands with about the same fire return interval, yet these species are split between three of the history groups. This indicates that none of the life history response groups are associated with particular fire return cycles.

2.4.5 CONCLUSION

Forming life history groups allows us to reduce the complexity of a system and extract recurrent patterns that can aid in predicting species' responses to disturbance. Four distinct life history groups were defined for South African *Encephalartos* species based on their key life history traits. These groups were not phylogenetically constrained and partially corresponded to their associated environmental variables. Groups 1 and 4 are the most robust and reliable groups made up of species with an easily recognizable life history. Caution should be taken with generalisations for Group 2 due to outliers and rare species. Species in Groups 2 and 3 represent a variety of growth forms and coning behaviours and seem to allow these species to occupy many different habitats and to respond to changing conditions. They may therefore require a more autecological approach to determine appropriate management strategies. Future studies could include new traits such as time to- and size at- maturity that could possibly better characterize species within Groups 2 and 3. Additionally, it may be valuable to develop a continuum of life history strategies rather than defined group boundaries to better interpret environmental associations and phylogenetic distances. It may also be valuable to conduct further multivariate analyses to better view the association between life history and environmental effects. This could be more valuable than using ANOVA to identify Group differences and can aid in better group identification. However, the aim of this study was to determine if life history traits alone could form the basis for grouping species. For the purpose of this study, further investigation into the consequences of life history types and possible emergent properties is needed, specifically the assessment of population stage structure. These are explored in the following chapter.

CHAPTER 3: THE POPULATION STRUCTURE AND SURVIVORSHIP OF SOUTH AFRICAN CYCADS AS AN EMERGENT PROPERTY OF THEIR LIFE HISTORY TRAITS

3.1 INTRODUCTION

3.1.1 POPULATION DEMOGRAPHY IN CONTEXT

Population demography is the study of populations and how their size, structure and distribution is affected by age- and size-specific variation in fecundity, migration and mortality, ultimately affecting variation in fitness (Stearns, 1992). Classical population demography was developed as a means to predict population growth (Stearns, 1992) by measuring, describing and explaining changes in population numbers (Harper & White, 1974). The demographic characteristics commonly used are population structure, growth patterns, age and fecundity, density and spatial distributions (Harper and White, 1974).

Population demography is expected to be strongly linked with life history traits, as both ultimately reflect the strength of natural selection on particular traits under different conditions (Stearns, 1992). If life history traits are fixed, species-wide characteristics, then they may result in predictable demographic responses under particular conditions. In this sense, demographic patterns may be an emergent property of the suite of life history traits (Price, 1994; De Roos *et al.*, 2003; Violle *et al.*, 2007; Adler *et al.*, 2014). For example, May (1976) discovered that chaotic behaviour in populations is not necessarily an environmentally driven fluctuation, but could be an intrinsic property arising from the set of species traits. If this is true of individual species, then groups of species that share the same suites of traits may be expected to share the same intrinsic properties and exhibit similar demographic responses. Understanding how life history traits affect population demographics is therefore an extension of the analyses undertaken in Chapter 2.

Although demography encompasses measures of birth, death and migration, one of the common starting points for understanding population demography is the study of population structure (Harper & White, 1974; Bongers, 1988; Franco & Silvertown, 1996;

Pérez-Farrera *et al.*, 2006; Jones *et al.,* 2014; Borsboom *et al.*, 2015). Typically, this would involve the delimitation of different age classes and then analysing populations by studying the relative proportion of the population in each age class. In many studies it is not possible to assign individuals to exact ages classes and this is particularly true for plants where age-specific markers may not be available (Raimondo & Donaldson, 2003; Borsboom *et al.*, 2015; Pulido *et al.*, 2015). In this case, population studies may focus on developmental stages rather than age classes. Stage based analysis and modelling are commonly used in population studies (Raimondo & Donaldson, 2003; Octavio-Aguilar *et al.*, 2008).

Apart from understanding the fundamental biology of different plants, these demographic dynamics have been useful in assessing the effect of habitat fragmentation (López-Gallego *et al.*, 2008; Octavio-Aguilar *et al.,* 2008), disturbance (Pérez-Farrera *et al.*, 2006), leaf longevity (Clark & Clark, 1992), predator defence (Cressler *et al.,* 2010) and trade-offs between recruitment and mortality (Forbis & Doak, 2004). Investigations into population stage structure and survivorship can also aid in the identification of the life history stages that contribute the most to population growth and allow for conservation management to target these stages (Shemske *et al.*, 1994; Negrón-Ortiz *et al.*, 1996; Octavio-Aguilar *et al.*, 2008).

3.1.2 POPULATION STAGE STRUCTURE AND SURVIVORSHIP OF CYCADS

There are a number of general population studies on assorted cycad species (Ornduff 1991a; Ornduff 1991b; Negrón-Ortiz *et al.*, 1996; Watkinson & Powell, 1997; Negrón-Ortiz & Gorchov, 2000; Pérez-Farrera *et al.*, 2000; Pérez-Farrera & Vovides, 2004; Pérez-Farrera *et al.*, 2006; López-Gallego, 2008; Octavio-Aquilar *et al.*, 2008; López-Gallego & O' Neil, 2010; López-Gallego, 2013; Borsboom *et al.*, 2015; Pulido *et al.*, 2015). Amongst other parameters, all of these studies investigate the stage structure of different populations and refer to their survivorship patterns. A population stage structure is often used when it is not possible to measure the exact age structure and typically divides the population into classes based on size and reproduction, such as the proportion of reproductive adults versus non-reproductive individuals (Gatsuk *et al.*, 1980). Survivorship refers to the patterns of mortality in the different stage classes

(Pacala & Silander, 1983) and is usually portrayed by a survivorship curve summarizing the information from a life table (Harper & White, 1974).

Studies of population structure and survivorship in cycads have highlighted differences between species indicating a lack of genus-specific patterns. López-Gallego (2014) found that seed germination and seeding establishment greatly affected population fitness in *Zamia* species as selection through mortality was most prevalent during these stages. Negrón-Ortiz and O'Neil (2009) investigated the life history stages of *Zamia amblyphyllidia* over 3 years in Puerto Rico and quantified the patterns of survivorship and fecundity characterizing each stage. In contrast to López-Gallego (2014), they found a high sum of elasticity for survival and a low sum of elasticity for growth and fecundity which indicates that the population growth rate is predominantly dependent on adult survival rather than growth and fecundity. Ultimately both studies emphasized the importance of conserving adult plants as even with low incidences of coning, low fecundity and seedling survival, population growth would decline extremely slowly and only occasional episodes of coning would be adequate for population persistence (Negrón-Ortiz *et al*., 1996). A further number of cycad studies agreed with other long-lived plant studies (Silvertown *et al*., 1995), showing that the persistence of reproductive adults is crucial as adults are the most important life stage for population survival (Valverde *et al*., 2004; Pérez-Farrera *et al*., 2006; Octavio-Aguilar *et al*., 2008).

Population structure and survivorship has been analysed and represented in a number of ways. According to Deevey's (1947) study on animal populations, three survivorship curves exist with respect to age distribution. Type I is a negatively skewed rectangular distribution which characterizes species where individuals are born at the same time, have a similar life span and die more or less at the same time. Type II is a diagonal distribution characteristic of species with a constant rate of mortality where no specific age has a higher tendency of dying than another. Type III is a positively skewed rectangular distribution (reverse J-curve) characteristic of species with very high mortality in early life, but high life expectancy for individuals which have survived to advanced ages. A few cycad studies have referred to Deevey's (1947) survivorship curves and suggested type III survival curves for Mexican cycad species such as *Ceratozamia matudai* (Pérez-Farrera *et al*., 2000; Pérez- Farrera & Vovides, 2004), and

Dioon edule (Octavio-Aguilar *et al*., 2008). This implies high seedling and juvenile mortality with persistence mostly restricted to the adult life history stage

A classification of different types of population structure by Bongers *et al.* (1988) has also been useful for cycad studies involving stage structure analyses. Bongers *et al*. (1988) evaluated the population structure of 31 rainforest plant species in Mexico and derived three patterns of recruitment that distinguish different population structure: 1) Continuously high recruitment, 2) discontinuously high recruitment and 3) continuously low recruitment . Pérez-Farrera *et al*. (2006) reported that the population structure of *Ceratozamia mirandae* in Mexico was consistent with Bongers (1988) type I structure with a high number of seedlings and juveniles but a low frequency of adults (continuously high recruitment). A diversity of factors can influence plant mortality schedules and so far no explicit pattern has been demonstrated for cycads (Octavio-Aguilar *et al*., 2008).

Very few population studies have been undertaken on *Encephalartos* species and those that have been done have only focused on species in South Africa. da Silva *et al*. (2011) focused on the population genetics of *E. latifrons*, Raimondo and Donaldson (2003) investigated the effect of harvesting strategies on two contrasting life history types and Donaldson (1995) theorized a classification of South African *Encephalartos* to ascribe population structure predictions onto different life history types.

Due to the diversity of life history types of South African *Encephalartos* species, investigating the population structure and survivorship of these species may indicate if certain patterns are emergent properties of life history types. Predictive ecological and managerial frameworks could be developed if predictable patterns are evident in cycad species with particular suites of life history traits. Specifically, I tried to establish if groups of species based on life history traits (Chapter 2) exhibited similar population structure and survivorship. The focus was on determining whether population structure was unique to each population or whether there were consistent patterns within species and within groups sharing key life history traits.

3.1.4 FACTORS INFLUENCING POPULATION STAGE STRUCTURE

The stage structure of a population can be influenced by any changes in the recruitment, growth and survival rates of the plants in the population (López-Gallego, 2008). If the life history traits are fixed, then the changes in growth and survival may be predictable under different environmental conditions. However, environmental differences can also cause physiological and morphological changes in plant life histories (Makana & Thomas, 2005; López-Gallego, 2008). Studies using age stage transition matrices have found that the population dynamics are determined by life history characteristics in combination with abiotic and biotic environmental variation (Valverde *et al*., 2004; Pérez-Farrera *et al*., 2006; Octavio-Aguilar *et al*., 2008). The influence of climatic variables on the derived groups from Chapter 2 should therefore be considered in conjunction with the life history type when assessing population structure.

The dynamics of populations can vary through time and studies investigating the stage structure of populations are helpful to understand the selection of different life histories as well as to identify the magnitude of disturbances (Octavio-Aguilar *et al*., 2008). Here, the demographic information obtained from the selected South African *Encephalartos* species was evaluated not only to measure and describe the different populations, but to compare whether or not species within the same life history group displayed a similar population stage structure. If the stage structure is similar within a life history type, then the demography and environmental responses of hard-to-study species can be predicted through their life history type without requiring field-study.

The hypotheses I tested in this chapter were:

1. That the population stage structure of South African *Encephalartos* species is an emergent property of their key life history traits (see Chapter 2) so that species in the same life history group will have a similar population structure.

2. That there would be discernible differences in population structure across life history groups due to major differences in life history traits affecting reproduction and persistence. This is linked to two sub-hypotheses:

- Species with single stems and little allocation towards vegetative tissue would display reverse-J type curves with a high numbers of seedlings and fewer adult plants.

- That species with many stems and high allocation to vegetative suckering would display a J-shaped curve with low numbers of seedlings and high adult persistence.

3. That groups with a strong consistency in life history traits (Groups 1 and 4) would exhibit little variation in population structure whereas groups with more variable traits (Groups 2 and 3) would also vary in population structure.

3.2 METHODS

3.2.1 STUDY SPECIES AND SITES

Data were collected from 35 populations, representing 13 species of *Encephalartos* (Table 1). These represent three sets of data.

- Data collected personally in 2014, focusing on species from the Eastern Cape Province of South Africa.
- Data obtained from a separate study of cycad populations using the same sampling protocol (D. Okubamichael & S. Jack, 2014).
- Data collected by Prof J.S. Donaldson during the period 1993-1995.

These data are from populations that have not been badly influenced by poaching.

Table 1: Summary of populations for which data were obtained that allowed an analysis of population stage structure. Data represent the number of plants measured in each population.

SPECIES	POPULATION	# Plants (2014)	# Plants (prior date)	Data Source
E. villosus	Umtiza Forest	99	51 (1993)	Own data (2014) Donaldson (1993)
E. villosus	Ocean View	151	65 (1993)	Own data (2014) Donaldson (1993)

E. caffer	Brooklands	240	-	Own data
E. caffer	GlenView	-	112 (1994)	Donaldson
E. middelburgensis	Middelburg	63	-	Okubamichael & Jack
E. lehmannii	Knoetze	54	-	Okubamichael & Jack
E. lehmannii	Weltevrede	26	-	Okubamichael & Jack
E. lehmannii	Jansenville	29	31 (1991)	Okubamichael & Jack (2014) Donaldson (1991)
E. lehmannii	Somerset East	34	-	Okubamichael & Jack
E. friderici-guilielmi	Middeldrift	189	-	Own data
E. friderici-guilielmi	Fincham's Nek	54	-	Okubamichael & Jack
E. friderici-guilielmi	Cathcart	120	-	Okubamichael & Jack
E. friderici-guilielmi	Thomas River	56	-	Okubamichael & Jack
E. natalensis	Hilton	84	-	Okubamichael & Jack
E. natalensis	Hopewell	112	-	Okubamichael & Jack
E. longifolius	Joubertina	53	61 (1993)	Okubamichael & Jack (2014) Donaldson (1993)
E. longifolius	Kritplaas	98	20 (1993)	Okubamichael & Jack (2014) Donaldson (1993)
E. longifolius	Van Stadens	119	58 (1993)	Okubamichael & Jack (2014) Donaldson (1993)
E. longifolius	Waterkloof	61	-	Okubamichael & Jack
E. longifolius	Saagkuilen	15	-	Okubamichael & Jack
E. longifolius	Alicedale	16	-	Okubamichael & Jack
E. lanatus	Botshabelo	30	-	Okubamichael & Jack
E. ferox	Kosi bay	25	-	Okubamichael & Jack
E. transvenosus	Modjadji	24	-	Okubamichael & Jack
E. horridus	Springs	46	46 (1994)	Okubamichael & Jack (2014) Donaldson (1994)
E. trispinosus	Helspoort	-	77 (1993)	Donaldson
E. trispinosus	Kenton-on-Sea	-	56 (1990)	Donaldson
E. cycadifolius	Venn Grove – East facing	122	-	Own data
E. cycadifolius	Venn Grove – West facing	52	38 (1993)	Own data (2014) Donaldson (1993)

GPS coordinates were recorded for each individual plant that was measured, but these are left out for reasons of security. The data obtained were from the healthiest populations available for sampling.

3.2.2 DATA COLLECTION PROTOCOL

The protocols outlined below apply to all samples in Table 1 except those collected by Donaldson (Table 1). The latter sample protocol used similar plots or transects but did not include all the plant measurements listed below. What is useful about the data collected by Donaldson is that he excavated around the stem to measure the diameter of subterranean stems in E*. villosus* and *E. caffer*. This made it possible to test whether measures such as leaf length could be used to estimate stage class. In some species there is a strong correlation between stem diameter and leaf length (Raimondo & Donaldson, 2003).

Sample area selection

At each population, 100 x 100 m plots were selected and all the cycads within the plot were measured. Using a plot ensured that an accurate profile was sampled with no selection bias. If there was a difficult environmental gradient, a 100 m line transect was used instead of a plot. The number of plots varied, with the aim being to sample a minimum of 50 individual plants per site, ideally 100.

Plant locality details

The GPS coordinates and altitude of each plant was recorded and a photograph taken with a ranging rod held next to the base of the plant. The degree of slope was recorded with an inclinometer. Rockiness was evaluated on a scale of 1-5, with 1 indicating that the base was in soil and 5 indicating that the base was in rock.

Plant measurements

The number of stems was counted and the height and diameter of each stem recorded with a semi-flexible metal tape measure to the nearest 0.5 cm. The canopy was measured as the distance from the longest leaf on one side to the longest leaf on the opposite side (cm). The number of leaves was counted and the maximum leaf length recorded to the nearest 0.5 cm. The stem and leaf health were assessed on a grading of

1- 5, with 1 being dead and 5 being very healthy. If there were any cones present, the gender was recorded as well as the number of cones and whether the cones were fresh or old.

3.2.5 STATISTICAL ANALYSES

3.2.5.1 DEFINING SPECIES-SPECIFIC CRITERIA TO DIFFERENTIATE STAGE CLASSES

It was necessary to develop a protocol for assigning individuals in each population to different stage classes. Ornduff (1991a) used leaf number or stem height to indicate size class. This has been successful in angiosperms (Werner & Caswell, 1977) as well as in some *Zamia* (Negrón-Ortiz *et al*., 1996; López-Gallego, 2008) and *Ceratozamia* (Pérez-Farrera & Vovides, 2004; Pérez-Farrera *et al*., 2006; Pulido *et al*., 2015) species. The production of cones is the most reliable indicator for sexually mature adults (Borsboom *et al*., 2015), and size of coning individuals has been used to determine adult stage classes (Ornduff, 1989). Not all adult cycads cone during a reproductive season, so mature plants cannot be identified based only on in-field coning evidence (Ornduff, 1991a;b). To identify adult plants of *Macrozamia riedlei*, Ornduff (1991a) used the number of leaves so that the coning plant with the fewest leaves was used as a reference point for adulthood. Thus, every individual with an equal or higher number of leaves was considered sexually mature.

Here I used a similar approach. Different characteristics were plotted for each species (with data from the most detailed, healthy and largest site) in order to differentiate stage classes (Appendix 3). It was anticipated that different criteria would need to be used for species with subterranean stems, arborescent stems or multiple short stems. As a result, analyses included: the relationship between stem diameter and/or stem height to the number of leaves and/or leaf length; the relationship between the number of stems to stem height and/or diameter and/or leaf length. Evidence of coning was overlaid on the scatter plot to indicate the point where plants would be assigned to the adult stage. The scatter plots for each species were then evaluated to determine the criteria that could be used to differentiate five age classes within each species. For this study, plants were assigned to one of five stage classes: S1 (seedling stage 1), S2

(Seedling stage 2), J (Juvenile), A1 (Adult stage 1) and A2 (Adult stage 2). Other studies (e.g. Pulido *et al*., 2015) have used more stage classes, particularly when the intention has been to track transitions between stage classes. For this study, fewer stage classes were used to enable a comparison between species with different life history traits. It was deemed necessary to separate S1 and S2 stages because in many cases there is high mortality of young single leaved seedlings. Similarly, it was necessary to distinguish between young adults, often with relatively low reproductive output, from older more established adults. An adult was defined as a reproductive individual, i.e. a plant that can produce cones. Stage 2 adults were somewhat arbitrarily assigned to the larger size classes in the adult stage. The age classes were assessed by taking note of asymptotes, a step in the data points and the earliest coning plants and their corresponding measurements (Appendix 3).

3.2.5.2 STAGE STRUCTURE GRAPHS AND CHI-SQUARED ANALYSES

Once the stage class criteria were developed for each species, each individual plant was assigned to a stage class. A total count of individuals in each stage class was recorded per site and a bar plot constructed using the package “ggplot2” (Wickham, 2009). The three populations of *E. cycadifolius* sampled in 2014 were spatially segregated, each one with different ecological conditions such as aspect and burn cycles. In this instance, the standard deviation between populations was included on the stage class columns. The same was done for the three segregated populations of *E. friderici-guilielmi* sampled at Middeldrift Farm in 2014. The skewness and kurtosis for each stage-structure barplot was obtained using the package, “moments”(Komsta & Novomestky, 2015) and presented in tables to represent each group.

Differences in the number of juveniles (J) and adults (A1 and A2) were assessed with Chi-squared tests (Pearson, 1900) manually calculated using Microsoft Excel 2007. These differences were examined for the observed stage structure (O_{ij}) for species within each group, as well as between groups and subgroups, using chi-square statistics (χ^2) with (r-1)(c-1) degrees of freedom. The expected values (E_{ij}) were calculated as: [(row sum)$_i$ × (column sum)$_j$] / *n*, the null hypothesis being $O_{ij} = E_{ij}$. Similar to a study on stage structure differences in the Mexican cycad, *Ceratozamia fuscoviridis* (Pulido *et al*., 2015), the significant differences were examined using Haberman's test of standardized residuals (Haberman, 1973). This test provided an adjusted Z-score which was represented in a contingency table with the observed and expected values and level of significance (Appendix 4, Figures 1,3,5 & 7).

Stage class categories that had significantly greater or fewer individuals were indicated with an (x) or (-) on the barplots respectively. *Encephalartos longifolius* populations from Saagkuilen and Alicedale, were excluded from the chi-squared analyses due to a small sample size. The population of *E. lehmannii* sampled at Jansenville in 2014 was also excluded because it has been impacted by poaching.

The juvenile and adult stages were chosen for analyses to give an indication of longer term trends. Seedling abundance can be influenced by one good recruitment event and only indicates a snapshot in time. However, as supplementary material, contingency tables, calculated in the same manner, were produced to show within- and between-group differences between seedlings (S1 and S2), juveniles (J) and adults (A1 and A2) (Appendix 4, Figures 2,4,6,8 & 9).

3.2.5.3 STATIC LIFE TABLES AND SURVIVORSHIP CURVES

Static life tables were constructed to assess survival rates and mortality (Begon *et al*., 1996). The total number of individuals per stage class (x) in each population was pooled to produce one life table per species, this integrated variation in the populations. Columns calculated were the number of individuals in each stage class (n_x), the proportion of surviving individuals ($l_x = n_x - n_0$), the proportion of dying individuals ($d_x = l_x - l_{x+1}$), the finite rate of mortality for each stage class ($q_x = (n_x - n_{x+1}) / n_x$) and the killing power of each stage class ($k_x = \log_{10} n_x - \log_{10} n_{x+1}$). All stage classes were included in this analysis unless they contained zeros. The life tables are presented in Appendix 5.

A survivorship curve for each species was produced using Microsoft Excel (2007). The proportions of surviving individuals (l_x) were plotted against the stage classes (x) for juveniles (J) and adults (A1 and A2).

3.3 RESULTS

3.3.1 STAGE STRUCTURE GRAPHS AND CHI-SQUARED ANALYSES

The chi-square test showed that the species stage structure was significantly different between the groups [$\chi^2(6, n = 12) = 237.238$, $p < 0.00001$] (Table 2). There was also a significant difference between the population stage structure within the sampled species of Group 1 [$\chi^2(10, n = 18) = 101.262$, $p < 0.00001$] (Figure 1) , Group 2 [$\chi^2(8, n = 15) = 44.111$, $p < 0.00001$] (Figure 2), Group 3 [$\chi^2(30, n = 48) = 387.469$, $p < 0.00001$] (Figures 3, 4 & 5) and Group 4 [$\chi^2(12, n = 21) = 148.996$, $p < 0.00001$] (Figure 6) . This indicated that a single generalized stage structure did not exist as a property of each group, although coherence of stage structure within some groups must exist due to the significant differences found between groups (Table 2).

Significantly more juveniles were present in the populations of Group 1 than expected from the average values for all species, as well as significantly fewer A2 adults (Table 2). This supports the hypothesis that Group 1 species have high levels of recruitment by seed and recurrent mortality of large plants. Conversely, there were significantly fewer juveniles than expected in Group 4 and more individuals in both adult classes (Table 2). This supports the hypothesis that Group 4 species rely predominantly on the persistence of adult plants (regeneration via suckering). There were no statistically significant differences between the observed and expected values for Group 2 or Group 3 (Table 2).

Table 2: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species between the four life history groups. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Group	Stage Class		
	J	**A1**	**A2**
Group 1	267	78	75
	(166)	(87)	(167)
	11.54**	-1.28	**-10.47****
Group 2	65	38	87
	(75)	(39)	(75)
	-1.58	-0.28	1.81
Group 3	327	153	319
	(316)	(166)	(317)
	1.11	-1.53	0.16
Group 4	46	102	228
	(149)	(78)	(149)
	-12.17**	**3.41****	**9.33****

*p < 0.05   ** p <0.01

Within Group 1, both *E. villosus* populations from 2014 had fewer A1 adults and more A2 adults than expected (Figure 1 A & C), with an increase in both adult stages in comparison with the populations sampled in 1993 (Figure 1 B & D). There appeared to be a trend within this group that if one stage class had a lower value than the expected value, at least one of the other classes had a value higher than expected, indicating intermittent but consistent recruitment events (Figure 1). However, the number of seedlings for the Umtiza Forest Reserve in 2014 was low (Figure 1A). *Encephalartos caffer* from GlenView had significantly more A1 adults than expected and showed the most symmetry between stage classes (Table 3). In addition, *E. caffer* from Brooklands was the only population with a negatively skewed distribution (Table 3), probably due to having very high numbers of S1 and S2 seedlings, suggesting recent recruitment events.

The general population structure observed for Group 1 species was that of a high juvenile (J) component with less adult plants (Figure 1). This is typical of a reverse J-shaped curve or Deevey type III curve. Although this pattern was not observed in all the populations, the emphasis on recruitment via seeds is evident.

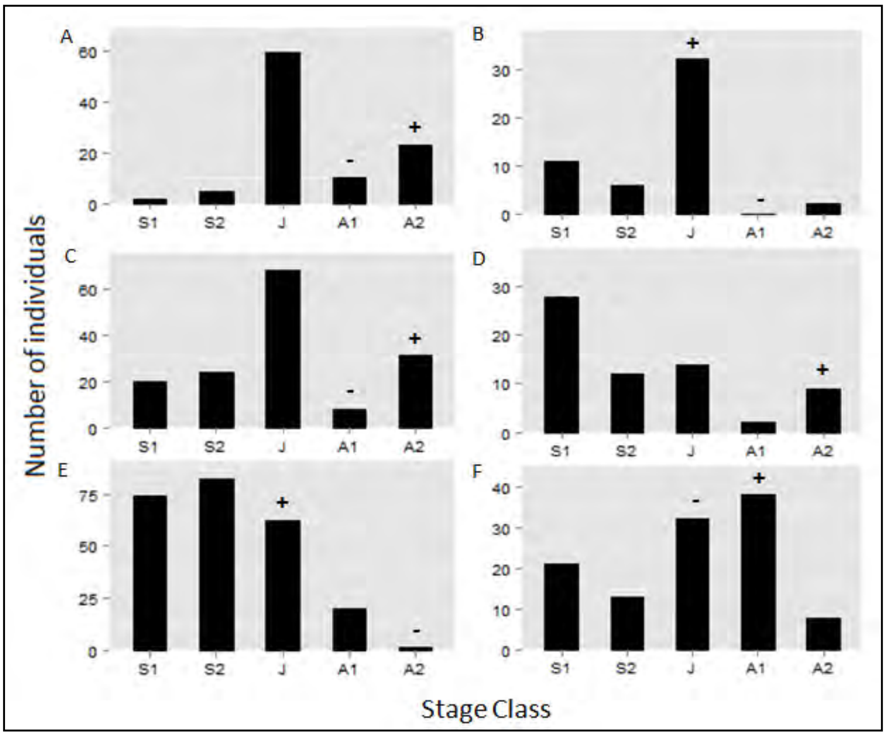

Figure 1: Stage classes of sampled *Encephalartos* species from Group 1. **A**: *E. villosus* from Umtiza Forest, 2014 **B**: *E. villosus* from Umtiza Forest, 1993 **C**: *E. villosus* from Ocean View farm, 2014 **D**: *E. villosus* from Ocean View farm, 1993 **E**: *E. caffer* from Brooklands Nature Reserve, 2014 **F**: *E. caffer* from GlenView, 1994.

Table 3: The skewness and kurtosis values for the population stage structure of *Encephalartos* species in Group 1.

Species	Population	Kurtosis	Skewness
E. villosus	Umtiza, 2014	2.653115	1.109145
E. villosus	Umtiza, 1993	2.732269	1.131545
E. villosus	Ocean View, 2014	2.693599	0.9954818
E. villosus	Ocean View, 1993	2.472678	0.6375263
E. caffer	Brooklands, 2014	1.425528	-0.3856482
E. caffer	GlenView, 1994	1.478106	0.1209484

Within group 2, *E. middelburgensis* and *E. lehmannii* from Knoetze had higher juvenile and A1 adult classes than expected (Figure 2 A & F). All the populations had a low seedling component with all *E. lehmannii* populations having a high A2 adult component (Figure 2 A - E). The *E. lehmannii* population at Jansenville had fewer adult plants than the same population in 1992 (Figure 2 D & E). This shows the effect of the poaching which is known to have occurred. However, the population had more juveniles in 2014 than in 1991, indicating a recruitment event after 1991.

In general, the survivorship pattern exhibited a J-shaped curve in half of the sampled populations (Figure 2 B, C & E) and a high juvenile component in the other half (Figure 2 A, D & F). The low number of seedlings in most of the populations (Figure 1, B – D, F) suggests that no recent recruitment events have occurred, although the high number of juveniles in some populations (A,D & F) indicate past recruitment events and therefore suggest that these populations have intermittent recruitment

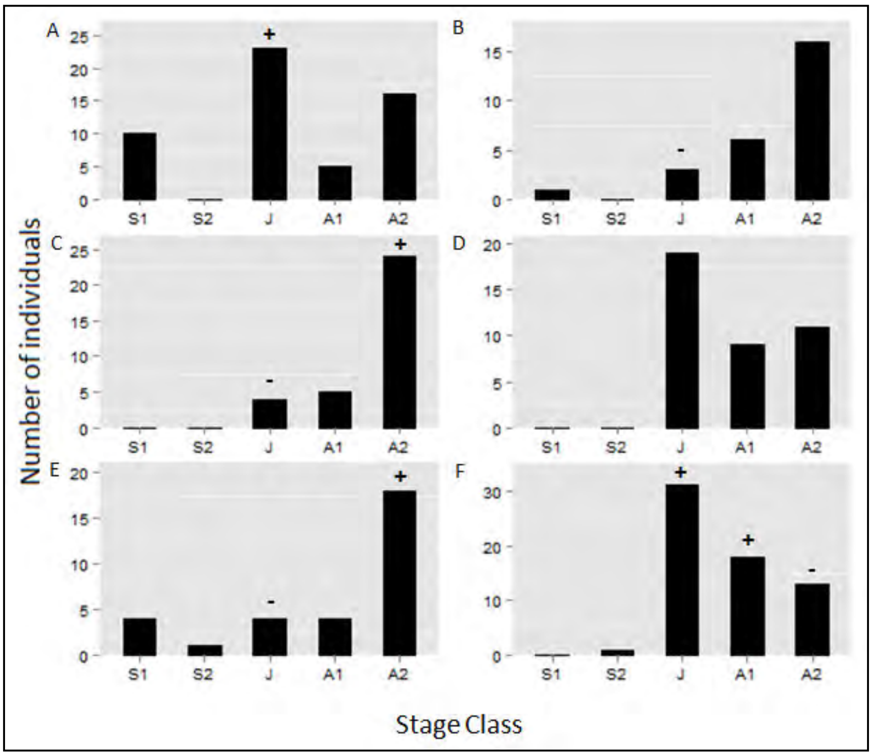

Figure 2: Stage classes of sampled *Encephalartos* species from Group 2. **A**: *E. lehmannii* from Knoetze, 2014 **B**: *E. lehmannii* from Weltevrede, 2014 **C**: *E. lehmannii* from Somerset East, 2014 **D**: *E. lehmannii* from Jansenville, 2014 **E**: *E. lehmannii* from Jansenville, 1991 **F**: *E. Middelburgensis* from Middelburg, 2014

Table 4: The skewness and kurtosis values for the population stage structure of *Encephalartos* species in Group 2.

Species	**Population**	**Kurtosis**	**Skewness**
E. lehmannii	Jansenville, 2014	1.735296	0.2633408
E. lehmannii	Jansenville, 1991	3.088109	1.352529
E. lehmannii	Knoetze, 2014	1.761333	0.1896722
E. lehmannii	Weltevrede, 2014	2.63657	1.07419
E. lehmannii	Somerset East, 2014	2.996688	1.309612
E. middelburgensis	Middelburg, 2014	1.815984	0.3716388

Within Group3, population structure differed significantly between the three subgroups and the remaining species [$\chi^2(6, n = 12) = 101.2199$, $p < 0.00001$] (Table 5). Subgroup (b) had more juveniles than expected and fewer adults, whilst Subgroup (c) and the unassigned remaining species had fewer juveniles and more adults than expected (Table 5).

Subgroup (b) is represented by populations of *E. longifolius* (Figure 3). The population sampled at Joubertina in 2014 had a high proportion of juveniles and A2 adults whereas in the same population sampled in 1993 there was a high proportion of S2 seedlings and adults. This could indicate a single recruitment event with seedlings that survived moving into the juvenile stage in the most recent population analysis (Figure 3 A & B). Some populations displayed limited survivorship to adult stages (Figure 3 D & G), which could be due to poaching of adult plants.

Both populations of *E. natalensis* displayed different dominant stage classes (Figure 4 A & B). An adult dominated population was observed for *E. lanatus* in Subgroup (c) (Figure 4C) with *E. ferox* displaying a relatively even distribution across stage classes (Figure 4D), being the only one with perfect symmetry (Table 6). *Encephalartos friderici-guilielmi* was unassigned to a subgroup and generally displayed a J-shaped curve (Figure 5 A – D). However, the population at Middeldrift was negatively skewed (Table 6). *Encephalartos transvenosus* displayed the opposite to *E. friderici-guilielmi* with a dominance of juveniles (Figure 5E).

It was evident that within Group 3, many different survivorship strategies were displayed with the emphasis on seedling recruitment versus suckering interchanged between populations. No explicit pattern can be derived for the population stage structure within this group.

Table 5: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* populations of species within Group 3's Subgroups. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Group 3 Subgroup	**Stage Class**		
	J	**A1**	**A2**
Subgroup a	55 (50) 1.10	32 (23) **2.21***	34 (48) **-2.88****
Subgroup b	159 (112) **7.17****	33 (52) **-3.65****	81 (109) **-4.26****
Subgroup c	9 (18) **-2.94****	23 (9) **5.61****	13 (18) -1.56
Unassigned	104 (147) **-6.27****	65 (69) -0.71	191 (144) **6.86****

*p < 0.05 ** p <0.01

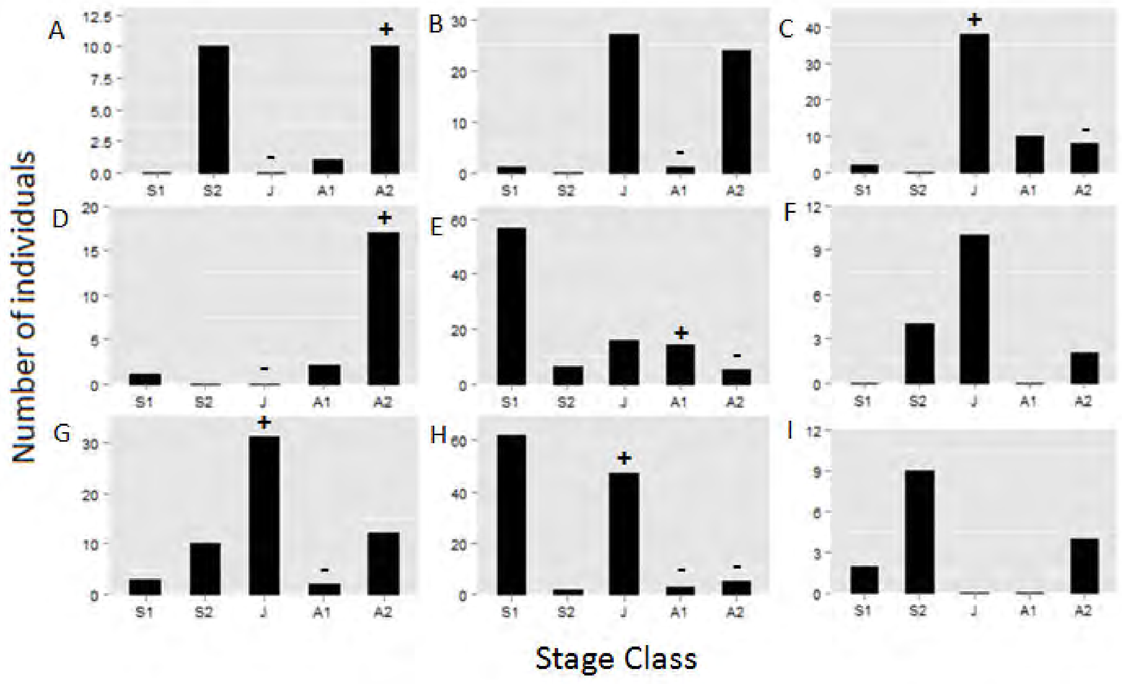

Figure 3**:** Stage classes of sampled *Encephalartos longifolius* species from subgroup b of Group 3. **A**: Sampled from Joubertina, 1993 **B** Sampled from Joubertina, 2014 **C**: Sampled from Waterkloof, 2014 **D**: Sampled from Kritplaas, 1993 **E**: Sampled from Kritplaas, 2014 **F**: Sampled from Saagkuilen, 2014 **G**: Sampled from Van Stadens farm, 1992 **H**: Sampled from Van Stadens farm, 2014 **I**: Sampled from Alicedale, 2014.

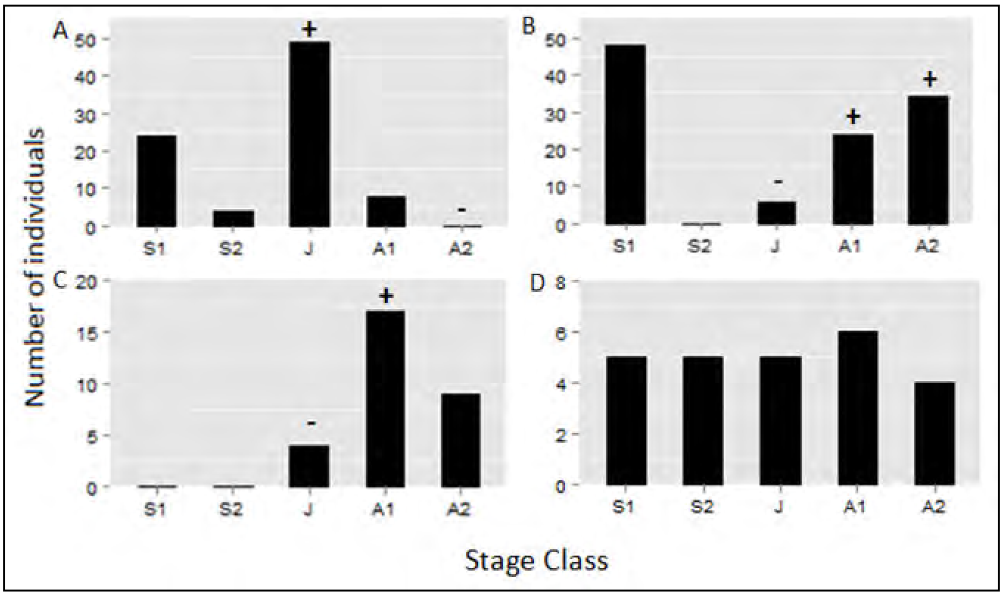

Figure 4**:** Stage classes of sampled *Encephalartos* species from subgroup a (A & B) and subgroup c (C & D) of Group 3. **A**: *E. natalensis* from Hilton, 2014; **B**: *E. natalensis* from Hopewell, 2014 **C**: *E. lanatus* from Botshabelo Village, 2014 **D**: *E. ferox* from Kosi Bay, 2014

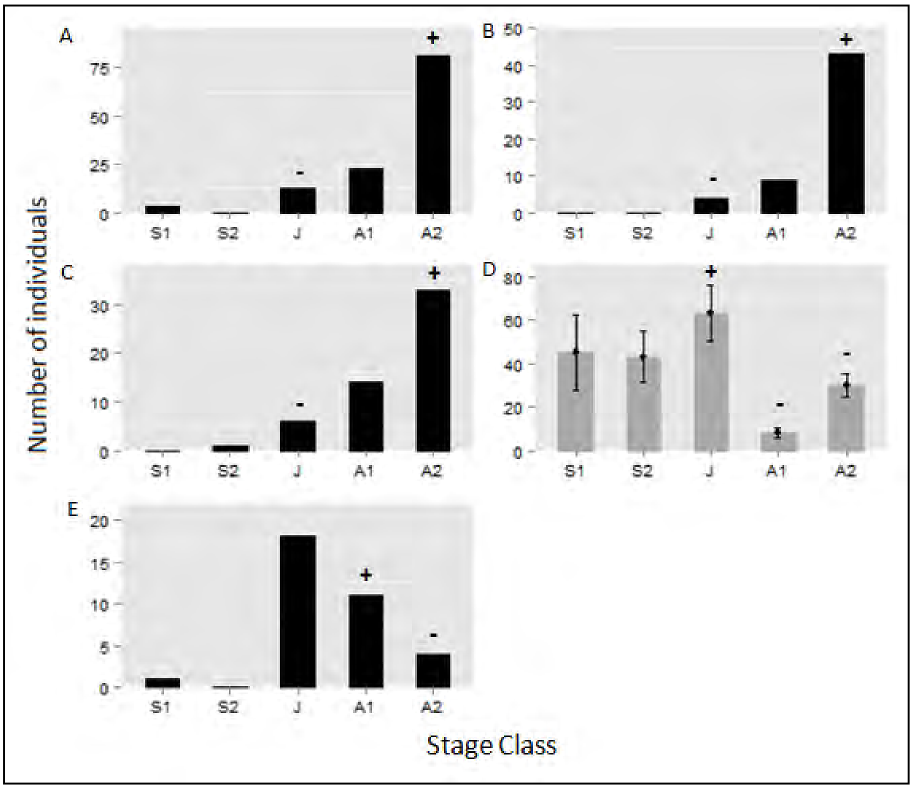

Figure 5: Stage classes of sampled *Encephalartos* species unassigned to a subgroup from Group 3. **A**: *E. friderici-guilielmi* from Cathcart, 2014 **B**: *E. friderici-guilielmi* from Thomas River, 2014 **C**: *E. friderici-guilielmi* from Fincham's Nek, 2014 **D**: *E. friderici-guilielmi* from Middeldrift, 2014 (±SD) **E:** *E. transvenosus* from Modjadji, 2014.

Table 6: The skewness and kurtosis values for the population stage structure of *Encephalartos* species in Group 3.

Species	**Population**	**Kurtosis**	**Skewness**
E. longifolius	Joubertina, 1993	1.175155	0.3906151
E. longifolius	Joubertina, 2014	1.208242	0.4239121
E. longifolius	Waterkloof, 2014	2.905167	1.235483
E. longifolius	Kritplaas, 1993	3.184776	1.452832
E. longifolius	Kritplaas, 2014	3.004894	1.315067
E. longifolius	Saagkuilen, 2014	2.327806	0.8644064
E. longifolius	Van Stadens, 1992	2.617672	1.01466
E. longifolius	Van Stadens, 2014	1.39223	0.5075533
E. longifolius	Alicedale, 2014	2.482693	0.970495
E. natalensis	Hilton, 2014	2.25053	0.8731263
E. natalensis	Hopewell, 2014	1.579052	0.09738956
E. lanatus	Botshabelo, 2014	2.041898	0.6942675
E. ferox	Kosi bay, 2014	2.5	0
E. friderici-guilielmi	Cathcart, 2014	2.881631	1.236819
E. friderici-guilielmi	Thomas River, 2014	3.038084	1.352292
E. friderici-guilielmi	Fincham’s Nek, 2014	2.439933	0.9645592
E. friderici-guilielmi	Middeldrift, 2014	2.168269	-0.3436735
E. transvenosus	Modjadji, 2014	1.818858	0.6042542

Within Group 4, *E. horridus* had fewer adult plants than expected for the populations sampled in 2014 and in 1993 (Figure 6 A & B); *E. trispinosus* had fewer juveniles and more A1 adults in both populations (Figure 6 C & D) and *E. cycadifolious* had more A2 adults than expected in the west- and east-facing populations from 2014 (Figure 6 E & F). The survivorship patterns reveal that the species within this group tend towards a J-shaped curve with a much higher proportion of adult plants than seedlings or juveniles (Figure 6). This aligns with the hypothesis that Group 4 species rely on vegetative persistence rather than regeneration through seed. Recruitment events do occur from time to time, which is evident from comparing the past and recent population samples where *E. horridus* had a higher proportion of juveniles in the recent population than from the past (Figure 6 A & B).

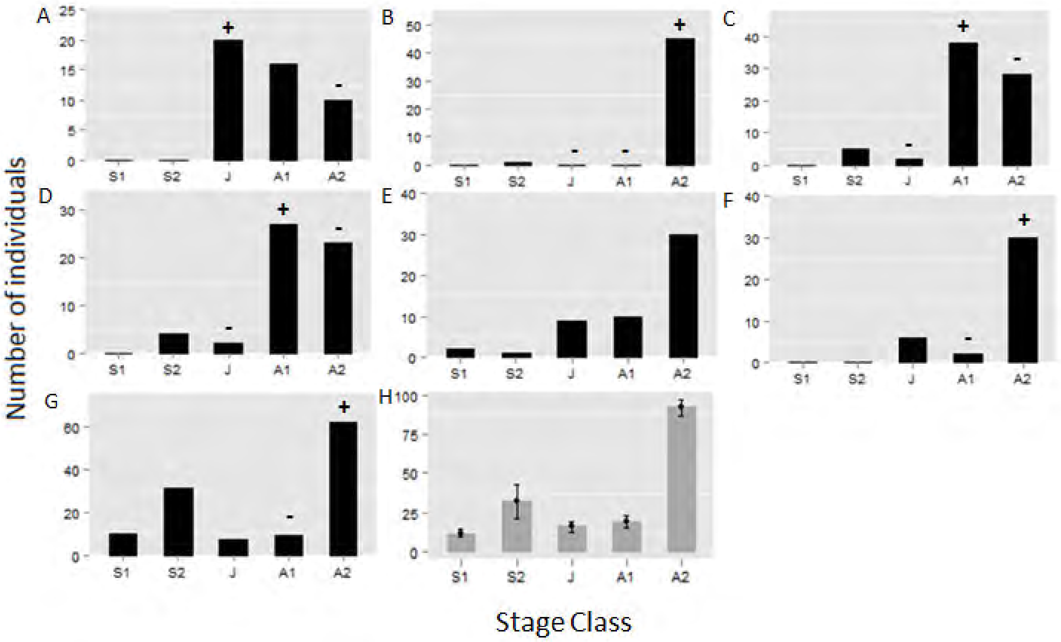

Figure 6: Stage classes of sampled *Encephalartos* species from Group 4. **A**: *E. horridus* from Springs, 2014 **B**: *E. horridus* from Springs, 1993 **C**: *E. trispinosus* from Kenton-on-Sea, 1990 **D**: *E. trispinosus* from Helspoort, 1993 **E**: *E. cycadifolius* west –facing population from Venn Grove farm, 2014 **F**: *E. cycadifolius* west-facing population from Venn Grove farm, 1993 **G**: *E. cycadifolius* east-facing population from Venn Grove Farm **H:** *E. cycadifolius* (all populations) from Venn Grove Farm (±SD).

Table 7: The skewness and kurtosis values for the population stage structure of *Encephalartos* species in Group 4.

Species	Population	Kurtosis	Skewness
E. horridus	Springs, 2014	1.357549	0.006364346
E. horridus	Springs, 1993	3.247635	1.498259
E. trispinosus	Kenton-on-sea, 1990	1.266637	0.408155
E. trispinosus	Helspoort, 1993	1.448948	0.5015587
E. cycadifolius	Venn Grove West-facing, 2014	2.697607	1.072077
E. cycadifolius	Venn Grove West-facing, 1993	3.05882	1.37005
E. cycadifolius	Venn Grove East-facing, 2014	2.365848	0.9841898
E. cycadifolius	Venn Grove all sites,2014	2.986317	1.322055

3.3.2 SURVIVORSHIP SCHEDULES DERIVED FROM THE STATIC LIFE TABLES

The static life table data (Appendix 5) provided additional information on the survival and mortality risk of different life history stages, as well as the differences in those parameters found between and within the life history response groups. Once more, Groups 1 and 4 exhibited the greatest consistency in patterns. Species in Group 1 showed a near consistent decrease in survival from the seedling to juvenile and adult stages (Appendix 5, Tables 1 & 2). However *E. villosus* displayed a reverse J-curve (Figure 7A) due to an increased proportion of A2 adult survival, whereas *E. caffer* corresponded to a Deevey type II curve (figure 7B) .These results showed that Group 1 species do not necessarily have the same survivorship pattern, but emphasize seedling recruitment with fewer adult plants.

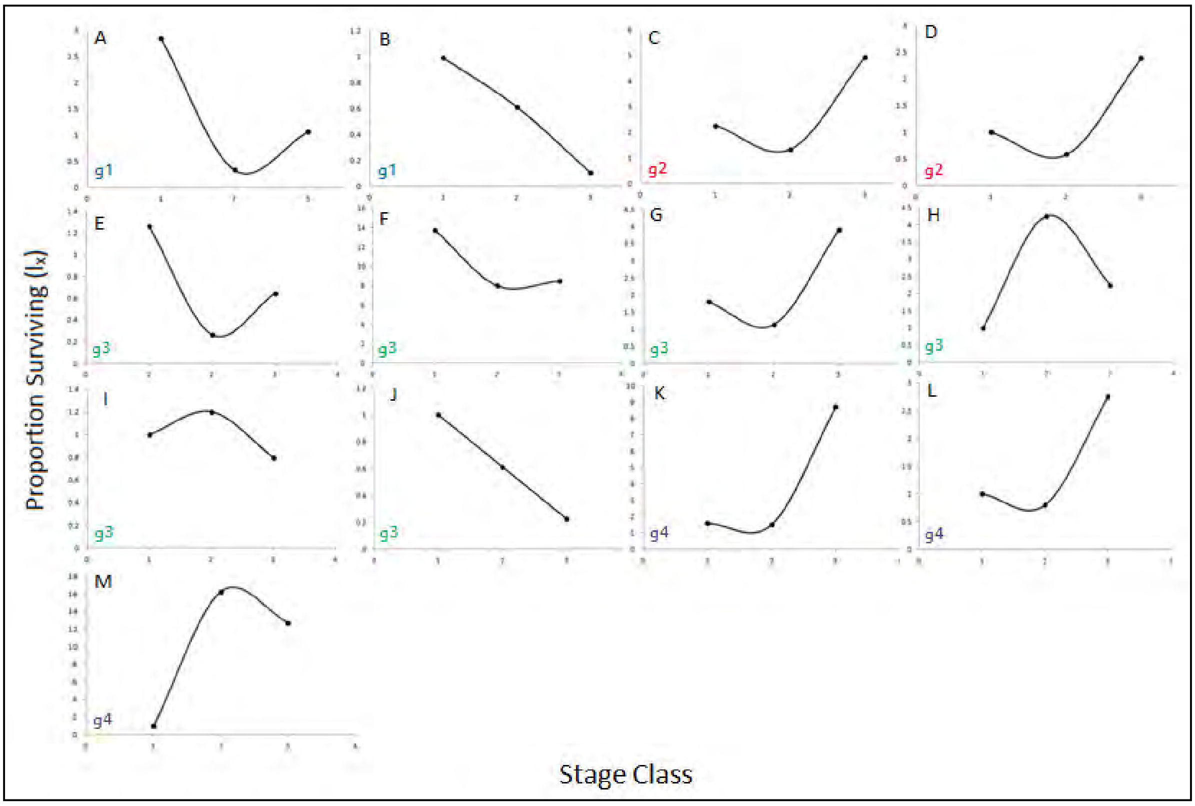

Figure 7: Survivorship curves for South African *Encephalartos* species. **A**: *E. villosus* **B**: *E. caffer* **C**: *E. lehmannii* **D**: *E. middelburgensis* **E**: *E. longifolius* **F**: *E. natalensis* **G**: *E. friderici-guilielmi* **H**: *E. lanatus* **I**: *E. ferox* **J**: *E. transvenosus* **K**: *E. cycadifolius* **L**: *E. horridus* **M**: *E. trispinosus*. Number on the X-axis refers to stage classes: 1 = Juveniles, 2 = A1 adults, 3 = A2 adults. The designation of g1-4 on each graph refers to the life history group.

Species within Group 4 all exhibited similar survivorship patterns with the highest risk of mortality in seedling and juvenile stages and a high proportion of surviving adults (Appendix 5, Tables 11 - 13). The A1 adult stage also had high vulnerability to mortality in *E. cycadifolius* and *E. horridus* despite a very large proportion of surviving A2 adults (Appendix 5, Tables 11 & 13). Both *E. cycadifolius* and *E. horridus* displayed J-shaped survivorship curves (Figure 7 K & L). Similarly, *E. trispinosus* displayed low proportions of juveniles with a concave-down curve due to some mortality of A2 adults (Figure 7M).

Similar to Group 4 species, the survivorship of both *E. lehmannii* and *E. middelburgensis* in Group 2 reflected a J-shaped curve (Figure 7 C & D), with S1 seedlings showing the largest risk of mortality (Appendix 5, Table3 & 4). This group also showed that A1 adults were vulnerable to mortality despite high proportions of A2 adults in the populations (Appendix 5, Tables 3 & 4).

Group 3 did not show consistent survivorship patterns with a reverse-J curve displayed by *E. longifolius* (Figure 7E), a J-curve displayed by *E. friderici-guilielmi* (Figure 7G), a concave-up curve displayed by *E. natalensis* (Figure 7F), a concave-down curve curve displayed by both *E. lanatus* and *E. ferox* (Figure 7 H & I) and finally a distinct Deevey type II curve displayed by *E. transvenosus* (Figure 7J). Life tables indicate the differences within this group (Appendix 5, Tables 5 - 10).

3.4 DISCUSSION

3.4.1 OVERVIEW

The aim of this chapter was to determine whether the population stage structure of South African *Encephalartos* species was a property determined by their life history types. If this was true, I expected to find (i) that species with similar life history traits would exhibit a similar population structure, (ii) that there would be discernible differences in population structure across life history groups because of major differences in reproduction and persistence, and (iii) that the greatest similarity in population structure would be found in those life history groups that had a suite of traits that were consistent across all the species in the group.

The results showed significant differences in population structure within all of the groups, most notably within Group 3. This does not appear to support the first hypothesis. However, the differences in population structure between groups were also significant and supported the second hypothesis. This suggests that, despite variation within groups, the range of population structures displayed in each group was small enough to show statistically measurable differences of population structure compared with the other groups. Finally, the data showed that there was a relatively consistent population structure within Groups 1, 2 and 4, but no consistency within Group 3. This partially supported the third hypothesis since Groups 1 and 4 contained species with the most consistent life history traits. Species in Groups 2 and 3 showed the most variation in their life history traits, yet species in Group 2 displayed consistency in their population structure. These components of the results are discussed further with additional details on the survivorship patterns between groups.

3.4.2 POPULATION STRUCTURE IN RELATION TO LIFE HISTORY TRAITS

Four response groups were identified for South African and Swaziland *Encephalartos* species based on their key life history traits (Chapter 2). The population stage structure of representative species in each group was assessed to examine whether a particular population structure was consistent for species within a group and differing for species between groups. If a distinct population stage structure can be identified as an emergent property of a life history type, autecological studies might not be essential for conservation management, since information relating to the status and ecological responses of cycad populations could be inferred from the species' group membership.

The results showed a relatively consistent population structure within Groups 1 and 4, the two life history types containing species which displayed consistent within-group suites of life history traits. The significant differences in stage structure between groups were also found between Groups 1 and 4, with Group 1 having fewer adults and more juveniles than expected and Group 4 having more adults and fewer juveniles than expected. Species in Group 1 are single-stemmed, subterranean cycads shown to occur in relatively stable and predictable environments with sufficient and consistent water availability and a mild temperature range. The general population structure of these species displayed a large proportion of seedlings and juvenile plants relative to the number of adults. This is in agreement with Raimondo and Donaldson (2003) who found a prevalence of seedlings as opposed to adults in *E. villosus* populations. The high proportion of seedlings and juveniles indicates that Group 1 species are dependent on recruitment via seeds for their population persistence and growth resembling a Bongers type I population structure characteristic of plant species with continuous recruitment. This is typical of species which do not invest in resources to resprout via vegetative suckers (Bond & Midgley, 2001) and are found in habitats optimal for germination and seedling establishment (Pérez-Farrera and Vovides , 2004; Pérez-Farrera *et al*., 2006). A Bonger's type I population structure was also reported for *Ceratozamia mirandae* (Pérez-Farrera *et al*., 2006) and *C. Fuscoviridis* (Pulido *et al*., 2015). This is also consistent with Donaldson (1995) who proposed that single-stemmed subterranean cycad species could be classified as reproducers.

In contrast to the reproducer life history type, species that invest in vegetative backup for resprouting are expected to produce fewer seeds and seedlings and show greater adult plant dominance (Bond & Midgley, 2001). This was evident for the species within Group 4 which were dwarf arborescent cycads that produce multiple stems and cone infrequently. Additionally, these species occurred in more variable habitats with a low, unreliable rainfall and periods of drought, winter frost and, in some cases fire (Kriticos *et al.,* 2012). These conditions do not favour seed germination and seedling establishment (Bazzaz *et al*., 2000). The population structure of species within Group 4 showed a high proportion of adult plants with low numbers of seedlings and juveniles resembling a Bongers type III population structure, characteristic of plants with poor recruitment. This is in agreement with Raimondo and Donaldson (2003) who found that *E. cycadifolius* had adult-dominated populations with almost no seedlings or juveniles present. Furthermore, Donaldson (1995) classified species with a high degree of vegetative suckering, as persisters and included *E. cycadifolius* as an example.

The species with the most variation in life history traits were placed as either Group 2 or Group 3 response types. Species in Groups 2 and 3 are tall with many stems. The separation between species in Group 2 and Group 3 is likely due to most species in Group 2 having shorter stems, relatively more stems and producing relatively fewer cones. The species in both of these groups inhabit a variety of environments and appear to be more flexible in terms of their investment in cones versus vegetative growth. The population structure of species in Group 2 showed a very low proportion of seedlings but a high proportion of adult plants in all populations. This suggests a Donaldson (1995) life history strategy of persisters, however the abundance of juveniles in half of the sampled populations suggests that episodic recruitment events do occur more so than for species in Group 4. This could indicate a Bongers type II population structure for plants with discontinuous recruitment, and is also in agreement with Donaldson (1995) who hypothesized that some species, such as *E. lehmannii*, would tend towards persistence but with greater reproduction than truly persistent species. These species rely on adult persistence via suckering, with episodic coning events.

The population structure of species within Group 3 did not illustrate consistent nor predictable patterns as a whole, or within the subgroups identified in Chapter 2. Some species exhibited high numbers of seedlings and juveniles, but none consistent with a Reproducer strategy due to higher numbers of adults either in the same population or in different populations of the same species (*E. longifolius, E. friderici-guilielmi, E. natalensis, E. transvenosus*). Three out of the four populations of *E. friderici-guilielmi* had a high proportion of adult plants relative to seedlings and juveniles, but the population sampled at Middeldrift showed recent recruitment. Furthermore, *E. ferox* displayed similar numbers of plants in each stage class. There is a lack of consistency in population structure within this group, but the manner in which populations of the same species differ in their seedling/juvenile to adult ratio may indicate a Bongers type II population structure similar to the general population structure for Group 2.

In summary, the population stage structure of South African *Encephalartos* species revealed three general strategies in line with Bongers (1988): i) Species with high proportions of non-reproductive versus reproductive individuals (adults) implying continuous recruitment (Group 1); ii) species with high proportions of adults versus non-reproductive individuals implying poor recruitment (Group 4) and iii) species with fairly high numbers of adults with intermittent increases in non-reproductive individuals implying discontinuous recruitment (Groups 2 and 3).

3.4.3 PATTERNS OF SURVIVORSHIP BETWEEN GROUPS

The survivorship of a species indicates the probability of mortality in different stage classes (Pacala & Silander, 1983). In conjunction with population stage structure, survivorship curves can help indicate which stage class is the most important for conservation to ensure species survival (Harper & White, 1974). It is expected that different life histories will have different survivorship patterns leading to different conservation requirements.

In Group 1, the low proportion of survival displayed in the A1 adult stage showed that *E. villosus* experienced a high risk of mortality of A1 adult plants. However, the survivorship pattern resembles a Deevey type III or reverse J-shape curve implying high juvenile mortality (Deevey, 1947). The same survivorship pattern was found for *Zamia debilis* (Negron & Breckon, 1989), *Dioon edule* (Vovides, 1990; Octavio-Aguilar *et al*., 2008), *Ceratozamia matudai* (Pérez-Farrera *et al*., 2000), *Ceratozamia mirandae* (Pérez-Farrera *et al*., 2006), *Macrozamia parcifolia* (Borsboom *et al*., 2015) and *Ceratozamia fuscoviridis* (Pulido *et al*., 2015). The life table for *E. villosus* also indicated considerable mortality in the seedling and juvenile stages and thus the survivorship may be explained by highest mortality in non-reproductive individuals with consistent mortality also present in later life stages. This is similar to *E. caffer* which better resembled a Deevey type II survivorship curve implying constant mortality over the stage classes (Deevey, 1947; Harper & White, 1974).

The high proportion of adult plant survival for the species in Group 4 would suggest a J shape survival curve. Both *E. cycadifolius* and *E. horridus* displayed this pattern, but *E. trispinosus* showed a slight decrease in the survival of A2 adults. In addition, *E. cycadifolius* and *E. horridus* showed mortality risk in the A1 adult stage. This was an unexpected result and may be due to the parameters used to classify the stage classes. It appears that the parameters defining the A1 adult class may have been too narrow and therefore not enough plants were represented in this category. In addition, *E. cycadifolius* showed a decrease in the number of surviving adults from juvenile to A1 stage by only one plant which does not warrant true mortality risk and is probably the result of misclassification of some A1 adults as juveniles. Octavio-Aguilar *et al*. (2008) suggests that the survivorship of *E. cycadifolius* resembles a Deevey type III curve. Although the life history and population structure of this species does imply high seedling mortality due to irregular coning and unfavourable conditions for seedlings, the survivorship pattern does not resemble the type III survivorship curve. This is probably due to the rarity of seedlings and the success of adult plant persistence (Donaldson, 1995) and the same is likely true for *E. horridus* and *E. trispinosus*.

A J-shaped survivorship curve was not confined to the species in Group 4 since both species sampled from Group 2 displayed a J-shaped survivorship curve with a high risk of mortality in the juvenile stage. Similarly, *E. friderici-guilielmi* and *E. lanatus* in Group 3 displayed a J-shaped curve and a similar curve to *E. trispinosus* in Group 4. Overall, there was no consistency in survivorship patterns for species in Group 3. In the same way, the survivorship patterns were not confined discretely to separate life history groups, nor were they always consistent within groups. Populations of the same species of cycads have displayed different survivorship patterns, possibly influenced by poaching of adult plants (Pulido *et al.*, 2015) or the availability of suitable habitat (López-Gallego, 2008). It is not uncommon that species with different life histories and population structure display similar mortality and survivorship patterns (Jones, 2014). This highlights the factors that need to be considered when assessing the association between life history types and their emergent population structure and survivorship patterns.

3.4.4 FACTORS THAT COULD BE INFLUENCING THE POPULATION STRUCTURE AND SURVIVORSHIP OF SOUTH AFRICAN CYCADS

There are a number of factors that can influence the population structure and survivorship patterns of cycad species. Most notably, the species within Group 3 showed the greatest inconsistency between species. This could be attributed to the fact that their life history group contains the most species with less well-defined life history attributes than those of Groups 1 and 4. Species in this group were also shown to occupy diverse habitats encompassing a large range of environmental conditions. These habitat inconsistencies may explain the differences in population and survivorship patterns. Seedling establishment can be affected by the surrounding floristic density (Pérez-Farrera *et al.*, 2000), composition, herbivory and weather (Pérez-Farrera *et al.*, 2000). Lower quality habitats have also been shown to have lower fecundity (Angelone *et al.*, 2007) and recruitment (Jacquemyn *et al.*, 2003) and therefore smaller population sizes (Vergeer *et al.*, 2003). However, López-Gallego (2008) suggests that habitat size is more notable than habitat quality in influencing recruitment in *Zamia* species. For *Dioon edule*, a cycad native to Mexico, disturbance may have caused variations in vegetative growth and sexual reproduction with disturbed sites having a higher reproductive component and undisturbed sites showing greater persistence attributes and decreased sexual reproduction (Octavio-Aguilar *et al*., 2008). Similar patterns were found by Negrón-Ortiz *et al*. (1996). Therefore both subtle and more noteworthy habitat differences, including disturbance and habitat size could be one explanation for the differences between the stage structure within populations of the same species (*E. natalensis* and *E. longifolius*), as well as among species within the same life history group.

Furthermore, resprouting ability allows for the ultimate survival and reproduction of plants through persistence during times of disturbance and drought (Longbrake & McCarthy, 2001). Many life history traits are correlated with each other resulting in a holistic response to stresses (Longbrake & McCarthy, 2001). Environmental signalling pathways have been connected to developmental transformations in plants resulting in different phenotypic responses (Nicotra *et al*., 2010). This phenotypic plasticity is controlled at a molecular level with these epigenetic variations helping species to persist in variable environments (Bräutigam *et al*., 2013). This is particularly relevant to species in Groups 2 and 3 which display alternation between vegetative persistence and recruitment. Therefore, phenotypic plasticity due to environmental stresses may also be responsible for the lack of explicit life history parameters and demographic patterns in these groups.

Another important consideration when assessing the demographic parameters of cycads is the illegal collection of adult plants which is a major threat to populations countrywide (Golding & Hurter, 2003; Donaldson, 2008; da Silva *et al*., 2012; Cousins *et al*., 2013). The populations of *E. longifolius* had fewer adults in the recent population assessment in comparison with the assessments of the same populations in 1992 and 1993. This could indicate illegal collection of adult plants which in turn influenced the results. The two populations of *E. natalensis* also showed different stage structures, with the population sampled in Hilton having fewer adult plants in contrast to the high number of adults in the Hopewell sample. This could also be the result of poaching. When assessing population structure as an emergent property of life history groups, healthy populations that accurately reflect the general stage structure are required. For this study, I attempted to limit the analyses to relatively healthy, natural populations with little evidence of poaching, but some populations were inevitably affected.

The threatened nature of the species in Group 2 is also important for the interpretation of their population dynamics. The rarity and small population size of species in group 2 render it possible that the displayed population stage structure for each of these species is not accurately representative. Although both sampled species show J-curve survivorship, these species had relatively small populations and *E. middelburgensis* was only represented by a total of 63 plants from one location. Small population size can result in a skewed population structure because small differences in the number of individuals in any given stage class will have a larger impact on the results (Sherbov & Ediev, 2011). This is also relevant for certain species in Group 3 (eg. *E. ferox, E. lanatus* and *E. transvenosus*).

Species-specific considerations may be needed to address conservation objectives. For example, the highly threatened species, *E. latifrons,* is regarded as naturally rare (Pearson, 1916). With less than 60 plants left in the wild and a male-biased sex ratio (da Silva *et al*., 2012), this species has not produced viable seed in wild populations for over ten years (Whitelock, 2002). The pollinators have not been observed and are likely extinct (da Silva *et al*., 2011). The sex ratio bias may be due to the illegal collection of female plants or increased female plant mortality (da Silva *et al*., 2012). It is the production of basal suckers as well as the longevity of individual stems that has allowed it to persist (da Silva *et al*., 2012). This shows the importance of certain life history traits since, for the survival of *E. latifrons*, it is obviously imperative to conserve all adult plants by protecting them from illegal collection or habitat destruction. This can be partially predicted from generalised responses of species with similar life histories but does benefit from additional species-specific information.

In future population studies of cycads, the protocol of Borsboom *et al*. (2015) should be considered to ensure the most accurate stage class classification. This information was not yet available at the start of this study when field measurements were being carried out. Borsboom *at al*. (2015) found that there was a size overlap between immature and mature plants when using leaf length and stem height. They suggest the use of the basal petiole width and longest leaf coupled with coning information to generate stage classes. This study did have a larger dataset than that of Borsboom *et al* (2015) with a greater diversity of life histories to consider. The use of leaf and stem number were very successful in identifying S1 and S2 seedlings and A2 adults, respectively. The most challenging parameter was to distinguish between juveniles and A1 adults, as coning information is lacking for many species. This implies that the characters recommended by Borsboom *et al* (2015) may not be significantly more useful since coning information is still limited. Ornduff (1991a) and Werner and Caswell (1977), advocated the use of stem height and leaf number to determine plant stage class classification and this is sometimes the only option when coning data are not available.

It should also be noted that the number of representative populations for species in Groups 1 and 4 is quite small due to the smaller size of these groups and available population data. Therefore the trend that species with a higher investment into reproduction have a higher proportion of juveniles and species with greater investment towards persistence have a higher number of adults, may not be related exclusively to life history strategies. As suggested in Section 2.4.5, if a continuum of life history strategies was developed rather than defined groups, the population properties could be represented as a distribution along the continuum with further regression analysis on the life history strategy versus the proportion of juveniles. This would give a more quantitative approach to assessing the association between life history types and population structure and be more powerful than contingency tables.

CHAPTER 4: SYNTHESIS AND CONCLUSIONS

This study had two primary aims. The first aim was to determine whether species of *Encephalartos* from South Africa shared suites of life history traits which could be used to classify species into life history groups. The second aim was to determine whether the life history traits used to define these groups, and which were expected to represent different ecological response groups, would result in emergent properties at the population level. In particular, the study tested whether the population structure and survivorship properties were predictable for different groups based on their shared life history traits. The traits used for this analysis were easily measurable attributes that were considered to influence survival or reproduction and which were common to, and available for, all *Encephalartos* species from South Africa and Swaziland. The purpose was not to understand the evolutionary implications of life history analysis, but rather to explore the use of life history (and ecological response) groups as an approach to guide management and conservation of rare and difficult to study species through a predictive understanding of cycad ecology.

Analysis of the life history traits of 35 South African and two Swaziland *Encephalartos* species showed strong statistical support for division into four main groups. Group 1 was represented by six single-stemmed, subterranean species and Group 4 consisted of four dwarf-arborescent species with clusters of multiple stems. Species in Groups 2 and 3 were less well defined in terms of their life history traits, with species in both groups producing many stems and cones. Group 2 was represented by nine species separated from the 18 species in Group 3 due to their production of slightly more and slightly shorter stems than the species in Group 3. Group 2 contained some of the most rare and threatened species as well as three detected outliers.

Phylogenetic constraints were not found to influence the species group allocation implying that the suite of traits expressed have been influenced by selection rather than constrained by ancestral character states. Furthermore, the groups showed some consistency in terms of the environments in which they occurred. Group 1 species occurred in more mesic habitats characterized by a high mean annual precipitation and low variation in annual rainfall. In contrast, species in Group 4 occurred in more variable habitats with unreliable rainfall and more xeric conditions characterized by a low mean annual precipitation and high variation in annual rainfall. The species in Groups 2 and 3 showed no consistency in the generalized nature of their habitats and occurred over a diverse range of conditions.

The analysis of population stage structure and survivorship patterns, derived from static life tables, for each species provided partial support for population structure being an emergent property of particular cycad life histories. Species in Group 1 displayed high proportions of seedlings and juveniles with fewer adult plants indicating investment in reproduction. These species generally showed consistent mortality throughout the stage classes. In contrast, species in Groups 2 and 4 displayed a high proportion of adult plants with very few seedlings showing the highest risk of mortality in the juvenile stage. However, the population structures of species in Group 2 indicated that recruitment occurred more frequently than for the species in Group 4 which indicated investment primarily into persistence but with some recruitment. Group 3 species showed no consistency in survivorship schedules, although their population structure did generally indicate a reliance on the persistence of adult plants with episodic recruitment, similar to species in Group 2.

The results of this study indicate that there was some consistency in the population structure of Groups 1 and 4. These groups can be considered as contrasting life history types and display a contrasting population structure. This implies that their particular population structure is an emergent property of their life histories and these two groups can be used in predictive ecology due to less plasticity in their population responses. Although species in Group 2 displayed a consistent population structure, this structure should not be considered an emergent property representative of the whole group. This is due to the rarity and small population size of the species within Group 2, as well as the lack of representative data for population analysis. Predictions for this group based on the population structure represented here may not be accurate. Similarly, species in Group 3 showed little consistency in terms of survivorship and population structure preventing reliable predictions. However, in a broad sense, Groups 2 and 3 can be considered discontinuous recruiters having the capacity to invest in both reproduction and recruitment.

Being able to infer general population stage structure patterns has important implications for species population management. Studies on population structure and survivorship have been used to highlight the susceptibility of species to management practices, disturbance and habitat fragmentation or destruction (López-Gallego, 2008; Octavio-Aguilar *et al*., 2008; López-Gallego & O' Neil, 2010), as well as to identify populations under stress (Raimondo & Donaldson, 2003; da Silva et al., 2012). The population stage structure of plants is important in indicating the health of a population and evaluating whether the current recruitment is adequate enough to ensure population viability. This is especially valid for long-lived plants like cycads (Borsboom *et al*., 2015). Different threats will have different implications depending on the species involved. Species which predominantly sprout to ensure persistence into future generations are more susceptible to disturbance in the form of habitat loss, fragmentation or illegal collection, as few recruitment events result in difficulties to recover from adult plant loss (Bond & Midgley, 2001; Octavio-Aguilar *et al*., 2008). Moreover, a lack of recruitment events in non-sprouting species could indicate population stress possibly due to disturbance (Cook, 1979), climate change (Cochrane *et al*., 2015) or habitat fragmentation (López-Gallego, 2008). This information can better inform IUCN-listing categories (Pérez-Farrera, 2006) and provide guidance for both *in situ* and *ex situ* conservation strategies.

Despite the variation detected in the population structure within some life history groups of South African *Encephalartos*, this study shows that it is possible to use life history groups to understand general demographic patterns in terms of the broader trends. Moreover, the variation detected in this study may be an indicator of stressors in those particular populations such as fewer adults due to illegal collection. In addition, this study was useful in assembling the life history data for South African and Swaziland cycads as well as the parameters which separate the different life history types. The collation of data on climate variables and fire return frequencies for 193 populations provides a dataset that will have many uses for conservation and ecological studies of South African cycads. One of the avenues for future study would be to assess the distributions of *Encephalartos* in South Africa and how these associate with particular environments, since investment in reproduction versus persistence would influence dispersal. Despite the variation between species observed in this study, the grouping of species into response groups and the assessment of group characteristics was worthwhile. It provided important insights into how primary investment in seeds versus persistence, or a combination of strategies, can influence population structure and should be considered in management frameworks. This approach may also be useful in a global context and could be replicated for cycads in other genera.

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APPENDIX 1: LIFE HISTORY TRAIT MATRIX WITH SOURCES

Table 1: Key life history traits of South African and Swaziland *Encephalartos* species used in the analyses described in chapter 2. Superscript numbers indicate the source of information. Categories with more than one reference were finalized by the average of values or maximum value present in the literature.

	Typical number of cones p/stem^{1}♦	**Seeds produced in a 10 year interval^{*,2,3,4,6}**	**ca. Coning interval (years)^{5}**	**Maximum stem height (cm)^{1,2,6}**	**Number of stems^{4,5}**	**Stem habit^{2,4,5}**
E. aemulans	2.5	1875	4	300	Few	Arborescent
E. altensteinii	3.5	7781.667	3	500	Few	Arborescent
E. aplanatus	1	966.6667	3	10	Single	Subterranean
E. arenarius	1	3400	3	100	Few	Arborescent
E. caffer	1	800	3	10	Single	Subterranean
E. cerinus	1	766.6667	3	10	Single	Subterranean
E. cupidus	1	514.2857	7	75	Clusters	Dwarf arborescent
E. cycadifolius	1	1142.857	7	100	Clusters	Dwarf arborescent
E. dolomiticus	2.5	2125	4	200	Many	Arborescent
E. dyerianus	3	1725	4	400	Few	Arborescent
E. eugene-maraisii	3	2400	3	250	Few	Arborescent
E. ferox	3	4500	3	100	Few	Arborescent
E. friderici-guilielmi	4	4200	3	400	Few	Arborescent
E. ghellinckii	4	3700	4	300	Few	Arborescent
E. heenanii	2	1050	4	300	Few	Arborescent
E. hirsutus	2	1600	5	400	Many	Arborescent
E. horridus	1	2400	6	50	Clusters	Dwarf arborescent
E. humilis	1	630	5	30	Few	Arborescent
E. inopinus	1.5	1560	5	300	Many	Arborescent
E. laevifolius	3	8662.5	4	300	Many	Arborescent
E. lanatus	2.5	2083.333	3	150	Few	Arborescent
E. latifrons	1.5	5925	6	300	Many	Arborescent
E. lebomboensis	2	4366.667	3	400	Few	Arborescent
E. lehmannii	1	2450	6	200	Many	Arborescent
E. longifolius	1.5	2193.75	4	400	Few	Arborescent
E. middelburgensis	5	6500	4	700	Many	Arborescent
E. msinganus	1.5	1575	4	300	Few	Arborescent
E. natalensis	3.5	5950	3	600	Few	Arborescent
E. ngoyanus	1	366.6667	3	10	Single	Subterranean
E. nubimontanus	2	2080	5	250	Many	Arborescent
E. paucidentatus	3	6000	3	600	Few	Arborescent
E. princeps	2	2925	4	400	Few	Arborescent
E. senticosus	2.5	4916.667	3	400	Few	Arborescent

E. transvenosus	2.5	6416.667	3	1200	Few Clusters	Arborescent
E. trispinosus	1	850	8	100		Dwarf arborescent
E. umbeluziensis	1	700	3	10	Single	Subterranean
E. villosus	1	1540	3	10	Single	Subterranean

[1]: Hill and Stevenson (1998)
[2]: Whitelock (2002)
[3]: Grobbelaar (2004)
[4]: Osborne (1993)
[5]: Advice of experts
[6]: Goode (2001)
♦ Decimal values imply the median between a min/max range

*The average number of seeds was calculated as:

$$[(average\ \#\ of\ seeds\ per\ cone) \times (average\ \#\ of\ cones\ per\ stem) \times (average\ \#\ of\ reproductive\ stems)] \times \left({}^{10}/_{coning\ interval}\right)$$

Sources of information:

-Average number of seeds per cone:

(Megasporophylls were counted for each species from the images displayed in Whitelock (2002), Osborne (1993) and Goode (2001). These were then multiplied by two to account for the opposite side. This total was then multiplied by two since each megasporophyll contains two ovules (Grobbelaar, 2004).

-Average number of reproductive stems: Osborne (1993); Expert opinion

Appendix 2: Cluster analysis (Single-Linkage method)

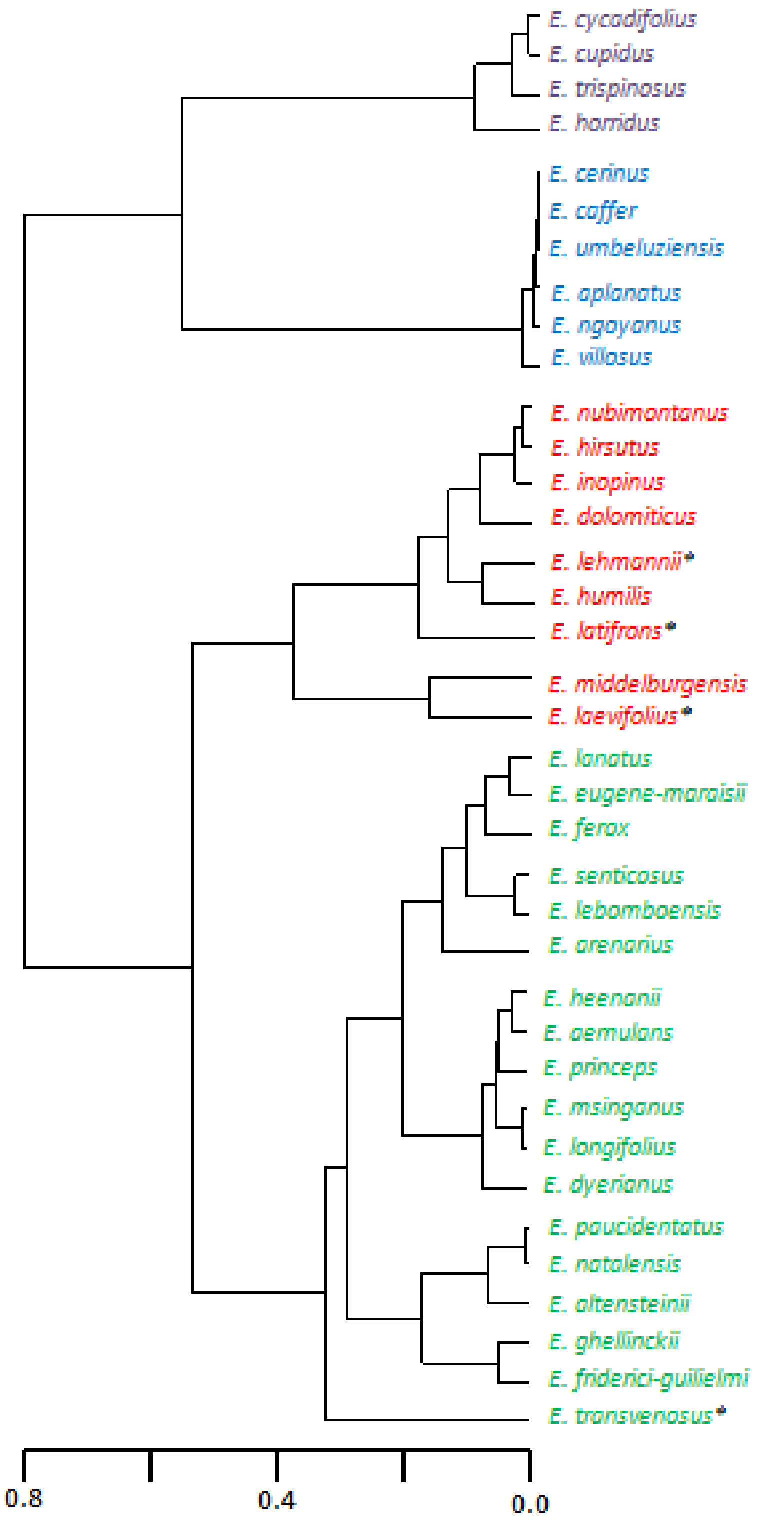

Figure 6: Horizontal dendrogram produced by a cluster analysis using Complete Linkage linkage method showing 35 South African and two Swaziland *Encephalartos* species hierarchically arranged in fewer clusters as the amount of dissimilarity permitted within each cluster increases, based on key life history traits. At 0.5 units of dissimilarity, there are four clusters, each represented by a different colour. Group 1 = blue; Group 2 = red; Group 3 = green and Group 4 = purple. Outliers identified by the multivariate outlier analysis are indicated by an asterisk (*).

APPENDIX 3: SCATTERPLOTS AND STAGE CLASS PARAMETERS

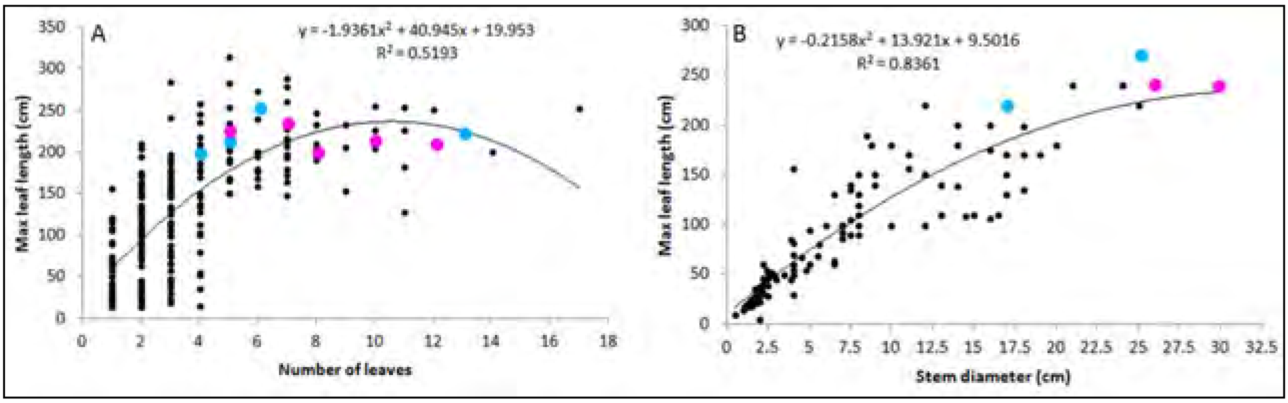

Figure 1: Correlations between the maximum leaf length and two other variables: **A**) Number of leaves and **B**) Stem Diameter, with cone records overlaid, ● indicates a male cone, ● indicates a female cone. **A**: *E. villosus* from Umtiza and Ocean View sampled in 2014; **B**: *E. villosus* from Umtiza and Ocean View sampled in 1993.

Table 1: Parameters used to classify stage classes for *E. villosus.*

Stage Class	Stage class classification parameters
S1	0 – 2.5 cm diameter (1993) or 1 leaf, ≤ 50 cm leaf length (2014)
S2	2.6 – 5 cm diameter (1993) or 2-3 leaves, ≤ 50 cm leaf length (2014)
J	50 cm < leaf length ≤ 180 cm
A1	180 cm < leaf length < 200 cm
A2	≥200 cm leaf length (2014)

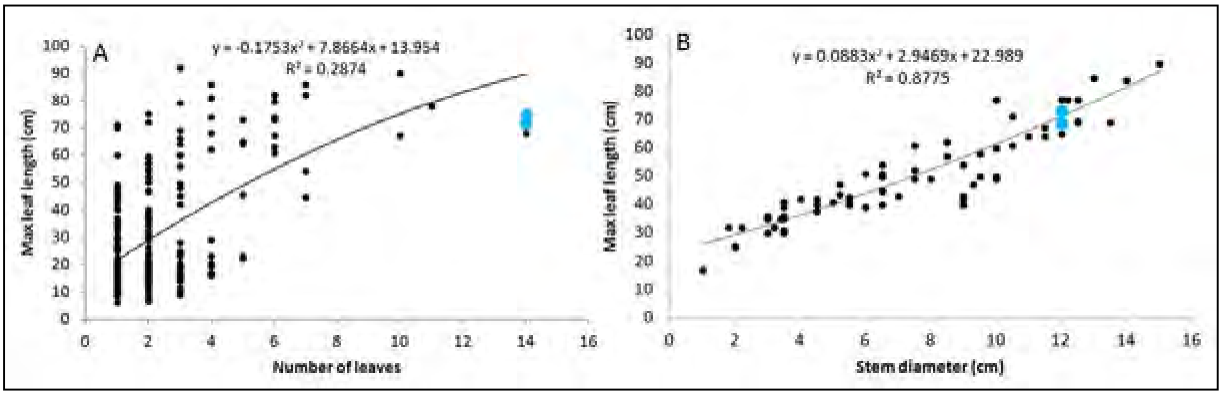

Figure 2: Correlations between the maximum leaf length and two other variables: **A**) Number of leaves and **B**) Stem Diameter, with cone records overlaid, ● indicates a male cone, ● indicates a female cone. **A**: *E. caffer* from Brooklands sampled in 2014; **B**: *E. caffer* from GlenView sampled in 1994.

Table 2: Parameters used to classify stage classes for *E. caffer.*

Age Class	Stage class classification parameters
S1	1 leaf, ≤ 40 cm leaf length
S2	2 leaves, ≤ 50 cm leaf length
J	3-4 leaves, ≤ 80 cm leaf length
A1	4– 10 leaves, > 40 cm leave length
A2	>10 leaves

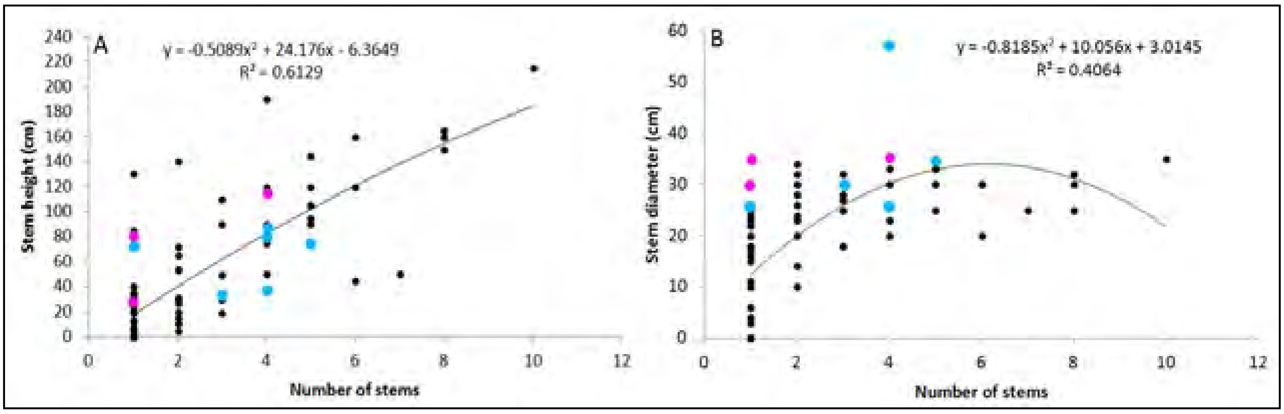

Figure 3: Correlations between the number of stems and two other variables: **A**) Stem height and **B**) Stem Diameter, with cone records overlaid, ● indicates a male cone, ● indicates a female cone for *E. lehmannii* from Knoetze and Somerset East sampled in 2014.

Table 3: Parameters used to classify stage classes for *E. lehmannii.*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, stem height <20 cm, diameter <20 cm
A1	1 stem, stem height >20 cm, diameter >20 cm
A2	>1 stem

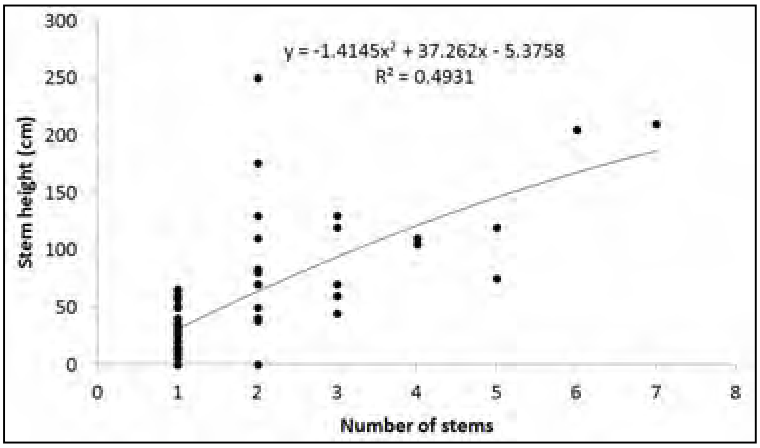

Figure 4: Correlations between stem height and number of stems for *E. middelburgensis* sampled in Middelburg in 2014.

Table 4: Parameters used to classify stage classes for *E. middelburgensis.*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, stem height ≤ 50 cm
A1	1 stem, stem height > 50 cm
A2	>1 stem

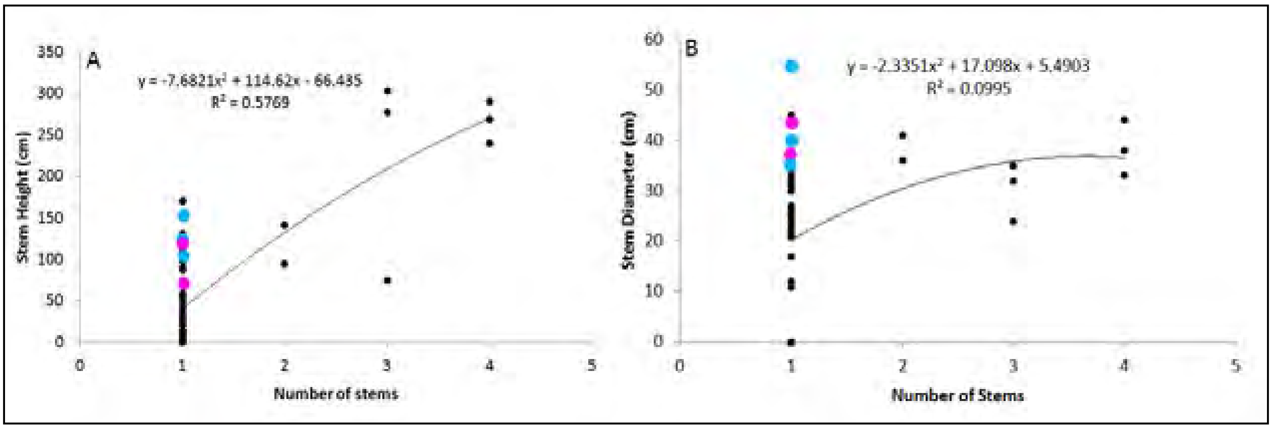

Figure 5: Correlations between the number of stems and two other variables: **A**) Stem height and **B**) Stem Diameter, with cone records for plants with 1 stem overlaid, ● indicates a male cone, ● indicates a female cone for *E. longifolius* from Waterkloof sampled in 2014.

Table 5: Parameters used to classify stage classes for *E. longifolius.*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, stem height ≤ 100 cm, diameter ≤ 30 cm
A1	1 stem, stem height > 100 cm, diameter > 30 cm
A2	>1 stem

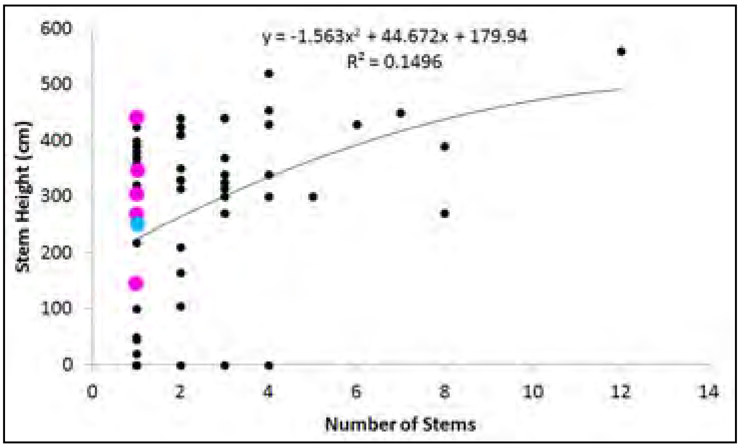

Figure 6: Correlations between the number of stems and stem height with cone records for plants with 1 stem overlaid, ● indicates a male cone, ● indicates a female cone, for *E. natalensis* from Hopewell sampled in 2014.

Table 6: Parameters used to classify stage classes for *E. natalensis*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, stem height ≤ 100 cm
A1	1 stem, stem height > 100 cm
A2	>1 stem

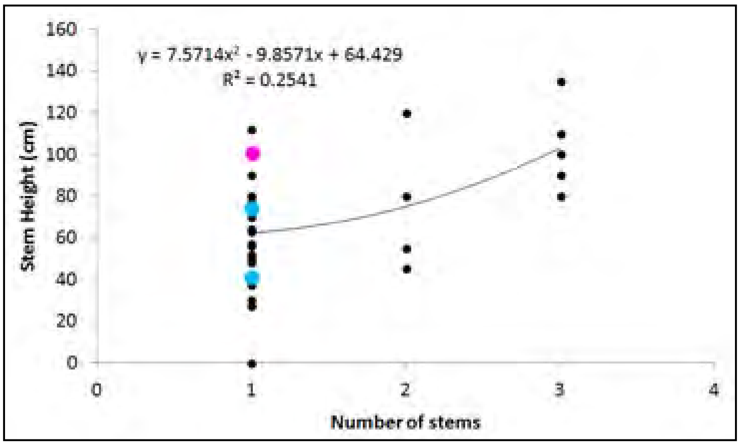

Figure 7: Correlations between the number of stems and stem height with cone records for plants with 1 stem overlaid, ● indicates a male cone, ● indicates a female cone, for *E. lanatus* from Botshebalo sampled in 2014.

Table 7: Parameters used to classify stage classes for *E. lanatus*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, stem height < 40 cm
A1	1 stem, stem height ≥40 cm
A2	>1 stem

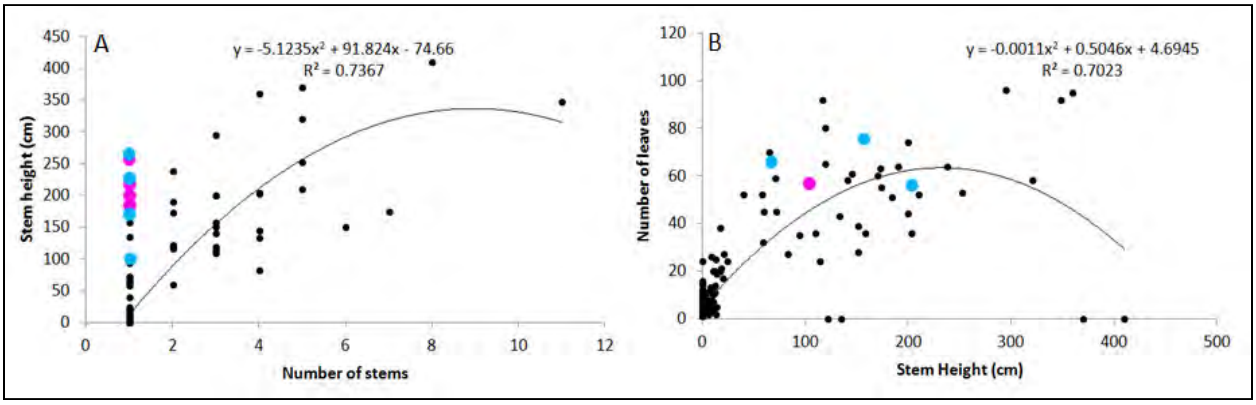

Figure 8: Correlations between the stem height and two other variables: **A**) number of stems and **B**) number of leaves, with cone records for plants with 1 stem overlaid, ● indicates a male cone, ● indicates a female cone for *E. friderici-guilielmi* from Middeldrift sampled in 2014.

Table 8: Parameters used to classify stage classes for *E. friderici-guilielmi*

Age Class	Stage class classification parameters
S1	1 leaf or classed on site
S2	2 - 3 leaves or classed on site
J	1 stem, 4 – 20 leaves, stem height < 70 cm
A1	1 stem, stem height ≥ 70 cm
A2	>1 stem

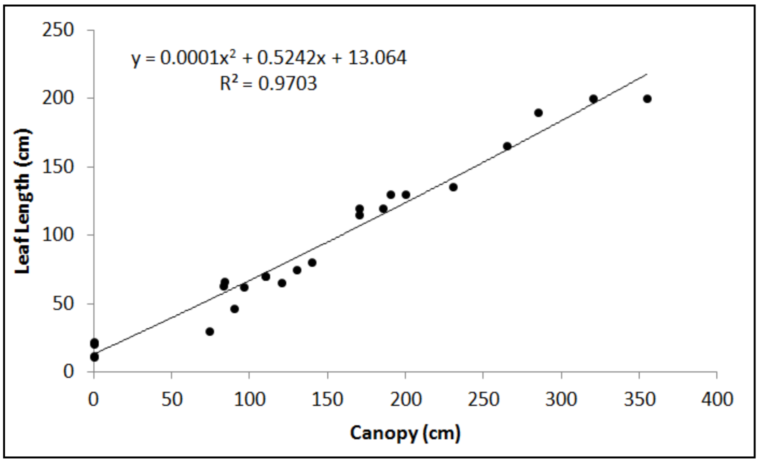

Figure9: Correlations between canopy length and leaf length for *E. ferox* sampled in Kosi Bay in 2014.

Table 9: Parameters used to classify stage classes for *E. ferox*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	Leaf length ≤ 100 cm leaf length
A1	100 > Leaf length (cm) ≤ 150
A2	Leaf length > 150 cm

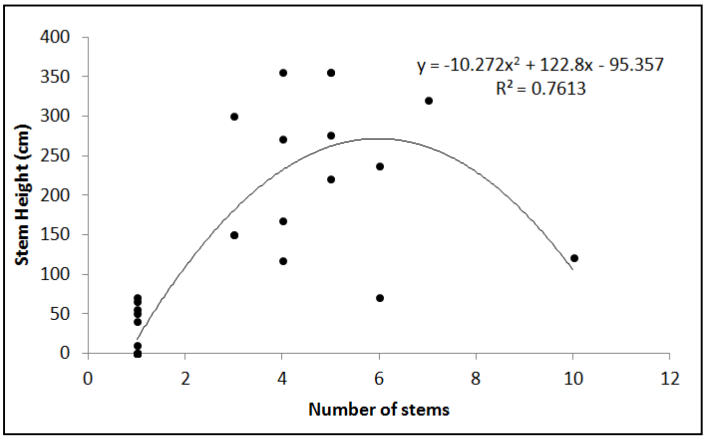

Figure 10: Correlations between number of stems and stem height for *E. transvenosus* sampled at Modjadji in 2014.

Table 10: Parameters used to classify stage classes for *E. transvenosus*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, stem height ≤ 100 cm
A1	2 – 5 stems, stem height > 100 cm
A2	>5 stems

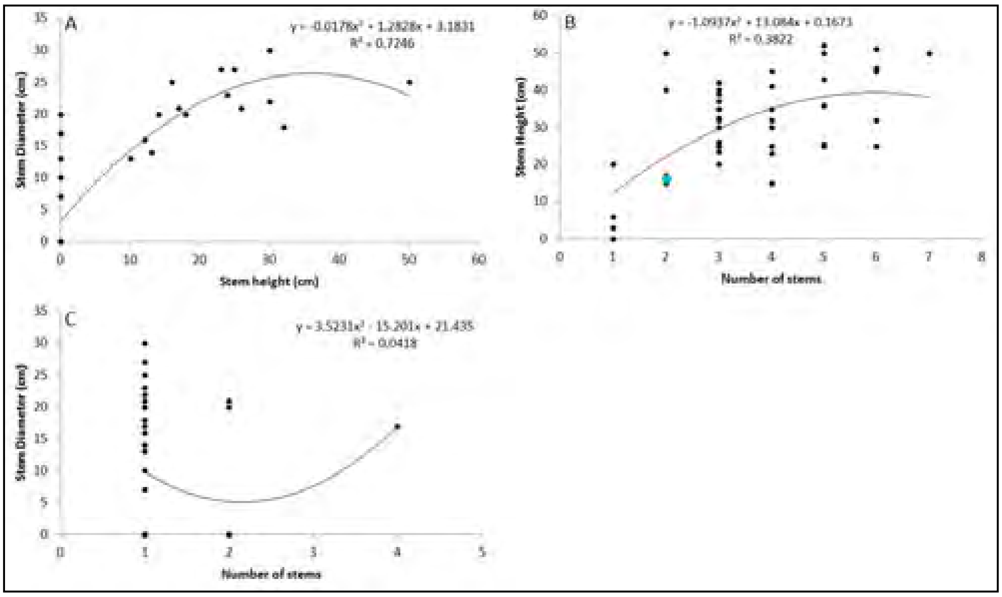

Figure 11: Correlations between: **A**) stem diameter and number of stems **B**) stem height and number of stems (● indicates a male cone) C) stem diameter and number of stems, for *E. horridus* sampled at Springs in 1994 and 2014.

Table 11: Parameters used to classify stage classes for *E. horridus*

Age Class	Stage class classification parameters (2014)	Stage class classification parameters (1994)
S1	1 leaf (classed on site)	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)	2 - 3 leaves (classed on site)
J	1 stem, diameter ≤ 10 cm	1 stem
A1	1 – 3 stems, 10 < Diameter (cm) ≤ 20	2 – 4 stems
A2	Diameter >21	>4 stems

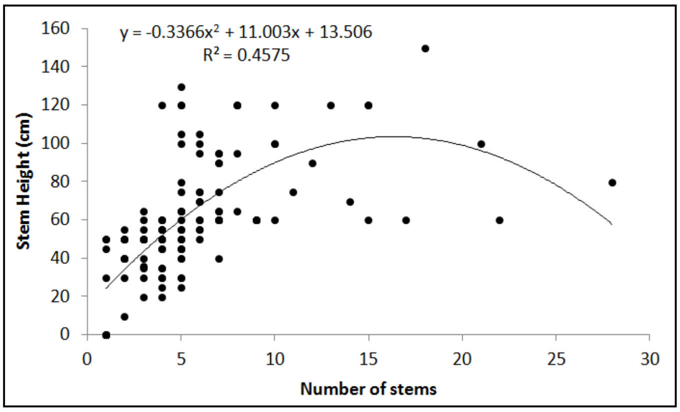

Figure 12: Correlations between number of stems and stem height for *E. trispinosus* sampled at Kenton-on-Sea in 1990 and Helspoort in 1993.

Table 12: Parameters used to classify stage classes for *E. trispinosus*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, 10 < stem height (cm) ≤ 50
A1	1 ≤ stems < 6
A2	>5 stems

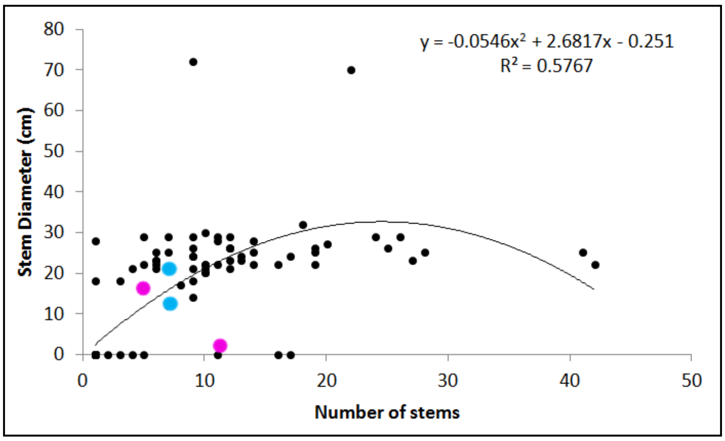

Figure13: Correlations between number of stems and stem diameter for *E. cycadifolius* sampled at Venn Grove in 2014. Cone records for the smallest plants, ● indicates a male cone, ● indicates a female cone.

Table 13: Parameters used to classify stage classes for *E. cycadifolius*

Age Class	Stage class classification parameters
S1	1 leaf (classed on site)
S2	2 - 3 leaves (classed on site)
J	1 stem, diameter 0 – 10 cm
A1	1 ≤ stems < 4
A2	>3 stems

APPENDIX 4: CONTINGENCY TABLES

Table 1: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 1. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**		
	J	**A1**	**A2**
E. villosus, Ocean View, 2014	68	8	31
	(68)	(20)	(19)
	0.00	**-3.42****	**3.48****
E. villosus, Ocean View, 1994	14	2	9
	(16)	(5)	(4)
	-0.81	-1.40	**2.44***
E. villosus, Umtiza Forest, 2014	59	10	23
	(58)	(17)	(16)
	0.13	**-2.15***	**2.02***
E. villosus, Umtiza Forest, 1994	32	0	2
	(22)	(6)	(6)
	3.86*	**-2.90****	-1.90
E. caffer, Brooklands 2014	62	20	2
	(53)	(16)	(15)
	2.18*	1.38	**-4.14****
E. caffer, Glenview, 1994	32	38	8
	(50)	(14)	(14)
	-4.59**	**7.59****	-1.94

*p < 0.05 ; ** p <0.01

Table 2: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 1. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**				
	S1	**S2**	**J**	**A1**	**A2**
E. villosus, Ocean View, 2014	20 (33) **-2.84***	24 (30) -1.35	68 (56) **-2.24***	8 (16) **-2.47***	31 (16) **4.56****
E. villosus, Ocean View, 1994	28 (14) **4.38****	12 (13) -0.28	14 (24) **-2.74****	2 (7) **-2.12***	9 (7) 0.94
E. villosus, Umtiza Forest, 2014	2 (22) **-5.12****	5 (20) **-3.96****	59 (37) **4.97****	10 (11) -0.26	23 (10) **4.48****
E. villosus, Umtiza Forest, 1994	11 (11) 0.00	6 (10) -1.49	32 (19) **3.92****	0 (6) **-2.59****	2 (5) -1.58
E. caffer, Brooklands 2014	74 (52) **4.19****	82 (47) **6.86****	62 (89) **-4.46****	20 (26) -1.54	2 (25) **-5.97****
E. caffer, Glenview, 1994	21 (24) -0.83	13 (22) **-2.36***	32 (42) **-2.05***	38 (12) **8.54****	8 (12) -1.24

*p < 0.05 ; ** p <0.01

Table 3: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 2. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**		
	J	**A1**	**A2**
E. lehmannii, Knoetze*,* 2014	23	5	16
	(15)	(9)	(20)
	2.88**	-1.63	-1.43
E. lehmannii, Weltevrede*,* 2014	3	6	16
	(9)	(5)	(11)
	-2.51**	0.54	1.96
E. lehmannii, Somerset East, 2014	4	5	24
	(11)	(7)	(15)
	-2.94*	-0.77	**3.42***
E. lehmannii, Jansenville*,* 1991	4	4	18
	(9)	(5)	(12)
	-2.18*	-0.63	**2.58****
E. middelburgensis, Middelburg*,* 2014	31	18	13
	(21)	(12)	(28)
	3.19**	**2.17***	**-4.78****

*p < 0.05 ; ** p <0.01

Table 4: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 2. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**				
	S1	**S2**	**J**	**A1**	**A2**
E. lehmannii, Knoetze*,* 2014	10	0	23	5	16
	(4)	(1)	(17)	(10)	(23)
	3.72†	-0.84†	**2.06***	**-2.01***	**-2.15***
E. lehmannii, Weltevrede*,* 2014	1	0	3	6	16
	(2)	(1)	(8)	(5)	(11)
	-0.72†	-0.54†	**-2.33***	0.66	**2.16***
E. lehmannii, Somerset East, 2014	0	0	4	5	24
	(2)	(1)	(10)	(6)	(14)
	-1.75†	-0.62†	**-2.60****	-0.52	**3.90****
E. lehmannii, Jansenville*,* 1991	4	1	4	4	18
	(2)	(1)	(10)	(6)	(13)
	1.32†	0.00†	**-2.41***	-0.85	**1.96***
E. middelburgensis, Middelburg*,* 2014	0	1	31	18	13
	(5)	(1)	(20)	(12)	(26)
	-2.66**	0.00†	**3.65****	**2.51***	**-4.12****

*p < 0.05; ** p <0.01; † No test because E_{ij} < 5

Table 5: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 3. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**		
	J	**A1**	**A2**
E. longifolius, Joubertina*,* 2014	27	1	24
	(21)	(10)	(21)
	1.67	**-3.26****	0.95
E. longifolius, Joubertina*,* 1993	0	1	10
	(5)	(2)	(4)
	-2.78**	-0.85†	3.48
E. longifolius, Kritplaas*,* 2014	16	14	5
	(14)	(7)	(14)
	0.59	**3.21****	**-3.17****
E. longifolius, Kritplaas*,* 1993	0	2	17
	(8)	(4)	(8)
	-3.67**	-0.97†	**4.46****
E. longifolius, Van Stadens*,* 2014	47	3	3
	(23)	(11)	(22)
	6.96**	**-2.67****	**-4.84****
E. longifolius, Van Stadens*,* 1992	31	2	12
	(18)	(9)	(18)
	3.93**	**-2.58****	-1.87
E. longifolius, Waterkloof*,* 2014	38	10	8
	(23)	(11)	(22)
	4.25**	-0.25	**-4.06****
E. natalensis, Hilton , 2014	49	8	0
	(23)	(11)	(23)
	7.18**	-1.02	**-6.39****
E. natalensis, Hopewell , 2014	6	24	34
	(26)	(12)	(26)
	-5.35**	**3.89****	**2.25****
E. lanatus, Botshabelo Village, 2014	4	17	9
	(12)	(6)	(12)
	-3.13**	**5.32****	-1.13
E. friderici-guilielmi, Middeldrift, 2014	63	8	30
	(41)	(19)	(40)
	4.69**	**-3.07****	**-2.24****
E. friderici-guilielmi, Fincham's Nek, 2014	6	14	33
	(22)	(10)	(21)
	-4.54**	1.39	**3.44****
E. friderici-guilielmi, Cathcart, 2014	13	23	81
	(48)	(22)	(47)
	-7.10**	0.15	**7.01****

E. friderici-guilielmi, Thomas River, 2014	4	9	43
	(23)	(11)	(22)
	-5.33**	-0.61	**5.84****
E. ferox, Kosi-bay, 2014	5	6	4
	(6)	(3)	(6)
	-0.60	2.07†	-1.06
E. transvenosus, Modjadji, 2014	18	11	4
	(14)	(6)	(13)
	1.63	**2.12***	**-3.33****

*$p < 0.05$; ** $p < 0.01$; † No test because $E_{ij} < 5$

Table 6: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 3. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**				
	S1	**S2**	**J**	**A1**	**A2**
E. longifolius, Joubertina*,* 2014	1	0	27	1	24
	(12)	(4)	(15)	(7)	(15)
	-3.65**	-2.07†	**3.63****	**-2.54****	**2.83****
E. longifolius, Joubertina*,* 1993	0	10	0	1	10
	(5)	(2)	(6)	(3)	(6)
	-2.48*	7.26	**-2.95****	-1.18†	**2.00***
E. longifolius, Kritplaas*,* 2014	57	6	16	14	5
	(22)	(7)	(28)	(13)	(28)
	8.94**	-0.42	**-2.87****	0.23	**-5.31****
E. longifolius, Kritplaas*,* 1993	1	0	0	2	17
	(4)	(1)	(6)	(3)	(6)
	-1.87†	-1.25†	**-2.88****	-0.46†	**5.70****
E. longifolius, Van Stadens*,* 2014	62	2	47	3	5
	(26)	(9)	(34)	(16)	(34)
	8.27**	**-2.45***	**2.70****	**-3.71****	**-6.15****
E. longifolius, Van Stadens*,* 1992	3	10	31	2	12
	(13)	(4)	(17)	(8)	(16)
	-3.21**	3.06†	**4.24****	**-2.30***	-1.30
E. longifolius, Waterkloof*,* 2014	2	0	38	10	8
	(13)	(4)	(17)	(8)	(16)
	-3.54**	-2.17†	**6.32****	0.85	**-2.50***
E. natalensis, Hilton , 2014	24	4	49	8	0
	(19)	(6)	(25)	(11)	(24)
	1.38	-0.91	**6.08****	-1.15	**-6.00****

E. natalensis, Hopewell , 2014	48	0	6	24	34
	(25)	(8)	(32)	(15)	(32)
	5.52**	**-3.10****	**-5.79****	**2.58****	0.54
E. lanatus, Botshabelo Village, 2014	0	0	4	17	9
	(7)	(2)	(9)	(4)	(8)
	-2.97**	-1.54†	-1.91	7.01†	0.22
E. friderici-guilielmi, Middeldrift, 2014	45	43	63	8	30
	(42)	(14)	(55)	(26)	(53)
	0.56	**9.11****	1.48	**-4.09****	**-4.12****
E. friderici-guilielmi, Fincham's Nek, 2014	0	1	6	14	33
	(12)	(4)	(16)	(7)	(15)
	-4.03**	-1.55†	**-2.95****	**2.73****	**5.51****
E. friderici-guilielmi, Cathcart, 2014	3	0	13	23	81
	(27)	(9)	(35)	(16)	(34)
	-5.50**	**-3.22****	**-4.61****	1.91	**10.13****
E. friderici-guilielmi, Thomas River, 2014	0	0	4	9	43
	(12)	(4)	(16)	(8)	(16)
	-4.11**	-2.13†	**-3.68****	0.57	**8.29****
E. ferox, Kosi-bay, 2014	5	5	5	6	4
	(6)	(2)	(7)	(3)	(7)
	-0.27	2.52†	-0.99	1.55†	-1.37
E. transvenosus, Modjadji, 2014	1	0	18	11	4
	(8)	(2)	(10)	(5)	(10)
	-2.75**	-1.64†	**3.14****	**3.26****	**-2.16***

*$p < 0.05$; ** $p < 0.01$; † No test because $E_{ij} < 5$

Table 7: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 4. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**		
	J	**A1**	**A2**
E. horridus, Springs , 2014	20 (6) **6.90****	16 (12) 1.25	10 (28) **-5.76****
E. horridus, Springs, 1994	0 (6) **-2.67****	0 (12) **-4.36****	45 (27) **5.76****
E. trispinosus, Kenton-on-Sea, 1990	2 (6) **-1.99***	27 (14) **4.33****	23 (32) **-2.61****
E. trispinosus, Helspoort, 1993	2 (8) **-2.58****	38 (18) **5.89****	28 (41) **-3.63****
E. cycadifolius, Venn Grove West-facing, 2014	9 (6) 1.40	10 (13) -1.13	30 (30) 0.00
E. cycadifolius, Venn Grove West-facing, 1993	6 (5) 0.71	2 (10) **-3.20****	30 (23) **2.44***
E. cycadifolius, Venn Grove East-facing, 2014	7 (10) -0.99	9 (21) **-3.48****	62 (47) **3.83****

*p < 0.05; ** p <0.01

Table 8: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species in Group 4. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**				
	S1	**S2**	**J**	**A1**	**A2**
E. horridus, Springs , 2014	0	0	20	16	10
	(1)	(5)	(5)	(11)	(24)
	-1.31†	**-2.38***	**7.65****	1.90	**-4.44****
E. horridus, Springs, 1994	0	1	0	0	45
	(1)	(5)	(5)	(11)	(24)
	-1.31†	-1.86	**-2.47***	**-3.98****	**6.49****
E. trispinosus, Kenton-on-Sea, 1990	0	4	2	27	23
	(2)	(6)	(6)	(13)	(29)
	-1.47†	-0.75	-1.84	**4.66****	-1.86
E. trispinosus, Helspoort, 1993	0	5	2	38	28
	(2)	(7)	(8)	(17)	(38)
	-1.71†	-0.97	**-2.40***	**6.29****	**-2.68****
E. cycadifolius, Venn Grove West-facing, 2014	2	1	9	10	30
	(2)	(5)	(6)	(12)	(27)
	0.00†	**-2.06***	1.67	-0.78	0.78
E. cycadifolius, Venn Grove West-facing, 1993	0	0	6	2	30
	(1)	(4)	(4)	(9)	(20)
	-1.18†	-2.14†	1.08†	**-2.78****	**3.40****
E. cycadifolius, Venn Grove East-facing, 2014	12	32	7	9	62
	(4)	(12)	(13)	(29)	(64)
	4.87†	**7.10****	**-2.07***	**-4.97****	-0.48

*p < 0.05; ** p <0.01; † No test because E_{ij} < 5

Table 9: Contingency table showing the observed and expected (in parentheses) frequencies, followed by the adjusted residuals (Z) of the sampled *Encephalartos* species between life history groups. Bold type font indicates groups where Z > 1.96 and observed values are significantly different from expected (α = 0.05).

Species, Site, Date	**Stage Class**				
	S1	**S2**	**J**	**A1**	**A2**
Group 1	20	24	68	8	31
	(24)	(12)	(40)	(24)	(52)
	-0.85	**3.86****	**5.44****	**-3.65****	**-3.78****
Group 2	15	2	65	38	87
	(32)	(16)	(54)	(32)	(72)
	-3.52**	**-3.88****	1.76	1.13	**2.38***
Group 3	252	81	327	153	319
	(178)	(88)	(298)	(177)	(391)
	9.54**	-1.26	**3.07****	**-3.08****	**-7.06****
Group 4	14	43	46	102	228
	(68)	(34)	(114)	(68)	(150)
	-8.08**	1.88	**-8.42****	**5.14****	**8.98****

*p < 0.05; ** p <0.01

APPENDIX 5: STATIC LIFE TABLES

Table 1: Static life table for *E. villosus* calculated from the sum of two populations from two different time points each (1993 and 2014).

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying l_x - l_x+1**	**Finite rate of mortality (n_x - n_{x+1}) / n_x**	**Killing power $\log_{10} n_x$ - $\log_{10} n_{x+1}$**
S1	61	1	0.229508	0.229508	0.113232
S2	47	0.770491803	-2.06557	-2.68085	-0.56595
J	173	2.836065574	2.508197	0.884393	0.937016
A1	20	0.327868852	-0.7377	-2.25	-0.51188
A2	65	1.06557377			

Table 2: Static life table for *E. caffer* calculated from the sum of two populations.

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying l_x - l_x+1**	**Finite rate of mortality (n_x - n_{x+1}) / n_x**	**Killing power $\log_{10} n_x$ - $\log_{10} n_{x+1}$**
S1	95	1	0	0	0
S2	95	1	0.010526	0.010526	0.004596
J	94	0.989473684	0.378947	0.382979	0.2097
A1	58	0.610526316	0.505263	0.827586	0.763428
A2	10	0.105263158			

Table 3: Static life table for *E. lehmannii* calculated from the sum of four populations.

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying l_x - l_x+1**	**Finite rate of mortality (n_x - n_{x+1}) / n_x**	**Killing power $\log_{10} n_x$ - $\log_{10} n_{x+1}$**
S1	15	1	0.933333	0.933333	1.176091
S2	1	0.066667	-2.2	-33	-1.53148
J	34	2.266667	0.933333	0.411765	0.230449
A1	20	1.333333	-3.6	-2.7	-0.5682
A2	74	4.933333			

Table 4: Static life table for *E. middelburgensis* calculated from one population.

x	*n_x*	*l_x*	*d_x*	*q_x*	*k_x*
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
J	31	1	0.419355	0.419355	0.236089
A1	18	0.580645	-1.80645	-3.11111	-0.61396
A2	74	2.387097			

Table 5: Static life table for *E. longifolius* calculated from the sum of four populations, three of which included two time points (1993 and 2014).

x	*n_x*	*l_x*	*d_x*	*q_x*	*k_x*
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
S1	126	1	0.777778	0.777778	0.653213
S2	28	0.222222	-1.03968	-4.67857	-0.75424
J	159	1.261905	1	0.792453	0.682883
A1	33	0.261905	-0.38095	-1.45455	-0.38997
A2	81	0.642857			

Table 6: Static life table for *E. natalensis* calculated from the sum of two populations.

x	*n_x*	*l_x*	*d_x*	*q_x*	*k_x*
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
S1	72	18	17	0.944444	1.255273
S2	4	1	-12.75	-12.75	-1.1383
J	55	13.75	5.75	0.418182	0.235213
A1	32	8	-0.5	-0.0625	-0.02633
A2	34	8.5			

Table 7: Static life table for *E. friderici-guilielmi* calculated from the sum of four populations.

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
S1	48	1	0.083333	0.083333	0.037789
S2	44	0.916667	-0.875	-0.95455	-0.29105
J	86	1.791667	0.666667	0.372093	0.202105
A1	54	1.125	-2.77083	-2.46296	-0.53945
A2	187	3.895833			

Table 8: Static life table for *E. lanatus* calculated from one population.

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
J	4	1	-3.25	-3.25	-0.62839
A1	17	4.25	2	0.470588	0.276206
A2	9	2.25			

Table 9: Static life table for *E. ferox* calculated from one population.

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
S1	5	1	0	0	0
S2	5	1	0	0	0
J	5	1	-0.2	-0.2	-0.07918
A1	6	1.2	0.4	0.333333	0.176091
A2	4	0.8			

Table 10: Static life table for *E. transvenosus* calculated from one population.

x	n_x	l_x	d_x	q_x	k_x
Stage Class	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x+1$**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
J	18	1	0.388889	0.388889	0.21388
A1	11	0.611111	0.388889	0.636364	0.439333
A2	4	0.222222			

Table 11: Static life table for *E. cycadifolius* calculated from two populations, one of which has two time points (1993 and 2014).

x	n_x	l_x	d_x	q_x	k_x
Category	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x$+1**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
S1	14	1	-1.35714	-1.35714	-0.37239
S2	33	2.357143	0.785714	0.333333	0.176091
J	22	1.571429	0.071429	0.045455	0.020203
A1	21	1.5	-7.21429	-4.80952	-0.76414
A2	122	8.714286			

Table 12: Static life table for *E. horridus* calculated from two populations, one of which has two time points (1994 and 2014).

x	n_x	l_x	d_x	q_x	k_x
Category	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x$+1**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
J	20	1	0.2	0.2	0.09691
A1	16	0.8	-1.95	-2.4375	-0.53624
A2	55	2.75			

Table 13: Static life table for *E. trispinosus* calculated from two populations.

x	n_x	l_x	d_x	q_x	k_x
Category	**Observed number**	**Proportion surviving n_x / n_0**	**Proportion dying $l_x - l_x$+1**	**Finite rate of mortality $(n_x - n_{x+1}) / n_x$**	**Killing power $\log_{10} n_x - \log_{10} n_{x+1}$**
J	4	1	-15.25	-15.25	-1.21085
A1	65	16.25	3.5	0.215385	0.105343
A2	51	12.75			