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

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

Keywords Conservation planning · Environmental predictors · Hotspot · Maximum entropy model · Suitable habitat

Introduction

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

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

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

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

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

Materials and methods

Study area and species

The study area lies in the eastern-most extreme of the Cape Floristic Region referred to as the Greater Cape Floristic Region (GCFR) (Bergh et al. 2014) within the Albany Centre of Endemism, South Africa (Smith van Wyk 2001). The area has a predominantly bi-modal rainfall pattern, with peaks in spring (September–November) and autumn (March–April). Populations of *Encephalartos latifrons* are associated with the Mediterranean-climate Fynbos Biome, specifically the Suurberg Quartzite Fynbos (SQF) (Rebelo et al. 2006). SQF is characterised by sandy, infertile soils, and can be distinguished from other types of fynbos as occurring on finer-textured soils, with relatively higher nutrient levels, where summer droughts are less pronounced (Cowling 1983; Campbell 1986). The study area (Fig. 1) was divided into two fire-climate zones, as adapted from Kraaij et al. (2014). In the western inland region, around Grahamstown, the fire frequency is typically every 4–6 years; in the coastal region, around the village of Bathurst, fires are typical at most every 15 years (Kraaij et al. 2014; unpublished records obtained from landowners). The SQF vegetation becomes patchy and fragmented in the coastal areas and surrounded by Kowie Thicket and Albany Thicket vegetation (Lubke et al. 1986; Hoare et al. 2006). This inland/coastal delineation roughly corresponds to the ecoregions described by Kleynhans et al. (2005) and the climate-gradient zones of Thuiller et al. (2004) within the GCFR.

Model development

Selection of the study area

The chosen area applied to the model represents the two ecoregions within which *E. latifrons* populations are found, namely the Southern Fold Mountains and the South-Eastern Coastal Belt ecoregions (as delineated by Kleynhans et al. 2005), derived from data on terrain and vegetation with altitude, rainfall, runoff variability, air temperature, geology and soil. Ecoregion GIS data were obtained from the South African Department of

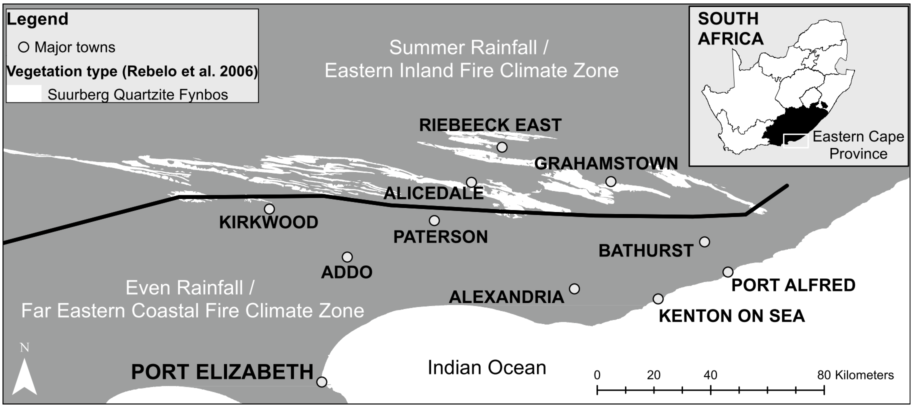

Fig. 1 Map of the study area showing Suurberg Quartzite Fynbos, a vegetation group of the Fynbos Biome associated with the distribution of the Albany cycad *Encephalartos latifrons*. The solid black line denotes separation of the study area into two rainfall regions (adapted from Rebelo et al. 2006) and different fire-climate zones (adapted from Kraaij et al. 2014)

Water and Sanitation (http://www.dwa.gov.za/iwqs/gis_data/ecoregions/get-ecoregions.aspx. Accessed 30/03/2015). The study area represents the geographical range considered accessible to this species, which is an important consideration in the modelling process (Fourcade et al. 2014). The biotic–abiotic–mobility (BAM) model proposed by Soberón and Townsend Peterson (2005) was used to describe the model for *E. latifrons*, where A = M ≠ B. Mobility (M) is the area accessible to the species, given its dispersal ability, and is derived from the two ecoregions (representing an area of relative homogeneity) where *E. latifrons* populations currently exist. The fundamental niche (A) would therefore be represented by the area M (Soberón and Townsend Peterson 2005). The limiting region B in the theoretical model represents the poorly understood biotic factors potentially affecting the distribution of the species but not included in the analysis.

Model resolution

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

Occurrence data

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

Three areas where populations of *E. latifrons* were known to have occurred were not included in the model and were used to test the model results: (1) Beggars Bush Nature Reserve, since unpublished permit records held at the DEDEA, as well as interviews with the managers who were in charge of the reserve at the time, indicated that this reserve once held a large population of *E. latifrons*. Because cycad theft was a major problem at the reserve, a decision was taken to remove all the wild plants in the reserve and place them at a nearby Forest Station, from where they subsequently disappeared. (2) A private farm in the Howieson's Poort area, a wild *E. latifrons* plant was growing according to herbarium records. (3) A private farm near Fraser's Camp, where an unpublished 1981 survey report (written by nature conservation authorities) mentions three large clumps of *E. latifrons* (> 20 plants), where males and females occurred in close proximity. The report also states that *E. latifrons* at the site were reproducing in a natural way since seedlings were evident. The plants were eventually stolen from the property (according to records detailing the court case), but subsequently found and confiscated. In all three cases, it was not possible to determine the exact location of the plants. These could not be included as locality points but were useful for testing the results of the model.

Environmental data

Four categories of environmental predictors were chosen for input into the model, based on relevance to *E. latifrons* distribution: climate, geology, vegetation, and topography (Table 1). Climate data were obtained from the WorldClim database, at a spatial resolution of 1 km^2 (Hijmans et al. 2005; http://worldclim.org/). To test autocorrelations of the climate data (a potential source of bias) the SDMtoolbox function was used in ArcGIS 10.2 (ESRI 2012; Brown 2014); climate predictors were considered highly correlated if Pearson's coefficient was ≥ 0.8. The 1:250,000 geological layer was obtained from the Council for Geoscience, South Africa. Geology was used as a substitute for soil data which were not readily available for the study area. Populations of *E. latifrons* are predominantly associated with rock outcrops of the Witteberg Group, where the soil is typically shallow, sandy and acidic as a result of the slow weathering of sandstones and quartzites (Shone and Booth 2005; DEA 2011). Three

Table 1 Categories of environmental data included in the MaxEnt model for identifying suitable habitat for *Encephalartos latifrons*

Category	Predictor	Grain	Source
Climate	BIO1	1 km	WorldClim database (www.worldclim.org.za)
	BIO3	1 km	
	BIO12	1 km	
	BIO5	1 km	
	BIO6	1 km	
Topography	Elevation (m above sea level)	1000 m	Generated in ArcGIS
	Slope (°)	1 km	
Geology	Substrate	1:250,000 geological layer	Council for Geoscience, South Africa
Landsat indices of vegetation	Albedo	30 m	Landsat 8 imagery (www.earthexplorer.usgs.gov, accessed 05/03/2015)
	TC brightness	30 m	
	TC wetness	30 m	
	TC greenness	30 m	

All layers were projected to the Transverse Mercator WGS84 datum coordinate system. WorldClim bioclimatic variables are coded as follows: BIO1—annual mean temperature (°C × 10), BIO3—isothermality (mean diurnal temperature range (BIO2)/temperature annual range (BIO7)) (unit less ratio × 100), BIO12—annual precipitation (mm), BIO5—maximum temperature in the warmest month (°C × 10), BIO6—maximum temperature in the coldest month (°C × 10)

vegetation indices as well as an albedo index (a measure of the Earth's surface reflectance, included as a predictor of rock outcrops) were extracted from remotely sensed data for input into the model. Remotely sensed data in the form of satellite imagery have been successful in predicting suitable habitats of rare and endangered species (Raxworthy et al. 2003; Lahoz-Monfort et al. 2010; Gogol-Prokurat 2011) and are appropriate for measuring the habitat characteristics of such species (Bradley et al. 2012). Albedo values vary based on land cover, where vegetation associated with rock outcrops has a higher value as compared with thicket and forest areas (Roy et al. 2014). Landsat Operational Land Imager (OLI) data (path 170, row 83; path 171, row 83), acquired for spring 2013 and 2014, was used to calculate albedo (total reflectance) and the three vegetation indices: tasselled cap (TC) brightness, TC wetness, and TC greenness. Tasselled-cap transformation converts original Landsat bands into three biologically meaningful indicators of vegetation (Kauth and Thomas 1976). Prior to transforming Landsat images into the indices mentioned, top-of-atmosphere reflectance (i.e. image correction for the fluctuating scattering and absorbing effects of atmospheric gases) was calculated from the raw calibrated digital numbers of the image. Topographical variables included elevation above sea level (m) and slope (degrees), calculated with ArcGIS Spatial Analyst tools (ESRI 2012). Hillshade (a predictor of shaded relief) and aspect (a predictor of slope direction) were excluded because model performance improved with their exclusion.

Model calibration

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

Model validation

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

Model parameters

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

Conservation gap-analysis

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

Conservation decisions

To assess the past conservation decisions involving *E. latifrons* plants made by conservation authorities (see Introduction), a decision-making scheme (see Guisan et al. 2013) was constructed based on the SDM results. The first step was problem identification: two conservation problems faced by conservation authorities involved the placement of *E. latifrons* plants (i.e. confiscated plants and seedlings for restoration) and a common set of objectives (explained in Table 2: the objectives apply to both problems, resulting in the same decision-making process). In this case, the plants (translocated and seedlings) originated from the same population. Once the objectives were defined, the translocation and restoration sites (both within formal protected areas) were compared with areas of suitable habitat identified by the SDM. The next three steps in the decision-making process (namely, defining possible actions, identifying the consequences of those actions, and a trade-off analysis) were followed according to Guisan et al. (2013).

Results

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

Environmental predictors

The geological group represented by the Witpoort Formation (Witteberg Group, Lake Mentz Subgroup, Paleozoic Cape Supergroup, and Cape Fold Belt) and associated SQF

Table 2 The first steps of structured decision analysis (Guisan et al. 2013) for the conservation problems faced by South African authorities in regard to placement of *Encephalartos latifrons* wild plants: problem identification and defining objectives

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

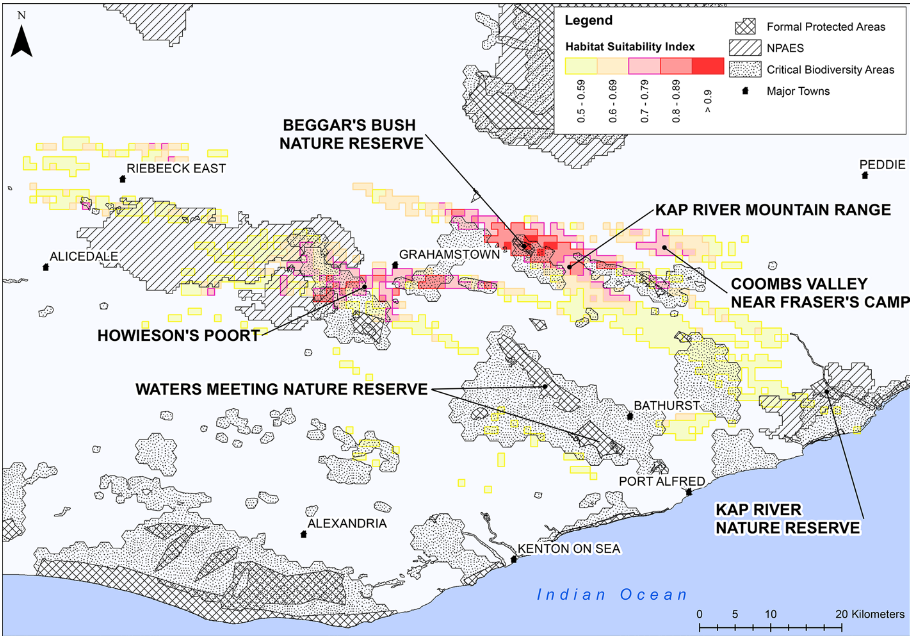

Fig. 2 Habitat suitability index map for the Albany cycad *Encephalartos latifrons*, including formal protected areas, areas forming part of the NPAES, and critical biodiversity areas (i.e. CBA1 areas, as defined in Berliner et al. 2007), Eastern Cape, South Africa

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

Protected and conservation areas

The model results show that an area of 5882 ha (0.51% of the study area) represents highly suitable habitat for *E. latifrons* (Table 3). Of this area, only 276 ha of highly suitable habitat are contained within one formal state protected area (Beggar's Bush Nature Reserve). In terms of the National Protected Area Expansion Strategy, a further 220 ha (0.17% of the NPAES within the study area) of highly suitable habitat is contained in the Howieson's Poort area and along the Highlands Road outside Grahamstown. There are large conservation gaps, however, with most of the suitable habitat in the hills south of Grahamstown and in the Kap River Mountains not included in this prioritised area. The CBAs within the study area contain a larger portion of highly suitable habitat (1.18%) over a wider extent

Table 3 Areas (in ha) of predicted habitat suitability within the study area (see Fig. 2) in relation to three conservation layers: the current network of formal protected areas, the network of the National Protected Area Expansion Strategy (NPAES), and critical biodiversity areas (i.e. CBAs of category CBA1)

Suitability values	Habitat suitability categories (subjectively defined)	Suitable habitat within the study area (ha)	Proportion of suitable habitat within the study area (%)	Proportion of suitable habitat within the current network of state protected areas (%)	Proportion of suitable habitat identified in the NPAES (%)	Proportion of suitable habitat within CBA1 (%)
0–0.39	Highly unsuitable	1,036,261	91.30	99.46	86.53	89.80
0.4–0.49	Unsuitable	35,608	3.14	0.13	5.98	3.15
0.5–0.69	Marginally suitable	46,935	4.13	0.21	6.6	4.13
0.7–0.79	Moderately suitable	10,472	0.92	0.03	0.7	1.74
0.8–0.94	Highly suitable (critical)	5881	0.51	0.17	0.18	1.18

(2446 ha), and also include more of the Highlands area extending towards Howieson's Poort and the hills south of Grahamstown. Some sections of the Kap River Mountains and the area around Beggar's Bush are also included as CBA1. The areas for *E. latifrons* protection previously listed by Osborne (1995a) were identified as highly unsuitable or unsuitable habitat in the Waters Meeting Nature Reserve and the Kowie Local Nature Reserve. Finally, no existing in situ populations of *E. latifrons* exist within a formal protected area, except for plants that were artificially placed there through restoration and/or translocation.

Discussion

Environmental predictors

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

Populations of *E. latifrons* appear to be restricted to quarzitic rock outcrops owing to their slow life history (less interspecific competition), dual fire avoidance/tolerance, and stress-tolerance strategies (first author's unpublished data). Accordingly, an albedo index was included in the model. It is not certain why albedo was not an important predictor for *E. latifrons* habitat in the broad-scale model, but this factor should be included in a finer-scale model for analysing local population distribution. Indices of habitat rockiness and fire-frequency were poor predictors in the case of other cycad species growing in arid-zone vegetation types in Australia (Preece et al. 2007). Though fire is an important environmental disturbance, its frequency was not included in the model here yet should be considered in local-scale modelling, depending data availability. SQF (also known as Grassy Fynbos) is prone to frequent fires, which includes the two core *E. latifrons* suitable habitat areas identified by the model. A high fire-frequency in the core *E. latifrons* area (Eastern Inland Fire Zone) is in contrast to the fire frequency nearer the coast (South-Eastern Coastal

Zone), where marginally suitable habitat was identified. The cycads in this coastal region may be outlier populations, based on interpretation of the model results predicting areas of marginally suitable habitat for *E. latifrons*. Finer-scale modelling may reveal smaller patches of suitable habitat in the coastal area with the inclusion of data for soils, fire history, and other factors not included in the broad-scale model.

Conservation decisions

Translocation site

Based on the results of the SDM, the symbol (+) indicates that the objective was met by the reserve, and the symbol (–) means it was not met (Table 4). The 1993 decision to translocate confiscated plants to the Waters Meeting Nature Reserve was assigned the symbol (–) for objective (a) in Table 4. The reserve's vegetation type and the characteristics of the underlying geology resulted in a habitat suitability score of 0 (highly unsuitable) in the SDM. Vegetation in this 4247-ha reserve consists of Kowie Thicket and Albany Coastal Belt vegetation (Hoare et al. 2006; Stickler and Shackleton 2014) overlying the Weltevrede Formation (oldest formation of the Witteberg Group). Stickler and Shackleton (2014) mention that two *Encephalartos* species are found on the reserve, *E. altensteinii* and *E. latifrons*, but fail to mention that *E. latifrons* was artificially translocated there (Daly et al. 2006). The results indicate that the geological and vegetation features of this reserve mark it as unsuitable for *E. latifrons*. The primary difference between the Witpoort Formation (an important predictor for *E. latifrons* distribution) and the Weltevrede Formation (the main geological group underlying the Waters Meeting Nature Reserve) is the proportion of quartzite to shales: the Witpoort Formation has a far greater proportion of quartz arenites (> 85%), in contrast to the Weltevrede Formation where shales occur as the greater proportion (Booth 2002). The quartz arenites of the Witpoort Formation form the weathered

Table 4 Table showing whether or not the defined conservation objective was met, based on the results of the species distribution model (SDM), for two conservation decisions made by South African authorities in regard to the placement of *Encephalartos latifrons* wild plants in 1993 (cf. Table 2)

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

The symbol (+) indicates that the objective was met by the reserve, and the symbol (–) means it was not met rocky outcrops to which species like *E. latifrons* and other Fynbos paleoendemics (such as the Near Threatened tree *Oldenburgia grandis*) are currently restricted (Meadows and Dewey 1986). Waters Meeting Nature Reserve is a formal protected area (+) but is approximately 20 kilometres from the origin population of the translocated plants (–), which is relatively far given the species' highly restricted distribution. Moreover, no historical records suggest that *E. latifrons* has ever occurred within the reserve's area. Security from theft is low (+) since access to the reserve is restricted and closely controlled. Lastly, the possible genetic contamination of wild plants at the translocation site is high (–) as it falls within the natural distribution range of *E. altensteinni* (Stickler and Shackleton 2014).

Restoration site

The decision to choose the Roundhill Nature Reserve as a restoration site for wild cycad seedlings was assigned the symbol (–) for objective (a) in Table 4. The reserve is situated in the middle of a Witpoort Formation quartzite ridge (forming the Kap River Mountains) that extends in a continuous band towards the coast. However, the reserve is overlaid by the remains of a limestone deposit belonging to the Bathurst Formation (Algoa Group), resulting in a habitat-suitability score of 0 in the SDM. The *E. latifrons* seedlings were planted on this limestone deposit (or *koppie*) (Donaldson 2003) and none have survived. The site is approximately 13 km from the original population (+), which is relatively close to the remaining wild population. The Roundhill Nature Reserve is a formal protected area (+), security there is inadequate (–). In addition, there is no historical record of *E. latifrons* or any other *Encephalartos* species on the reserve, thus the possibility of genetic contamination would be low (–) had the plants survived.

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

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

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

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

Conservation planning

Areas of suitable habitat for *E. latifrons* are poorly protected in the current network of formal state protected areas, as shown in the broad-scale model. The total area identified as suitable habitat may be slightly increased with finer-scale modelling, perhaps with smaller patches of SQF identified nearer the coast or on reserves, such as the Kap River Nature Reserve. Even so, it is proposed that formal protected areas will play a small role for *E. latifrons* conservation in the future, based on the areas of suitable habitat encompassed in the NPAES. No *E. latifrons* populations occur in formal protected areas (as currently known) except for those translocated there (Daly et al. 2006). The SQF is classified as

Least Threatened throughout its range, with only 1% of the areas transformed (Rebelo et al. 2006) and approximately 32% of the vegetation type conserved (the conservation target is 23%). Margules and Pressey (2000) advise that areas containing rare and/or threatened species should be allocated protection status irrespective of their contribution to conservation targets, and they refer to these as 'commitment areas.' Another solution to the gaps in formal protected areas as regards rare species like *E. latifrons* (with many other rare and endangered species particularly prevalent in the Cape region: Cowling et al. 2003) is the establishment of micro-reserves. Micro-reserves have played an important role in protecting rare and endangered flora in eastern Spain (Laguna et al. 2004), for example, and provision for the formation of these reserves (as 'special nature reserves') is accommodated within South African conservation legislation. The formal protected areas previously identified as '*E. latifrons* reserve' by Osborne (1995a) included the Waters Meeting Nature Reserve (incorporating the Bathurst State Forest), yet the present investigation found it is not representative of suitable habitat for *E. latifrons* based on the modelling results. The one formal protected area that stood out as containing critical habitat for *E. latifrons* is Beggar's Bush Nature Reserve—a conclusion supported by both the SDM results and historical records. The network of areas identified by the NPAES includes a slightly greater amount of suitable habitat for *E. latifrons*, although an essential conservation gap remains around Grahamstown and the Kap River Mountain Range. Among all the conservation layers considered in this study, the CBA1 areas provide the largest area of suitable habitat for *E. latifrons*; unfortunately, these are not legally binding areas of conservation but their identification serves only as a guideline for conservation planning.

Future research

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

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

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

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