Environmental barriers to the distribution of the genus Lithops: present, past and future

Article *in* Bradleya · May 2022

DOI: 10.25223/brad.sp40.2022.a5

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Bradleya special **2022** pages 43–50

Environmental barriers to the distribution of the genus *Lithops*: present, past and future

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Photograph: Ivor Crook

Summary: The genus *Lithops* (Aizoaceae; Ruschioideae) is widely distributed across South Africa, Namibia and into Botswana. Using the environmental niche modelling software Maxent, 416 *Lithops* localities were examined against environmental variables of climate, dominant soil, geology, ecoregion and altitude. Predictions obtained suggested that a combination of suitable soil or geology and climatic conditions determine the limits of the range of distribution of the genus. Predictions for paleoclimatic conditions at the last glacial maximum suggested the area of distribution of the genus *Lithops* was significantly contracted at this time but that all current species had at least one locality suitable to sustain them. Predictions using future climate simulations suggest a significant reduction in the range of the genus and potential extinction of two species due to habitats becoming unsuitable. A prediction using suitability of different ecoregions supports the hypothesis for an origin of the genus near to the mouth of the Orange River.

Keywords: *Lithops*, Maxent niche-modelling, climate change, geology, distribution

Zusammenfassung: The genus *Lithops* (Aizoaceae; Ruschioideae) is widely distributed across South Africa, Namibia and into Botswana. Using the environmental niche modelling software Maxent, 416 *Lithops* localities were examined against environmental variables of climate, dominant soil, geology, ecoregion and altitude. Predictions obtained suggested that a combination of suitable soil or geology and climatic conditions determine the limits of the range of distribution of the genus. Predictions for paleoclimatic conditions at the last glacial maximum suggested the area of distribution of the genus *Lithops* was significantly contracted at this time but that all current species had at least one locality suitable to sustain them. Predictions using future climate simulations suggest a significant reduction in the range of the genus and potential extinction of two species due to habitats becoming unsuitable. A prediction using suitability of different ecoregions supports the hypothesis for an origin of the genus near to the mouth of the Orange River.

Introduction

The genus *Lithops* (Aizoaceae; Ruschioideae) contains about thirty-eight species of dwarf, highly succulent plants. They occur either as a single pair of leaves or as a small cluster of paired leaves (Figure 1). Examination of the morphological appearance of *Lithops*, as in other plant genera, often leads to differing classification systems. Most studies of the genus focus on one or more of geographical locality, morphological features of the upper surface of the plant or the seed structure to define the species (Cole, 1988; Jainta, 2017; Earle & Young, 2020). Opinion varies on what constitutes a species and how many species the genus contains. The genus has one of the largest areas of distribution of any genus within the dwarf Ruschioideae. This includes

Figure 1. *Lithops localis*, Eastern Cape, South Africa.

	Source Website and page	Source document URL
Occurrence data		
Lithops Localities	Interactive *Lithops* Locality Map (https://mesemb.ru/map/index.en)	https://mesemb.ru/map/lithops-coles-mesemb_ru.kmz
Environmental data		
Present world climate	Global Climate and Weather Data (http://www.worldclim.org)	https://www.worldclim.org/data/v1.4/worldclim14.html
Paleoclimate data	Global Climate and Weather Data (http://www.worldclim.org)	https://www.worldclim.org/data/v1.4/paleo1.4.html
Future Climate Simulation	Global Climate and Weather Data (http://www.worldclim.org)	https://www.worldclim.org/data/v1.4/cmip5_2.5m.html
Surficial Geology	USA Department of the Interior (https://catalog.data.gov/eu/dataset/surficial-geology-of-africa-geo7-2ag)	https://catalog.data.gov/eu/dataset/surficial-geology-of-africa-geo7-2ag/resource/58c8fb31-7050-44ed-bfd5-08627a8a3c7b
Dominant Soil	Soil and Terrain Database for Southern Africa (SOTERSAF) (https://data.isric.org/geonetwork/srv/api/records/3571c1f3-159d-442c-b324-0af53d03f12e)	https://files.isric.org/public/soter/SAF-SOTER.zip
Altitude	DIVA-GIS (http://www.diva-gis.org/gdata)	Complete the form to select country and resource type
Ecosystem	World Wildlife Fund (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	https://files.worldwildlife.org/wwfcmsprod/files/Publication/file/6kcchn7e3u_official_teow.zip?_
Software		
DIVA-GIS	DIVA-GIS (http://www.diva-gis.org/download)	https://biogeo.ucdavis.edu/programs/diva/diva75.zip
QGIS	QGIS (https://qgis.org/en/site/forusers/download.html)	https://qgis.org/downloads/QGIS-OSGeo4W-3.16.10-1.msi
MaxEnt	American Museum of Natural History (https://biodiversityinformatics.amnh.org/open_source/maxent/)	Complete the form and submit

Table 1. Categories of data, software and their sources.

South Africa, Namibia and the south-eastern edge of Botswana. Unusually for southern African Aizoaceae (mesembs) its range covers all of the different areas of seasonal precipitation including winter, summer, biennial spring and autumn rainfall areas and fog belt (Hartmann, 2017).

Due to the exploratory work of Desmond Cole and others in the last one hundred years, many populations have been discovered. Cole assigned each of these populations a number. In an attempt to avoid habitat depletion he provided approximate information on the locality of each population. Over 400 populations are known and assigned a Cole number.

A molecular analysis of the genus using the sequences of two DNA markers failed to produce a robust relationship between the various taxa although some resolution was obtained from a whole genome AFLP approach (Kellner et al, 2011). It is often considered that such a lack of clarity of the relationship between various taxa is related to the relative recent evolution and radiation of a genus (Manning et al, 2014). DNA evidence does however, throw some light on dating the origins of the genus *Lithops*. Recent evidence suggests the subfamily Ruschioidiae could have arisen and rapidly diversified from the Aizoaceae in southern Africa as recently as 1.3 to 6.49 million years ago (Valente et al, 2014). This study also suggests that the genus *Lithops* may have been one of the more recent genera of the Ruschioideae to have evolved. It suggests the genus originated approximately 190,000 years ago, with a confidence interval of between 10,000 and 440,000 years (Jainta, 2020). During this time the underlying soil and surficial geology of the area of distribution of *Lithops* has changed little. However, there have been considerable changes to the Earth's climate. *Lithops* have continued to survive during these changing conditions.

Spatial niche modelling is a relatively new tool to help understand the distribution and limitation of plant species and genera. The models compare environmental variables at the localities for the taxon under investigation and produce a map showing the relative suitability of all areas to sustain that taxon. They also identify the relative importance of environmental variables to the model of the taxon under investigation.

The purpose of this study was to examine how environmental factors of climate, geology, soil, altitude and ecoregion affect the distribution of *Lithops* at the present time, to compare this with climate simulations of the past at the last glacial maximum (LGM), approximately 22,000 years before present, and to predict how future climate change may affect the distribution of *Lithops*.

Materials and method

All data used is freely available on the Internet. The locations for the first 416 Cole numbers were obtained as a kmz file from an online source (Boldyrev, 2010). Whilst this does not cover all currently known localities it does include at least one locality from every species. Table 1 lists the categories of environmental data and software used in the study, their source and the website details. The vector datasets were converted into raster format, at the same spatial resolution as the climate data (2.5 minutes of arc), using QGIS (version 3.18).

The choice of the various 'current' climate conditions was driven by consideration of which model was most contemporaneous with the discovery of the localities. Given that Cole's first monograph of the genus was published in 1988, this coincides most closely with the interval used for version 1.4 of the WorldClim climate database which was constructed from an average of the years 1960 to 1990.

Two separate simulations of paleoclimatic conditions derived from this version of the database were used, both generated as part of the Coupled Model Intercomparison Project Phase 5 (CMIP5) of the World Climate Research Programme. We chose the simulations generated at the Max Planck Institute for Meteorology, Hamburg, Germany (MPI) and the National Centre for Atmospheric Research (NCAR), Boulder, USA (CCSM4)

Several different simulations are available that predict future climatic conditions, each being dependent on differing predicted increases in atmospheric CO_2. The scenario chosen was RCP8.5 at 2070. This is a high-emissions scenario predicting mean planetary temperature rises of 2.5 to 3ºC. It was chosen because it is comparable with the highest global mean temperature during the existence of Lithops. Simulations generated at MPI and CCSM4 were chosen.

Maxent software for modelling species niches and distributions was then used to obtain projections of areas of suitability to sustain Lithops (Phillips et al, 2004). Models were generated for several combinations of the sets of environmental variables. This is a well-established method to produce niche probability maps showing the relative degree of environmental suitability for a taxon (Simoes et al, 2019). Default parameters were used for all options except the regularisation multiplier which was set to a value of 2.0. With these options the primary output of Maxent is a map representing the probability of presence of the taxon within each cell of the geographic grid. However, it is difficult to superimpose and identify individual localities over these maps. The Maxent output maps were imported into either DIVA-GIS (version 7.5) or QGIS to enable examination of the predictions in more detail. This permits a clearer view of the fit of the locations to each of the variables.

Results

Multiple predictions were obtained using a variety of combinations of the different environmental variables to understand the influence of each

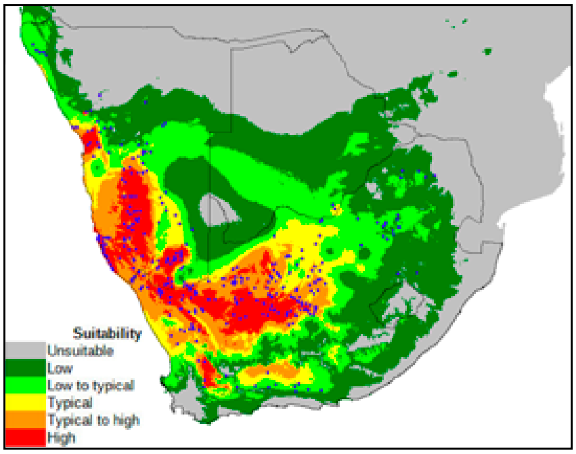

Figure 2. Areas which indicate favourable climatic conditions for the genus *Lithops* using current climate data. The blue dots show locations of Cole numbered Lithops sites C1 to C416.

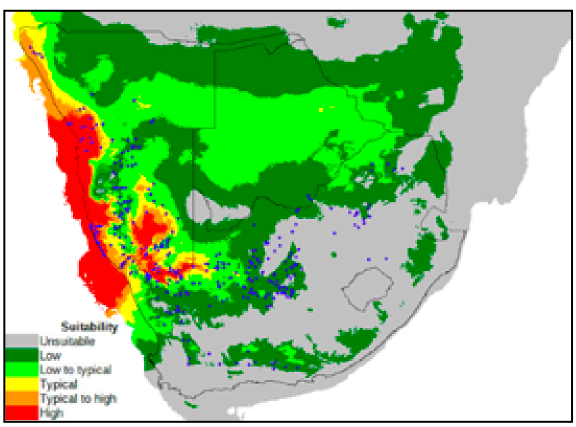

Figure 3. Areas which indicate favourable climatic conditions for the genus *Lithops* using Max Planck Institute for Meteorology Paleoclimate simulation for Last Glacial Maximum, 22,000 years ago. Note the increased land area due to lower mean sea level.

of these on the distribution of *Lithops*. Models using only climatic variables were examined first. Examination of the quality of the predictions using area under the ROC curve (AUC) shows values greater than 0.9 across all predictions indicating a high level of performance of the models. Modelling *Lithops* localities against current climate shows both the relative importance of each of the nineteen climatic variables in isolation (RIi) towards the overall model as a percentage and also the relative importance in combination (RIc) with the model. The latter reveals how much the prediction would differ if certain climatic variables were excluded from the model. Results suggest that some climatic variables are statistically more important than others for defining suitable conditions to sustain *Lithops*. Climatic variables with the greatest importance to predict areas of suitability were – precipitation in the wettest quarter (RIi = 46.7 %) and mean temperature of the coldest quarter (RIi = 21.1%). Four variables substantially reduced the performance of the model if they were excluded. These were – precipitation in the wettest month (RIc = 26.5%), mean temperature in the coldest quarter (RIc = 17.5%), annual mean temperature (RIc = 12.7%) and minimum temperature in the coldest month (RIc = 9.7%). All other variables each contributed less than 6% towards the overall model. Seasonality of rainfall shows poor correlation to the distribution of the genus (2.1%) but this was to be expected as *Lithops* are distributed across all seasons of rainfall. However, the total annual amount of rainfall does have significant importance. It has also been suggested that the importance of individual climatic variables differs significantly from species to species within the genus (A. Young, pers. comm.). A model using all climatic variables was produced and displayed in DIVA_GIS so each locality could be visualised against suitability of climate to sustain the genus. Adjusting the colour map showed the lowest probability of presence that included all except one locality was 0.05. This value for the minimal suitability of conditions to sustain *Lithops* was then used as the cut off point for unsuitable conditions across all projection maps. It is also noted that the area of land suitable to sustain *Lithops* is not a close fit to its current localities. There is a large area of southern Botswana to the north of the main east to west arm of distribution where the climate is suitable to sustain *Lithops* but no colonies have been found. (Figure 2).

Once a model of required conditions to sustain Lithops is established for the recent climate it is then possible to analyse the locations against simulations of past climate at the coldest part of the last glacial period. This can predict suitable areas of distribution for the genus at this point in the past. Using the MPI simulation, predicted areas of climatic suitability at LGM, about 22,000 years ago, are shown in figure 3. The Maxent projections for both MPI and CCSM4 simulations of climate at LGM look slightly different. However, both show two important details. The area of suitability for the genus *Lithops* contracts significantly at LGM with many current localities no longer in areas suitable to sustain them. Analysis of the localities however, shows that all the current species had

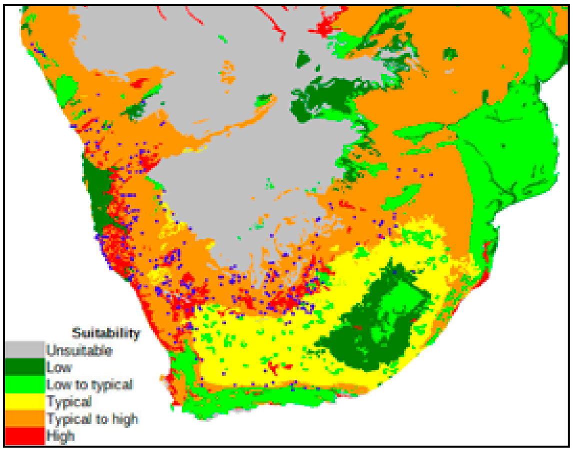

Figure 4. Areas which indicate favourable surficial geology for the genus *Lithops*.

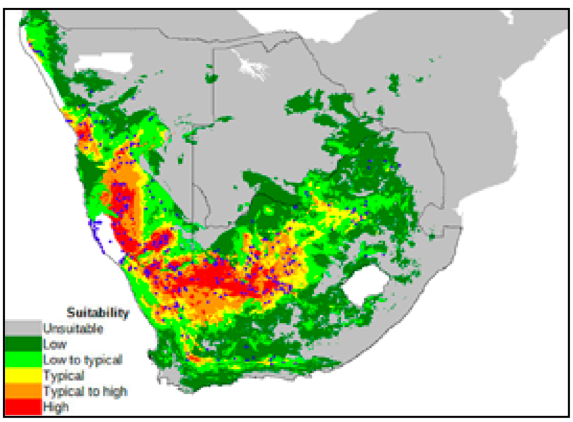

Figure 5. Areas indicating suitability to sustain *Lithops* predicted using both current climate and dominant soil.

at least some or all of their current distribution within areas of climate suitable to sustain them. This suggests it is likely that the current complement of species could have been present through the last glacial maximum.

Predictions generated using surficial geology and dominant soil look similar. This is not surprising as there has been no large-scale glacial event affecting southern Africa during the existence of *Lithops* so there cannot have been a major disconnection between dominant soils and surficial geology. (G. Lees Pers. Comm.). Over large areas, these predictions show a closer fit of localities to the area of distribution of *Lithops* than climate based predictions alone. Interrogation of the map shows the most suitable bedrock geology to be Precambrian rock but there is also a preference for other Paleozoic geology and igneous Mesozoic rock. The results also suggest several ages of rock may be unsuitable to sustain *Lithops*. These include the mainly Cenozoic rock of southern Botswana, coastal Holocene rock of central Namibia and Triassic rocks of the Eastern Cape. Examining the dominant soil map there is an area of no available data in southwest Namibia. This corresponds with the Tsaukhaeb (Sperrgebiet) National Park. The map shows that there are large areas of Arenosols covering most of eastern and north-western Botswana and large parts of eastern Namibia. Arenosols that form in hot, arid environments are usually sandy soils. There are no known *Lithops* localities where Arenosols are the underlying dominant soil. (Figure 4). A combined prediction of current climatic variables and dominant soils is shown in figure 5. This shows a closer fit of *Lithops* localities to suitable environmental conditions than either climatic or dominant soil predictions alone.

Anthropogenic climate change is frequently considered to be a threat to the continued survival of plant localities due to the associated changes in climatic conditions, particularly increased temperature. Predictions using MPI and CCSM4 simulations of potential future climate produced similar but slightly different maps. (Figue 6). Both show a substantial contraction of the overall area suitable to sustain *Lithops.* Northern and eastern Namibia as well as much of the eastern part of South Africa and Botswana are predicted to have climatic conditions unsuitable to sustain *Lithops* by 2070. For the majority of affected species this predicts a loss of range but some localities are retained within areas of climatic conditions suitable to sustain *Lithops*. However, in the future *Lithops werneri* and *Lithops coleorum* are predicted to no longer retain locations in areas of climatic suitability.

Ecoregions are large areas each tending to have their own characteristic biodiversity. At the present time, *Lithops* are distributed across eight ecoregions. The prediction examining suitability of these ecoregions to sustain *Lithops* is shown in figure 7 and indicates the most suitable ecoregions to be the Nama and Succulent Karoo. Namib desert and Namib savannah woodlands are predicted to have typical to high suitability. Kaokoveld desert and Kalahari xeric savannah display typical suitability and high veld grasslands and South African bushveld a lesser suitability. There appear to be no *Lithops* localities within the southern Fynbos ecoregion.

A prediction of suitability generated from the altitude of each locality failed to produce significant results. This was unsurprising since

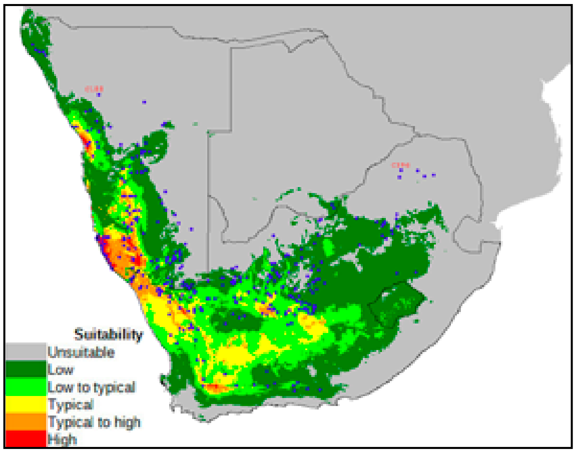

Figure 6. Areas indicating suitability to sustain *Lithops* predicted using both future climate simulation (RCP8.5@2070) and surficial geology. C396 = *Lithops coleorum*, C188 = *Lithops werneri.*

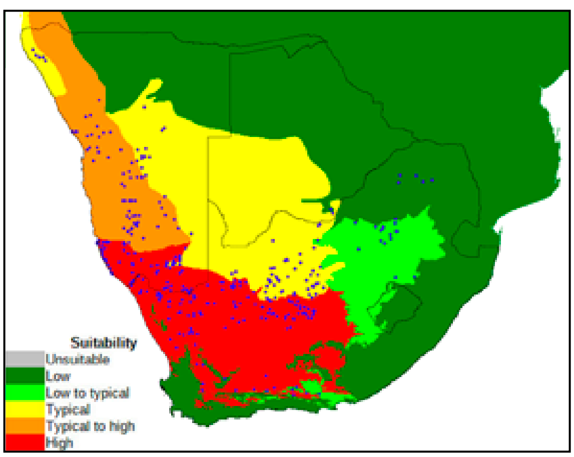

Figure 7. Areas indicating suitability to sustain *Lithops* predicted using ecoregions alone.

Lithops populations have been found at sea-level (e.g. C81) and at altitudes in excess of 2,000m on the Brandberg Mountain in Namibia (e.g. C383).

Discussion

The genus *Lithops* differs from many other genera of dwarf mesembs in two crucial ways. It occupies a large area of distribution and is spread across all areas of seasonality of rainfall.

Lithops appear to tolerate a wide range of climatic conditions. Figure 2 shows that *Lithops* populations can be sustained with climatic conditions as low as a probability of 0.05 suitability. This suggests that *Lithops* can be considered as niche specialists, whose localised conditions may provide some resilience. Predictions for *Lithops* using recent climatic variables alone show a poor fit of known localities to the area of suitable climate to sustain them. A detailed examination of figure 2 shows that there are areas with favourable climatic conditions where *Lithops* are not currently known to grow. Large areas of Botswana and beyond are predicted to have a suitable climate to sustain *Lithops* but where plants have not been observed. There are at least two explanations for this. It could be because they are there but yet to be discovered. Despite new colonies still being discovered in isolated and remote areas it seems unlikely that large numbers of colonies remain undiscovered given that *Lithops* are considered horticulturally important plants and a lot of effort has been expended over many years to discover new colonies in different places. There is perhaps a more likely explanation. Other factors, such as the lack of suitable underlying geology, soil or vegetation type, prevents *Lithops* from colonising these areas. If the latter explanation is accepted then most of Botswana cannot support *Lithops* due to factors independent of climate. Comparison with figure 3 at the LGM shows roughly the same large area of Botswana as having suitable climate to sustain *Lithops* at that time. As *Lithops* do not currently occupy this area due to non-climatic factors it seems likely that they would not have done so in cooler times. Thus the possibility that they could have migrated north into this area during climatic cooling before the LGM then south with subsequent climatic warming seems unlikely. There are also some current localities that fall outside areas with suitable climate to sustain *Lithops* at the LGM. One suggestion is that they may have existed through the LGM in these localities in small pockets of suitable microclimate. However, it is probably more likely that *Lithops* were not present in these areas during the LGM.

Models for *Lithops* using dominant soil better explain the distribution. In parts of southern Botswana that possess a suitable climate but for which there are no known localities the dominant soil type is arensols. Arenosols, in dry, arid environments produce sandy soils. This indicates the most likely cause for the absence of *Lithops* populations in much of Botswana is due to the dominant sandy soils which are unsuitable to sustain them as previously observed by Cole (1988). A similar tight fit model for surficial geology strengthens the assumption that dominant soil and surficial geology are closely linked. Therefore, using soil and surficial geology in the predictions may bias the results of the prediction. This is because there is expected to be little dissociation between surficial geology and dominant soil. Almost identical data for soil and surficial geology used twice in the prediction leads to it taking on twice the importance in the final model.

If we accept the origin of *Lithops* as about 190,000 years ago (Jainta 2020) then for a great percentage of the time *Lithops* has been in existence, global mean annual temperatures have been lower than the present. However, during this time, global mean annual temperatures have, for short intervals, been up to 2.0°C higher than at the present time (NOAA, 2021). This suggests that with a 2.0°C increase in mean global temperature, conditions remain suitable to sustain at least some species of *Lithops*. The prediction for a 2.5 – 3.0°C rise in global mean temperature shows that the area suitable to sustain *Lithops* contracts to a greater degree than it did during the LGM (Figure 6). In Namibia, areas to the centre of the country and the northern coastal region are predicted to become unsuitable to sustain *Lithops* and the southern coastal areas become more suitable. In South Africa, many of the north-eastern localities including the two localities in Botswana are predicted to become unsuitable to sustain *Lithops*. In common with predictions from the LGM, many species may undergo contraction of their distribution range but some populations remain within suitable areas. There are predicted to be two exceptions: *L. coleorum and L. werneri*. Each is only known from one small area of a few square kilometers and are already assessed as vulnerable according to IUCN criteria. Each locality is a significant distance from where climatic conditions are predicted to be suitable to sustain *Lithops* in the future. For *L. coleorum* this distance is about 340km and for *L. werner*i approximately 100km. Whilst both populations appear to have a corridor of suitable climatic and geological conditions to areas of future suitability, the distance involved in such a short time span, considering their limited dispersal by seed, must only intensify the vulnerability of their continued existence in nature.

The prediction made using ecoregions shows different ecoregions have differing suitability to sustain *Lithops*. The Nama and Succulent Karoo ecoregions are predicted to have the highest suitability to sustain *Lithops*. The degree of suitability of ecoregions falls with increasing distance from Nama and Succulent Karoo ecoregions. There are two competing hypotheses as to the origin of the genus *Lithops*. One suggests an origin near Gqeberha, (Port Elizabeth), on the central part of the south coast of South Africa with radiation in a northerly direction (Fearn, 1969a, 1969b). The second suggests an origin in the Gariep centre of endemism close to the mouth of the Orange River on the West coast which separates South Africa from Namibia with radiation outward from this area (Jump, 1988; Kellner et al, 2011). Several factors favour this second hypothesis. These include the vicinity having the greatest species diversity, plants with the most primitive morphological features of flat, smooth, unmarked upper surfaces and that these appear basal in a DNA study. This second hypothesis appears strengthened by the ecoregion prediction. This shows the most suitable conditions occur in the Nama and Succulent Karoo ecoregions which include the area around the Gariep centre and that the genus has potentially evolved and radiated into less suitable ecoregions and climatic conditions over time.

Predictions using altitude failed to show any significant results. All parts of the current range and beyond show typical and high suitability to sustain the *Lithops*. The only exception to this being a thin, coastal band near sea level where suitability drops to typical to low. As already mentioned this is unsurprising as *Lithops* species can be found from sea level to above 2,000m.

Conclusions

The genus *Lithops* appears to have well defined environmental requirements which determine and limit areas suitable to sustain the genus. The most important climatic variables are precipitation in the wettest month and the wettest quarter, mean annual temperature and minimum temperature of the coldest month and mean temperature of the coldest quarter. *Lithops* also show high specificity to certain rock and soil types. Both suitable climatic conditions in combination with dominant soil at a given location must be optimal to sustain *Lithops*. *Lithops* have survived in the past when global mean temperature was up to two degrees higher than present. This suggests that the genus will not become extinct with this degree of planetary warming. However, this model predicts that the extent of occurrence and area of occupancy of the genus will both become smaller. Some species may occupy locations that will no longer have climatic conditions suitable to sustain *Lithops*. This model predicts that *Lithops coleorum* and *Lithops werneri* are at significant risk of extinction with future climate change.

Acknowledgements

The authors would like to thank Peter Bint, Harald Jainta and Graham Lees for their helpful suggestions during preparation of the manuscript and Professor Andrew Young for his comments on multiple drafts leading to the final manuscript.

The authors declare they have no interests in the material and conclusions presented in this paper. ML was responsible for the preparation of data and production of the predictions. He also wrote the Materials and Methods Section. IC was responsible for the development of original objectives of the paper and drafts of all other sections. Both authors contributed to the final version of the manuscript.

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