MODELING THE ENVIRONMENTAL NICHE OF A SOUTH AFRICAN FYNBOS ENDEMIC TREE ALOE, *KUMARA PLICATILIS*, AND PREDICTING IMPACTS OF CLIMATE CHANGE ON THE SPECIES' DISTRIBUTION

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A research report submitted to the Faculty of Science, University of the Witwatersrand, in partial fulfilment of the MSc by Coursework Degree (in Resource Conservation Biology)

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Declaration

I declare that the work presented in this research report is, to the best of my knowledge and belief, my own original work, except as acknowledged in the text. This report is being submitted for the degree of Master of Science and it has not been previously submitted for a degree at this or any other university.

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Abstract

Understanding why species occur where they do and, predicting where species might migrate to under different global change scenarios is an important aspect of biodiversity conservation. Regions that harbour high levels of species diversity and endemism arising from sharp local climatic and ecological gradients are highly susceptible to changing conditions. *Kumara plicatilis* is a tree aloe endemic to the Boland mountain ranges in the species-rich fynbos region in the Western Cape Province of South Africa. The species is currently listed as Least Concern as far as habitat degradation, population decline, invasive species and direct-use threats are concerned although impacts of anthropogenic climate change on this habitat specialist remain undocumented. This study used species distribution models to successfully classify the environmental niche of the species as well as delineate spatial patterns of probable occurrence and abundance based on this niche. In addition, models based on the IPCCs 2014 'best-case' and 'worst-case' climate change scenarios provide projections of changes in the spatial occurrence patterns of *Kumara plicatilis* expected under conditions of shifting climates. Niche-based statistical analyses were further used to draw temporal comparisons between current and future projected ranges to ascertain the degree and properties of shared niche space now and in the future. Results indicate that suitable habitat conditions for the species distribution is irregularly spread around the central and southwestern fynbos region constrained by several climatic and biophysical variables including winter rainfall and temperature conditions as well as vegetation type. The species is expected to experience limited to severe declines in the area of suitable habitat available under mild and harsh climate change conditions, respectively. The patterns arising from these models are in line with the environmental niche measurements which show large degrees of overlap between current and future niche space of the species. These outcomes suggest that *Kumara plicatilis* displays traits of environmental niche conservatism where unsuitable climate and biophysical conditions can limit its geographic range and local extinction of populations can occur due to global change. Whilst the results of this study offer a useful and initial insight into the possible impacts of shifting climates on this species, outcomes from modeling should be interpreted with caution to reach the best management decisions and conservation action for this endemic species.

Key words: conservation, diversity, endemism, global change, niche properties, species distribution models

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Glossary of Abbreviations

AUC	Area Under the Curve
CCR	Core Cape Subregion
CFR	Cape Floristic Region
GCM	Global Climate Model
GPS	Global Positioning System
IPCC	Intergovernmental Panel on Climate Change
LC	Least Concern
m.a.s.l	Meters above sea level
MODIS	Moderate Resolution Imaging Spectroradiometer
NASA	National Aeronautics and Space Administration
NDVI	Normalized Difference Vegetation Index
RCM	Regional Climate Model
RCP	Representative Concentration Pathway
ROC	Receiver Operating Characteristic (analysis)
SCD	Size Class Distribution
SDM	Species Distribution Model

Modeling the environmental niche of a South African fynbos endemic tree aloe, *Kumara plicatilis*, and predicting impacts of climate change on the species' distribution

1. Introduction

1.1 Research problem

Modeling species geographic distributions based on the environmental conditions at known occurrence localities is an important tool in investigative ecology (Phillips *et al.* 2006; Guisan *et al.* 2013). This method is widely used to inform conservation decisions, such as the planning of land use and protected areas, wildlife and invasive species management, as well as interventions for challenges that may arise in the face of global environmental change (Guisan and Thuiller 2005; Jetz *et al.* 2012). Climate change is a significant contributor to global species loss and abundant research focuses on predicting extinctions of many extant species due to shifting climates (Thomas *et al.* 2004; Lewis 2006, Chen *et al.* 2011). One way to lessen the impact of climate change on species and the ecosystems they exist in is to understand why a species occurs where it does. This enables researchers to gain insight into locations where species may move to in future, as well as transitional areas they might need to overcome in the face of changing conditions (Lewis 2006; Dawson *et al.* 2011). Predictive modeling allows us to gather information about species habitats and projected movements, which benefits action against habitat degradation and has the potential to reduce climate change impacts on biodiversity.

Southern Africa is a hotspot for botanical diversity and the region is particularly celebrated for its diversity of Aloe species (Cousins and Witkowski 2012). *Kumara plicatilis* (the fan aloe) is a tree aloe that is endemic to mountain ranges in the Western Cape Province of South Africa (Cousins *et al.* 2013; 2014). The species has been listed as Least Concern on the Red Data List of Southern African Plants and, whilst there is no immediate threat posed by human disturbance or alien invasive species, the potential threat of climate change on this localized habitat specialist remains unclear. As global temperatures are predicted to rise (IPCC 2014), the species could potentially be facing range shifts and population decline similar to that observed and projected for other indigenous plants across the region (Midgley *et al.* 2003 & 2008; Foden *et al.* 2007). This study is intended to identify the environmental factors which contribute to the habitat suitability and distribution of *K. plicatilis.* The outcomes could help to better understand the species niche requirements, locate additional populations of plants, as well as provide a first insight into the potential impacts of climate change on *K. plicatilis*. This pro-active research approach is important in the conservation of present and future distribution ranges of this iconic species.

1.2 Literature Review

1.2.1 Species distribution modeling and its applications in conservation ecology

Understanding why species occur where they do and predicting where species might migrate to under different global change scenarios is an important aspect of conservation (Ahmed *et al.* 2015). Over the last two decades, methods have been developed to estimate distributional ranges based on associations between known occurrences and environmental variables (Guisan and Thullier 2005; Peterson and Soberon 2012). This derived 'environmental profile' is based on observed records and can be used to describe and measure the importance of specific variables and to predict species' distributions across non-surveyed areas, as well as to study environmental change and its ecological consequences (Miller 2010). Building on this concept, there are now several available algorithms (of varying complexity) that underpin species distribution models and fulfil a range of different modeling needs, including ecological niche models, bioclimatic envelope models and habitat suitability models. These various approaches have successfully integrated statistics, biology, and geography to create realistic patterns of current and future species distributions based on the ecology of the species (Peterson 2003b; Miller and Rogan 2007; Ahmed *et al.* 2015).

Species distribution models (SDMs) have changed from being basic resource inventories, used to map and describe animal and plant distributions, into useful, globally applied, decision-making tools for a range of biogeographical and conservation purposes (Miller 2010). SDMs have increasingly been used in several challenging applications including the identification of potential protected areas and important habitats, wildlife management, monitoring vector-borne disease and the spread and risk of alien species, as well as elucidating the impending impacts of anthropogenic change on rare and endangered species (Peterson 2003a; Thuiller *et al.* 2005; Witkowski and Lamont 2006; Moffett *et al.* 2007; Kumar and Stohlgren 2009; Wang *et al.* 2009; Pereira *et al.*, 2011; Khanum *et al.* 2013; Zhang *et al.* 2016).

While active population monitoring remains key to understanding species' ecology, behaviour, and conservation status, SDMs offer a simple way to gain an initial insight and understanding of these aspects based on the limited available information at hand. Long-term population monitoring is expensive and can be detrimental to biodiversity if data accumulation slows down the decision-making process in situations where a species is in rapid decline. Furthermore, observed records usually provide information on just a portion of a species geographic range and there is typically no information available for un-surveyed areas or areas that may be occupied in the future due to global change (Hernandez *et al.* 2006). Modeling future predictions of species distribution based on environmental suitability can provide useful information for

future surveys as well as for the prioritization of conservation needs (Guisan and Thuiller 2005). One of the most notable changes in environmental conditions has been the observed rise in global average temperatures since the mid-twentieth century (Rosenzweig *et al.* 2008). Increases in anthropogenic greenhouse gas emissions has been linked to the rise in global temperatures which is subsequently causing significant changes in the physical and biological systems across the worlds' land surfaces and oceans (Rosenzweig *et al.* 2008). Shifts in species ranges and physiology are now well-documented responses to anthropogenic climate change (Chen *et al.* 2011; Midgley and Thuiller 2011; Fordham *et al.* 2012).

1.2.2 South Africa, its' Global Biodiversity Hotspots and conservation challenges

South Africa has a vast wealth of the globe's biodiversity (Driver *et al.* 2012; DEA 2015). Covering only 2% of the earth's land surface, the country is home to 8% of the world's bird species, 6% of the world's plant and mammal species, and 5% of the world's reptile species, many of which are endemic (Driver *et al.* 2012). With a total of nine biomes, ranging from desert to dense forest, the country comprises a notable variety of habitats, ecosystems and landscapes. In addition, three of the 36 globally recognised biodiversity hotspots fall entirely within South Africa (i.e., the Cape Floristic Region) or incompletely within its borders (i.e., the Succulent Karoo and the Maputaland-Pondoland-Albany hotspot; Driver *et al.* 2012; CEPF 2016). The country also rests between two major oceans, and the coastline is home to 15% of all known coastal marine species (Driver *et al.* 2012).

More than 22 000 plant species are endemic to southern Africa (SANBI 2016). The Cape Floristic Region (CFR), or the Core Cape Subregion (CCR), covers approximately 90 760 km^2, and is home to an estimated 9383 indigenous plant species, about 68% of which are endemic (Bond and Goldblatt 1984; Manning and Goldblatt 2012). Four biomes and several distinct vegetation types (Mucina and Rutherford 2006), each comprising its own set of species and physical features, make up the Subregion (Manning and Goldblatt 2012). This diversity is attributed to a number of different environmental variables and a steep ecological gradient (i.e., the CFR is more geologically and climatically varied compared to its surrounds; Bradshaw 2009), which makes the region unique and able to support a large number of different vegetation types and species (Campbell 1983 & 1986; Cowling *et al*. 2002 & 2014).

The geology of the region consists of an alternating series of quarzitic sandstones and fine-grained shales giving rise to coarse-grained sandy soils which are poor in vital plant nutrients, and richer, clay soils which have a nutrient-intermediate grading respectively (Groves *et al.* 1983; Witkowski and Mitchell 1987; Manning and Goldblatt 2012). Mosaic effects of soils are further influenced by fluctuations in the precipitation across the region (Manning and Goldblatt 2012). Rainfall varies across the region, with

precipitation occurring predominantly or only in the winter months (May-October) in areas west of about 20.5˚E (Mediterranean climate- hot and dry summers); whilst the eastern half of the region receives extensive summer precipitation experiencing seasonal rainfall patterns (Manning and Goldblatt 2012; Bradshaw and Cowling 2014). Inland areas generally have a low total rainfall that comes in mainly in winter (Manning and Goldblatt 2012). Further variation in rainfall is experienced in mountainous areas, with higher levels of precipitation occurring along the mountain slopes facing the prevailing winds compared to the slopes in the lee of these winds (Preston-Whyte and Tyson 1989; Manning and Goldblatt 2012). Across the landscape, rainfall drops from 2 000 mm/year on the high coast-facing mountain ranges, to less than 200 mm/year on the shielded slopes of the interior ranges (Manning and Goldblatt 2012). Elevation and aspect further affect precipitation conditional to the direction of moisture-bearing winds (Manning and Goldblatt 2012; Cowling *et al.* 2014). Fire is another element that plays a fundamental part in the ecology of the CFR and many aspects of the flora have evolved in response to regular and periodic fires (Cowling *et al.* 2005; Keeley *et al.* 2012; Manning and Goldblatt 2012).

The Intergovernmental Panel on Climate Change (IPCC) predicts that sub-Saharan Africa will experience greater warming than the global average and the variability in climate is likely to come with a number of changing phenomena including fluctuating rainfall patterns, and an increase in the occurrence of extreme weather events and natural disasters. Climate change brings novel challenges to the conventional approach of conservation, which focuses on creating and maintaining protected areas, as fluctuating climates are expected to shift the distribution of suitable habitat for many species (Williams *et al.* 2005; Yates *et al*. 2010). With one of the richest and most botanically diverse regions in the world, it is not surprising that climate model predictions place South Africa's biodiversity as highly susceptible to climate change. When assessing the spatial shift of optimum climate conditions for each of South Africa's biomes under future climate conditions, the potential impact is evident with the fynbos region (which makes up a large part of the CFR) being the third most threatened biome projected to experience significant area reduction after Grasslands and the Nama-Karoo (SANBI *et al.* 2013).

The fynbos biome is already threatened by a water crisis and climate change has the potential to additionally alter regional rainfall patterns, with drying experienced in the western areas, as well as an increase in the intensity and frequency of fires (Freeth *et al.* 2008). The species in the CFR have adapted via physiological tolerances to the specific natural climates within the region. Climate change is expected to cause shifts in suitable climate zones and habitats and species are likely to (i) adapt over time to new conditions, (ii) shift their geographic range towards more suitable conditions or, (iii) become locally extinct (globally extinct in the case of endemic species; Freeth *et al.* 2008). Some species will only survive if they are able to colonize new areas and this may be hindered by limited dispersal abilities (Williams *et al.* 2005).

Mitigation and adaptation approaches provide complementary aspects towards reducing risks associated with climate change (IPCC 2014), and understanding the response of species to different environmental changes can help inform these approaches and guide conservation actions needed to protect species from extinction.

1.2.3 The species: Kumara plicatilis

Taxonomy and Description

The fan aloe, previously *Aloe plicatilis* (L.) Mill, was recently moved into the reinstated genus of *Kumara* Medikus (Xanthorrhoeaceae: Asphodeloideae) and is currently accepted under the taxonomic name of *Kumara plicatilis* (L.) Klopper & Gideon F. Smith (Klopper *et al.* 2013). The species is a stout, succulent tree with adult plants (over 50 years old) reaching about 2-5 m in height (Klopper and Smith 2012). The stem branches dichotomously and each branch ends in a set of 12–16 alternate, fleshy leaves arranged in a fan-like array (Carter *et al.* 2011). The leaves are broadly linear to lorate with a rounded apex. They are ± 30 cm long and dull green to glaucous-green in colour (Klopper and Smith 2012). These thick fleshy leaves have a lot of moisture, filled with clear sap and resist burning (Notten *et al.* 2016). The thick corky bark also affords protection from fynbos fires (Cousins *et al.* 2014 & 2015). *Kumara plicatilis* flowers between August and October (sometimes in November) with the fruits appearing in early November (Van Wyk and Smith 2008). The florets are simple, tubular, scarlet in colour and arranged on 50 cm long racemes (Klopper and Smith 2012). The fruits are coloured green with a pink tinge, and they measure about 20 mm long and 16 mm in diameter with a longitudinal-dehiscent (Killick 1988).

Distribution and Habitat

Kumara plicatilis is a range restricted species, endemic to the Western Cape Province of South Africa (von Staden and Helme 2008). The species is confined to the lower slopes of the Boland Mountains in the south-western Cape occurring from the Groot Winterhoek Mountains near Tulbagh in the north to the Franschhoek Mountains in the south, and from the Du Toit's Kloof Mountains near Rawsonville/Worcester in the east to the Paardeberg between Malmesbury and Wellington in the west (see Figure 1 later in the text; Cousins *et al.* 2014). This area forms part of the fynbos biome (the most distinctive and common biome in the CFR, covering just over half the region; Mucina and Rutherford 2006). Of the six known indigenous South African tree aloes, *K. plicatilis* is the only one found in this region (Van Wyk and Smith 2008).

The species is highly habitat specific requiring extremely rocky sites that are protected from fire (von Staden and Helme 2008). These succulent trees grow in well-drained, acidic soils on the steep rocky slopes

and outcrops. Surveyed populations were found growing in one of only four vegetation types; Kogelberg sandstone fynbos, Hawequas sandstone fynbos, Boland granite fynbos and Winterhoek sandstone fynbos (Cousins *et al.* 2014). The area receives winter rainfall (400–2000 mm/year) with an average annual temperature of 14–18 °C, and monthly wind speeds averaging around 4.5–10.4 km/h (Cousins *et al.* 2013). Fires sporadically occur in this part of the region (Cousins *et al.* 2014 & 2015). *Kumara plicatilis* occurs strictly on sandstone and is often found on sandstone screes overlying granite on lower slopes (von Staden and Helme 2008). The phosphorus content in these soils is generally very low (Witkowski and Mitchell 1987). Populations occur at altitudes of between 200 m and 950 m above sea level (Cousins *et al.* 2014).

Population Ecology

There are currently 31 known (fragmented) populations of this species with some populations accommodating just under 40 plants, whilst others host more than 110 000 individuals (Cousins *et al.* 2014). The species is long-lived and fairly slow-growing with adult plants measuring 4+ m in height, aged at approximately 130-150 years old (Cousins *et al.* 2013). *Kumara plicatilis* regenerates predominately by sexual reproduction; they produce seeds every summer, but plants can also propagate asexually by re-rooting branches that break off (Cousins *et al.* 2014). The species adopts an adult-persistence population survival strategy (i.e., populations consist mainly of medium-to-large adults, with low recruitment) and populations also show no evidence of having persistent seed banks, with the germination and establishment of limited number of seedlings occurring possibly only over longer periods of time in the absence of major disturbances (Cousins *et al.* 2013 & 2014). This distribution of size classes is typical for long-lived slow growing species like *K. plicatilis*, where population viability is hinged on adult persistence rather than regular large-scale recruitment (Venter and Witkowski 2010; Cousins *et al.* 2014). Populations of *K. plicatilis* display a bell-shaped size class distribution (SCD), with low recruitment rates but good 'health and stability' (Cousins *et al.* 2014).

Pollination is primarily by insects and occasionally by birds, whilst the small, black winged seeds are wind-dispersed (Cousins *et al.* 2013). Seed dispersal is limited (Cousins *et al.* 2013), partially due to the species' ecology (i.e. limited seed production and survival) but may also be a result of other extrinsic influences such as interspecific competition, predation, or geographic barriers. Whilst no relationship between population size and density has been established, density of plants does influence recruitment, with populations of greater density showing high recent recruitment as opposed to the low-density populations that showed no signs of recent recruitment (Cousins *et al.* 2014). This could potentially have longer-term consequences for the persistence of smaller, fragmented populations.

Conservation Status

Since 2008, the species has been listed as Least Concern (LC) according to the IUCN Red List criteria, with the global population displaying a stable trend (von Staden and Helme 2008). The growth habit of the species, on steep rocky slopes and rocky outcrops, affords it some protection from unplanned, sporadic fires (Van Wyk and Smith 2008). The species has also adapted to its fire prone habitat, with a thick, corky bark as well as the ability to sprout from apical meristems (Van Jaarsveld 1989; Cousins *et al.* 2015). Predation on plants by rock hyraxes, or *dassies* (*Procavia capensis),* in one area has also previously been observed where animals had caused intense debarking of plants in order to get to the inner fibrous parts after which they'd chew right through until the stems collapsed. This behaviour is thought to be associated with periods of drought (Notten *et al.* 2016). *Kumara plicatilis* is a prized species in the horticultural trade of succulent plants, but plants propagated in nurseries meet most of the demand for the species and the limited illegal wild harvesting has had a negligible impact on the species (Cousins 2013). Invasive alien species, including pine trees and Australian acacias are present within the habitat, but these are either at too low densities to cause any past or present threat or are otherwise actively managed (von Staden and Helme 2008). In addition, most *K. plicatilis* populations occur in mountain catchment and conservation areas, with some also occurring on privately owned land (Cousins *et al.* 2014).

Climate change has been shown to have impacts on the population size and distribution of several plant species (e.g., *Brachystegia spiciformis* and *Aloidendron dichotomum*; Foden *et al.* 2007; Chen *et al.* 2011; Fordham *et al.* 2012; Pienaar *et al.* 2015). Previous studies done in the region project severe impacts on biodiversity in the fynbos biome (von Maltitz *et al.* 2006) with a loss in fynbos area initially projected to be between 51% and 65% by 2050 (Midgley *et al.* 2002). More recent estimates however, show a less extreme decline in range owing largely to hotter and drier conditions arising only in the latter half of this century in the face of anthropogenic climate change (Driver *et al.* 2012; DEA 2015). Nevertheless, changing temperature patterns that are predicted to decrease rainfall and increase fire frequency may influence species persistence in certain areas of the fynbos. In addition, the complexities of dispersal and biotic interactions could result in some species being unable to navigate to suitable habitats in time as climates continue to change (Loarie *et al.* 2009; Urban *et al.* 2013). Several studies have further found that habitat loss is generally greater for mountain species (i.e., those distributed at higher elevations; Paulie *et al.* 1996; Loarie *et al.* 2009; Engler *et al.* 2011).

1.3 Aim and Objectives

Given that the floral communities in the CFR are well adapted to the environmental conditions present in the region, the aim of the study is to examine the potential implications of anthropogenic climate change on the long-lived habitat specialist, *Kumara plicatilis.*

The objectives of this study are as follows:

1) Estimate the current distribution of *Kumara plicatilis* using known occurrence data (as well as population size estimates).
2) Identify the environmental factors associated with *K. plicatilis* habitat suitability.
3) Identify additional areas of suitable habitat and in turn, identify possible additional populations of the plants.
4) Predict possible shifts in suitable habitat distributions for the species under future climate change scenarios.
5) Contrast and compare known suitable habitat with projected suitable habitat using comparative indices.

1.4 Applications in Ecological Niche Modeling

There are many methods available to predict species distributions (Elith and Leathwick 2009). Regression methods are most commonly used by ecologists (Guisan *et al.* 2002; Elith and Leathwick 2009). General linear models (GLMs) and generalized additive models (GAMs) allow for the modeling of the disparities that exist in species occurrence within an area based on linear and non-linear relationships with different environmental variables respectively (Guisan *et al.* 1999; Jaberg and Guisan 2001; Meynard and Quinn 2007). Based on the model outcomes, the most important predictor variables can be selected to fit ecologically realistic relationships into predicting new sites within the area of occurrence at present (i.e., interpolation to unsampled sites) as well as into predicting new and unsampled geographic regions (i.e., extrapolation or forecasting; Guisan and Thullier 2005; Aráujo and New 2007). Furthermore, regression methods can be applied to compounded data such as records with imperfect detection of presence, data without known absences and abundance data with many zeros (Elith and Leathwick 2009). Examples of species distribution models include genetic algorithms such as Genetic Algorithm for Rule Set Production (GARP), multivariate adaptive regression splines, classification and regression trees and ensembles of trees, support vector machines and maximum entropy models (Elith and Leathwick 2009).

The general process of building a SDM includes several steps: conceptualization, data preparation, model fitting, model evaluation, spatial predictions, and assessment of model applicability (Guisan and Zimmerman 2000). The objectives of this study provide a basis for the conceptual model to be simulated based on the information available for *K. plicatilis*. Model realism and robustness is partial to the choice of appropriate (and ecologically relevant) predictor variables along with other factors such as the extent of extrapolation (Elith and Leathwick 2009). Furthermore, uncertainties in SDM predictions can occur due to differences among scenarios of future climate (Beaumont *et al.* 2008). Whilst Global Climate Models (GCM) are the most reliable available tools for simulating future climate scenarios at the moment, discrepancies within and among different climate models poses some challenges for end users (Beaumont *et al.* 2008). It is therefore important to select GCMs in a way that will reduce the uncertainty. Finally, the choice of the model to be used as well as further statistical analysis needed for gauging the predictive accuracy of the model requires careful consideration to ensure successful and realistic predictions of habitat needed for the species' conservation (Guisan and Thuiller 2005).

1.4.1 Maximum entropy (Maxent) modeling

Maxent is a program for modeling species distributions using presence-only records (Phillips *et al.* 2006; Elith *et al.* 2011). With a simple and precise mathematical formula, Maxent fits the covariation between environmental variables and occurrence data onto non-linear regression functions, accounting for the complex interactions that a species may exhibit with the environment (Phillips *et al.* 2006; Elith *et al.* 2011; Merow *et al.* 2013). Maxent is one of the most frequently applied models for predicting species geographic distributions from occurrence data (Warren and Siefert 2011). When compared to other presence-only methods, Maxent provides a clearer discrimination of suitable versus unsuitable habitat for species (Phillips *et al.* 2006; Hernandez *et al.* 2006). The model achieves high predictive accuracy and has several useful features that add to its performance (Phillips and Dudik 2008).

Maxent is centered on the idea of 'how much selection choice is involved in an event' (Shannon 1948) and the model essentially estimates a target probability distribution by finding the probability distribution of maximum entropy (the one with the greatest choice), subject to a set of limitations which represents the incomplete information about the target distribution (Phillips *et al.* 2006). Hence, the probability distribution maximizes entropy adhering to constraints placed by the incomplete data, so that the inferred distribution agrees with everything that is known whilst carefully avoiding anything that is unknown (Jaynes 1990) and thus provides an accurate prediction based on the available information.

The program uses a list of species occurrence data as input as well as a set of environmental predictors (e.g., precipitation or vegetation type) across a user-defined area that is divided into grid cells (Merow *et al.* 2013). From this defined area, the model extracts a sample of background locations (where presence is unknown), and contrasts it against the presence locations. The model then predicts the probability of presence in each cell based on the environmental predictors at that location (Phillips *et al.* 2006; Phillips and Dudik 2008; Merow *et al.* 2013). This probability of occurrence is explained by a range of graphical and statistical outputs generated in the program. Habitat suitability maps use colour indices to indicate predicted probability that conditions are suitable (e.g., red indicates high predicted suitability (p =1) and blue indicates low predicted suitability (p = 0)) whilst known presence locations and predicted presence locations are displayed as points on the map (Phillips 2010). Statistical outputs include binomial tests of omission, receiver operating characteristic analysis (ROC) plots (measures the model fit) as well as jackknife tests and response curves that provide an indication of the environmental variables which matter most for a species and those which are highly correlated (Phillips 2010). Maxent supports three output formats (raw, cumulative and logistic), each with its own interpretation, and the package also has a range of additional settings which enables further data exploration (Phillips and Dudik 2008; Phillips 2010).

1.4.2 Measuring niche characteristics

Understanding ecological niche dynamics within and between taxa is important in studies concerned with how global change is likely to impact species and their distributions across space and time. Measuring niche overlap across species ranges provides a basis for evaluating the ecological and biogeographical differences and similarities between and within species (Broennimann *et al.* 2011). To date, a range of metrics have been applied to quantify niche overlap in the context of understanding competition between species (Horn 1966; Schoener 1970; Colwell and Futuyama 1971; May and Arthur 1972; Popielarz and McPherson 1995). More recently however, quantifying niche characteristics has become important in allowing conservationists to conceptualize impacts of environmental change and even understand patterns of evolutionary change (Jump and Penuelas 2005; Petitpierre *et al.* 2012; Broennimann *et al.* 2014). Methods for quantifying niche characteristics ordinarily rely on ordination techniques or SDMs (Broennimann *et al.* 2011) where the environmental conditions which influence species distributions are identified and an approximation of the species realized niche (subset of a fundamental niche that the species actually occupies) is obtained. Niche overlap is then calculated across geographic space, where gridded environmental cells (each with its own unique set of environmental conditions) supporting species niches are compared. These techniques can be used to quantify niche overlap between two species or two individual populations of the same species as well as, niche overlap

among the same species at different times (e.g. before and after climate change; Broennimann *et al.* 2011). Ordination techniques enable visualization and statistical comparisons of species occupying environmental space and produce complementary results to better SDM techniques, which use projections based on geographical predictions of occurrences to calculate overlap (Broennimann *et al.* 2011). The choice of technique is critical to obtaining accurate calculations of niche overlap (Broennimann *et al.* 2011). Further statistical tests of niche hypotheses (i.e., niche equivalency and similarity) offer additional insight into niche evolution and understanding species distribution patterns (see Warren *et al.* 2008).

2. Methods

2.1 Study area and species data

The study area spans the entire Western Cape Province of South Africa, covering approximately 129 462 km^2 of land, which includes the natural distribution range of *Kumara plicatilis*. The terrain has an elevation gradient ranging from sea level to 2400 m above sea level (Bradshaw and Cowling 2014). In addition, six of the nine described South African biomes (Mucina and Rutherford 2006) can be found covering the landmass of the province. These biomes are largely shaped by climatic zones where environmental conditions, such as moisture and temperature strongly influence the establishment and survival of plant species (Rutherford and Westfall 1986).

Data for *K. plicatilis* was obtained from expert field surveys conducted over a two-year period (2010-2012) across the known distribution range of the species (Cousins *et al.* 2014). The data consists of several hundred GPS coordinates of individual plants gathered from more than 18 populations, as well as, the population size estimates (based on the approximate number of individuals) of each of the surveyed populations (Cousins *et al.* 2014). Building on methods explored by Bradley (2016), I created two presence-only datasets from this field data (Fig. 1). 'Dataset 1' consisted of all the GPS records (3245 points) and was used simply to identify geographical areas of suitable habitat for the species across the study area. 'Dataset 2' comprised a portion of these GPS records (1896 points (~58%)) and was used to test whether points based on locations of known high abundance (i.e., populations with > 1000 individual plants) could be effective in distinguishing areas of varying species abundance across the region.

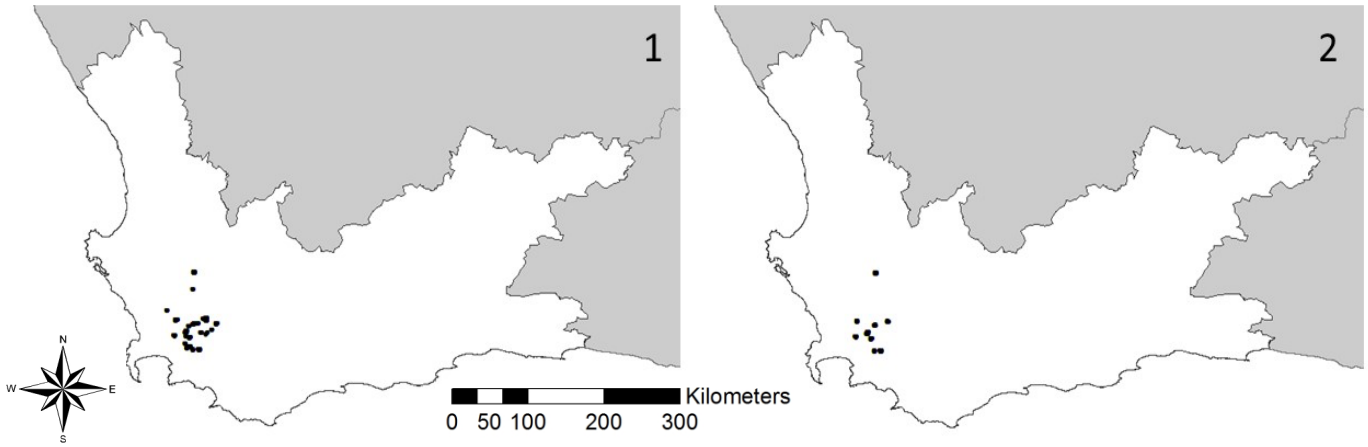

Figure 1: Map of the Western Cape Province of South Africa showing the two datasets used to create distribution models for *Kumara plicatilis*: 1) All records of occurrence, and 2) Occurrence records for populations of high abundance (>1000 plants).

2.2 Environmental data

Twenty-seven environmental variables were considered as possible predictors of *K. plicatilis* habitat. I included 19 bioclimatic variables downloaded from the WorldClim database (Hijmans *et al.* 2005; http://www.worldclim.org/) at a 30-arc second (~1 km) resolution. These climatic variables are derived from measurements of altitude, temperature and rainfall from weather stations across the world (averaged over the time period ~1950 – 2000, Hijmans *et al.* 2005) and are often used in species distribution models as they offer biologically meaningful platforms to define the eco-physiological tolerances of species' (Graham and Hijmans 2006; Kumar and Stohlgren 2009; Yates *et al.* 2010; Khanum *et al.* 2013). In addition, I obtained a Digital Elevation Model (DEM) from the WorldClim database and used these data to generate estimates of aspect and slope for the study region. Owing to the observed physical habitat of the species, I also included geological and vegetation cover data of the study area. A geology layer for the region was obtained from the University of the Witwatersrand (pers. comm. J. Fisher 2016), whilst information on the bioregions and vegetation types (based on the classifications done by Mucina and Rutherford 2006) occurring across the study area was extracted from the South African National Biodiversity Institute's BGIS website (http://bgis.sanbi.org/). The Normalised Difference Vegetation Index (NDVI), at a 1 km spatial resolution, and as an average for the 2001 – 2016 period was another variable considered for mapping the species distribution. The NDVI data comes from the Moderate Resolution Imaging Spectroradiometer (MODIS) web managed by NASA and offers an optimized vegetation signal for detecting areas of high biomass which is useful in modeling the distribution of plant species (Bradley and Flieshman 2008; Aguirre-Gutierrez *et al.* 2014). For the purpose of this research, NDVI was included in an attempt to assess whether the species preferred habitat is defined in more rocky areas with lower biomass compared to the surrounding areas. Finally, I used global fire data obtained from the NASA FIRMS database (MCD14DL MODIS Active Fire Detections, Collection 6) to create a fire frequency map for the study area for the 2001-2016 period. The fire frequency data represents the number of years each pixel (~1 km) has been burned over the aforementioned period (i.e., 0 to 16). This variable was included to assess whether sporadic fire occurrences has any contribution to the species distribution. I retained variables with a Pearson's pair-wise correlation coefficient $<|0.7|$. In cases where two variables were highly correlated, I kept the variable least correlated to others, except in two instances where two highly correlated variables (i.e. minimum temperature (bio_6) and temperature annual range (bio_7)) were both included owing to the variable contributions and biological relevance to the distribution of the species. Additional step-wise reductions were conducted following subsequent model runs to remove variables with low contribution to the distribution of the species and further simplify the final model. Pre- and post-processing of environmental data layers and maps were carried out in ArcGIS 10.3 (Environmental System Research Institute, Redlands, CA, USA).

2.3 Future climate data

The WorldClim database offers datasets of future climate projections generated by several GCMs under four different climate scenarios for two extended time periods (viz. for the years 2050 and 2070). The data selected for this study were projected using the HadGEM2-ES GCM, which offers a representation of several processes within the climate system and presents a valuable model for predicting impacts of future climate change (Bellouin *et al.* 2011). The future climate scenarios are based on the Representative Concentration Pathways (RCPs) that explore a range of plausible changes in climate due to anthropogenic activities (van Vuuren *et al.* 2011) and have been adopted by the IPCC in the fifth assessment report of 2014.

The four RCPs cover the range of radiative forcing values (defined as the difference of energy absorbed by the Earth and energy radiated back to space) calculated from existing literature from 2010 up to the year 2100 (viz. values range from 2.6 to 8.5 W/m^2 (van Vuuren *et al*. 2011; Shindell 2013). Each one of the RCPs is conceptually plausible, although the middle scenarios (RCP 4.5 and RCP 6.0) account for emissions levels that are roughly more probable than the two extreme scenarios (RCP 2.6 and RCP 8.5). Nevertheless, RCP 2.5 and RCP 8.5 were modeled to ascertain any shifts in the distribution of suitable habitat of *K. plicatilis* under a 'best case' and 'worst case' scenario. These scenarios represent CO_2 increases to 490 ppm and 1370 ppm and resultant temperature increases of between 0.3 °C to 1.7 °C and 2.6 °C to 4.9 °C above preindustrial levels by 2100 respectively (Moss *et al.* 2010, IPCC 2014).

2.4 Model building and interpretation

I applied Maximum entropy modeling using the Maxent algorithm (Phillips *et al.* 2006) to ascertain the probable distribution of *K. plicatilis* as well as to identify the environmental variables important in contributing to the species preferred habitat (i.e., estimate the environmental niche). I set the Maxent models to run using the auto-features option and the logistic output format for ease of interpretation. Random background samples (or pseudo-absences) were selected from an area around the occurrence points where I assumed *K. plicatilis* could be found (defined by a minimum convex polygon). This approach is more objective than drawing samples from the entire study region which has not been sampled and provides Maxent with a background file that has a similar bias as the presence data (Phillips and Dudik 2008; Young *et al.* 2011). Maxent automatically discards redundant points that occur in the same cells and this further reduces spatial clumping and sampling bias. To test the reliability of my model, I used a ten-fold cross-validation. The method randomly splits the data into k sections of equal size (here, k = 10) and generates a model, while sequentially leaving out one section. This allows for a more robust outcome of

the predicted distribution and variable contributions. Finally, the model trained on the set of environmental variables contributing to the current distribution of *K. plicatilis,* was used to make projections of future distributions using the future climate datasets.

The calculated probabilities of species presence (i.e., habitat suitability values ranging from 0 to 1) provided an indication of the probable distribution of *Kumara plicatilis* across the landscape under current climate conditions, as well as probable shifts in this distribution under future climate conditions. In addition, the analysis of variable contributions and the ecological response curves which reflect the importance and association of each environmental variable to the species habitat was used to draw conclusions on the species preferred environmental niche. Finally, the goodness-of-fit of the distribution models was assessed by the Area Under the Receiving Operator Curve (AUC), which typically varies from no-better-than-random (0.5) to perfect (1) (van Gils *et al.* 2014).

2.5 Measuring characteristics of projected current and future niche space

I applied a novel statistical framework used to describe and draw temporal comparisons on the niche of *K. plicatilis* based on current environmental conditions (entity 1) and on conditions projected for the future (entity 2), in order to ascertain the degree of shared current and future environmental space. The method described by Broennimann *et al.* (2011) uses a range of ordination techniques where species occurrences are plotted on a gridded environmental space (r x r cells) and a kernel smoothing method is applied to calculate the density of occurrences and environmental variables along the first two axes for each cell in the dataset (Broennimann *et al.* 2011). By applying a kernel density function to the smoothing method, the over- or under- estimation of species density across the space (arising from bias in occurrence data) is addressed and a reliable indication of environmental conditions suited to the species is obtained. The ordination technique used in this study is based on a principal component analysis adjusted across the complete environmental space existing in the study area (hereafter referred to as 'PCA-env'). Measurements of niche overlap are then computed using Schoener's D statistic (Schoener 1970), which ranges in value from 0 (no overlap) to 1 (complete overlap). This test statistic has been widely applied in applications assessing the degree of shared geographic or temporal space within and between species (Warren *et al.* 2008; Petitpierre *et al*. 2012; Glennon *et al.* 2014; Aguirre-Gutierrez *et al.* 2014).

Statistical tests of niche equivalency and similarity are also included in the framework (built on previous tests by Warren *et al.* (2008)). The test of niche equivalency assesses whether niches of two entities are equal (display constant overlap), moderately similar (show some overlap) or, significantly different (display no overlap) when occurrences are randomly shuffled across the ranges. The framework tests this by

comparing the niche overlap (*D*) values for the two entities to the overlap of a null distribution, which is created by the extraction of climate variables from a randomly selected set of co-ordinates across the background region of the study area. This is replicated 100 times (Broennimann *et al.* 2011). If the observed niche values are significantly lower than the overlap value from the null distribution ($P \leq 0.05$), then the null hypothesis of niche equivalency is rejected (Broennimann *et al.* 2011). A limitation of this test is that it only evaluates whether the two entities are indistinguishable in their niche space using exact locations whilst not accounting for the environmental conditions in the surrounding space of available habitat (Warren *et al.* 2008; Aguirre-Gutierrez *et al.* 2014).

The test for niche similarity asks whether the niches of two entities are more similar (or different) than would be expected by chance and takes into account the surrounding environmental conditions of the geographic space across the study area (Warren *et al.* 2008). Rejection of the null hypothesis ($P \leq 0.05$) shows that the niches are more similar (or different) than expected by chance and there is probably an underlying explanation (e.g., habitat suitability) for this pattern rather than it being just an artefact of the similarities (or differences) in environmental conditions available to the species (Warren *et al.* 2008). Niche breadth (viz. the variety of resources available to the species) for the species presently and in the future, was also obtained using Levins' inverse concentration statistic (Levins 1986; Warren *et al.* 2010). This value ranges from 0, when all but one grid cell has non-zero suitability, to 1, when all the cells in the area are suitable. Data for this section were prepared in ArcGIS (V10.3) and statistical analysis was conducted in R v.3.3.2 (R Development Core Team, 2016) using a range of packages enlisted in the scripts from Broennimann *et al.* (2011).

3. Results

3.1 Model performance and outcomes

The models trained on either dataset both presented high AUC values (dataset 1 AUC = 0.987; dataset 2 AUC = 0.986) showing that the data fit the models better than random (Table 1). Both model projections identified similar range areas of highly suitable and moderately suitable habitat between and around the current known locations of the species, showing some degree of overlap across certain regions of the study area (Fig. 2). Hotspots of projected occurrence appear well distributed around the central area of the fynbos region (Fig. 2).

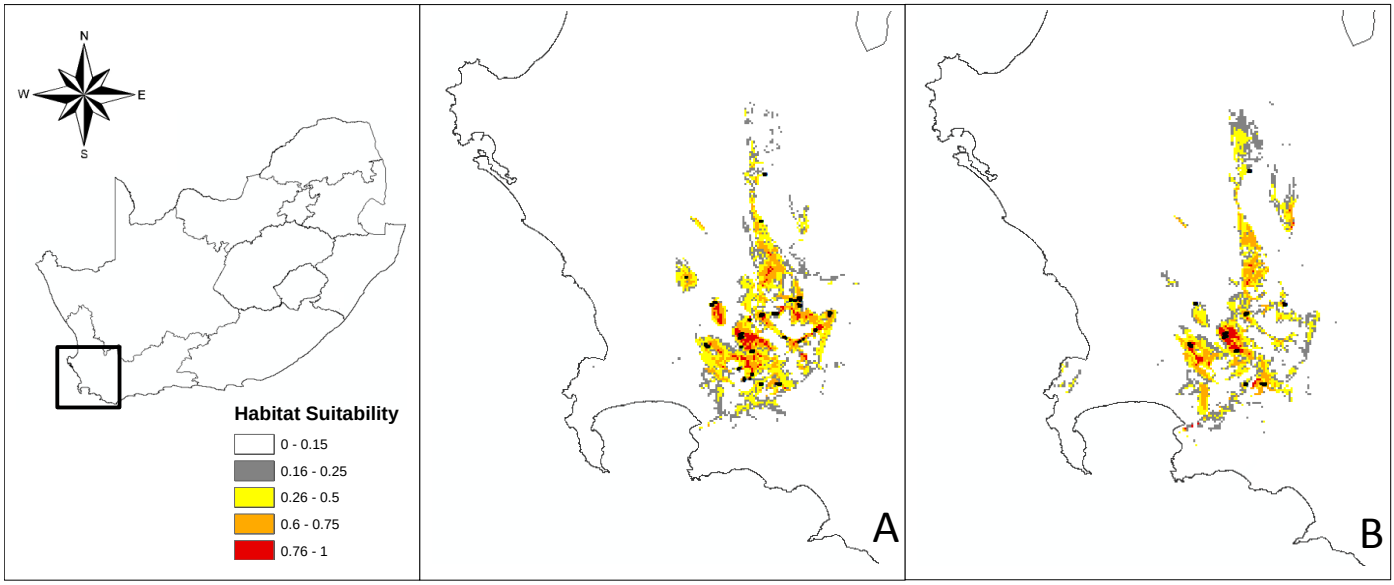

Figure 2: Environmental habitat models for the fan Aloe (*Kumara plicatilis*) representing areas of high (suitability > 0.75), moderate (0.75 > suitability > 0.5) and low (0.5 > suitability) habitat suitability. A) Results from the model trained with 'dataset 1'. B) Results from the model trained with 'dataset 2'. Black dots represent GPS points from each of the two datasets used to train the models.

The model trained on the complete set of occurrence points (dataset 1) offered a higher AUC score than the second model trained only on occurrence points from locations of known high abundance (dataset 2). The first model was therefore more robust in identifying likely areas of suitable and unsuitable habitat across the study region projecting a distribution range that closely matches the current known distribution of the species (Fig. 2a; Fig. 3). This model however, projected almost equal probabilities of presence across populations of different sizes and dataset 1 therefore appeared as a poor predictor of species abundance (Fig. 3). The second model presented a narrower overall distribution of suitable habitat for the species but the model was able to distinguish between areas of varying abundance with higher suitability projected for

large populations (>1000 individuals) and lower suitability for smaller (<1000 individuals) populations. Dataset 2 therefore offers the potential of predicting species abundance from presence-only models (Fig. 3).

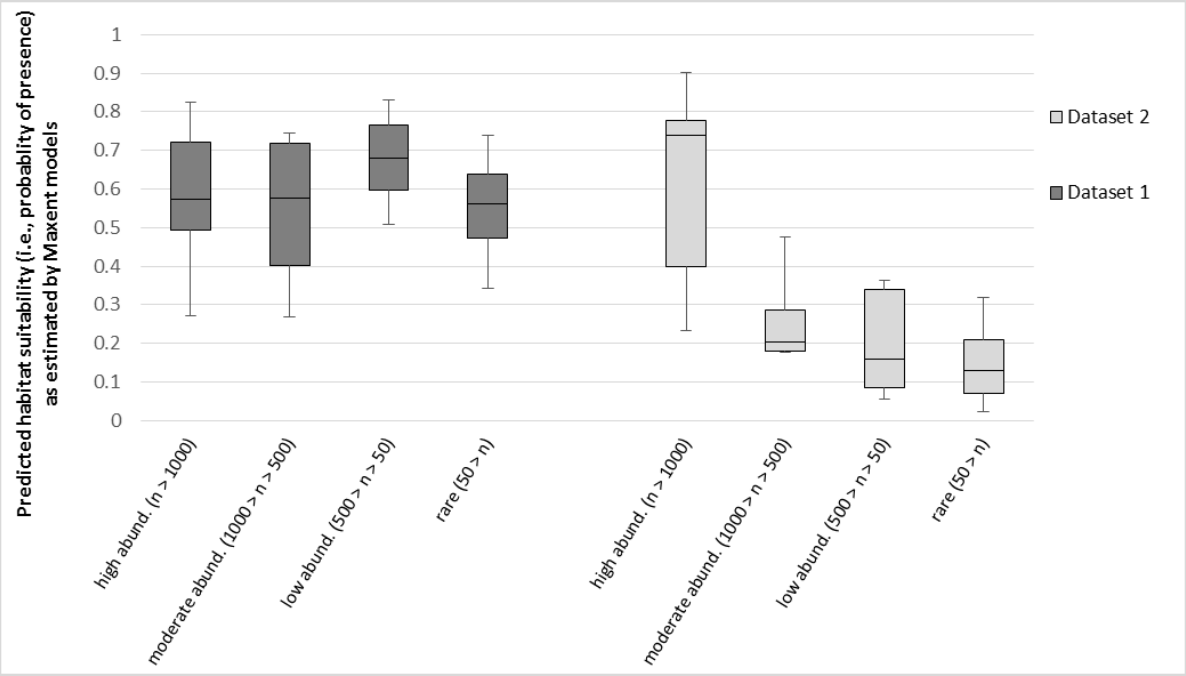

Figure 3: Model outputs constructed from dataset 1 (using all occurrence points) are effective in projecting areas of suitable habitat across a range of population sizes (n) but offer poor predictions of species abundance. In comparison, models trained on dataset 2 (using a subset of occurrence points from locations of known 'high abundance'), whilst most effective in identifying suitable habitat for large populations (n > 1000), offers the potential of predicting species abundance with projections of lower habitat suitability made across areas where smaller populations occur. Plots are box and whisker (minimum and maximum values limited to 1.5 times the interquartile range) estimates of habitat suitability derived from Maxent models trained on the two datasets. Ranked abundance estimates were obtained from a previous study of *Kumara plicatilis* (Cousins *et al.* 2014).

3.2 Favoured environmental conditions

The presence of *Kumara plicatilis* appears to be constrained by a combination of several variables including precipitation seasonality, precipitation of the wettest quarter, mean temperature of the warmest quarter and minimum temperature of the coldest month, as well as vegetation type (Table 1). Highly suitable habitat has been identified in areas with high winter rainfall (> 400 mm per wettest quarter and a rainfall seasonality of between 60 and 65%). This indicates that the species prefers wet conditions with mean winter precipitation greater than 60% (Fig. 4). The species is also influenced (to a lesser degree) by

temperature, tolerating areas that have warm conditions in the warm periods (~18 ˚C – 26 ˚C) and close to freezing conditions (between -4 ˚C and 6 ˚C) during the cold (winter) months. Annual temperature range of suitable habitat is between 19 ˚C and 26 ˚C (Fig. 4). The temperature annual range (bio_7) and minimum temperature variable (bio_6) are highly correlated and were both included based on their individual contributions to the model gain. *Kumara plicatilis* seems to be well suited to growing in the southwest fynbos bioregion and shows preference for certain vegetation types and geology, particularly sandstone and granite fynbos (Table 1; Fig. 4). Whilst the percent variable contribution differed between the two models (trained on dataset 1 and dataset 2), the general indication of which environmental variables are important for the species were largely consistent (Table 1). Many of the initial predictor variables had little to no impact on the distribution of the species and the model performance and were excluded in the final model runs (see APPENDIX for more detail).

Table 1: Percentage of variable contribution to the model construction, derived from the permuation importance analysis in Maxent. The results represent a drop in the AUC (as a percentage) once the values of the variables have been permuted and the model is re-evaluated on the permuted data. Values shown are averages over 10 replicate runs. Variables with the highest experimental contributions to the final model are highlighted in bold.

Variable	Dataset 1 (AUC = 0.987, *N*=53)	Dataset 2 (AUC = 0.986, *N*=23)
Bioregion	4.7	0.2
Precipitation in the wettest quarter (bio_16)	**28.3**	**59.5**
Temperature annual range (bio_7)	**5.3**	**9**
Geology	4.3	6.1
Slope steepness	3.9	1.8
Vegetation type	**5.7**	**10.6**
Precipitation seasonality (CV) (bio_15)*	**32**	3.5
Mean temperature of warmest quarter (bio_10)	**5.7**	0.7
Aspect	0.2	3
Minimum temperature of coldest month (bio_6)	**8.4**	NA
Temperature seasonality (CV) (bio_4)[a]	*NA*	3.4
Mean temperature of wettest quarter (bio_8)	1.2	0
Isothemality (bio_3)[b]	0	2

Null model AUC = 0.698

N represents the total number of occurrence points used to train the models after Maxent reduces spatial clumping

*bio_15 = Precipitation Seasonality (CV) is a measure of **the variation in monthly precipitation totals over the course of the year** and is based on the standard deviation of the monthly total precipitation to the mean monthly total precipitation (also known as the coefficient of variation), expressed as a percentage.

[a]bio_4 = Temperature Seasonality (CV) representing **the amount of temperature variation over a given period** (i.e. 1950-2000) based on the standard deviation (variation) of monthly temperature averages.

[b]bio_3 = Isothermality, the mean diurnal temperature range (between the months maximum and minimum temperature) divided by the annual temperature range (between the max temperature of the warmest period and the min temperature of the coldest period)

NA = not applicable

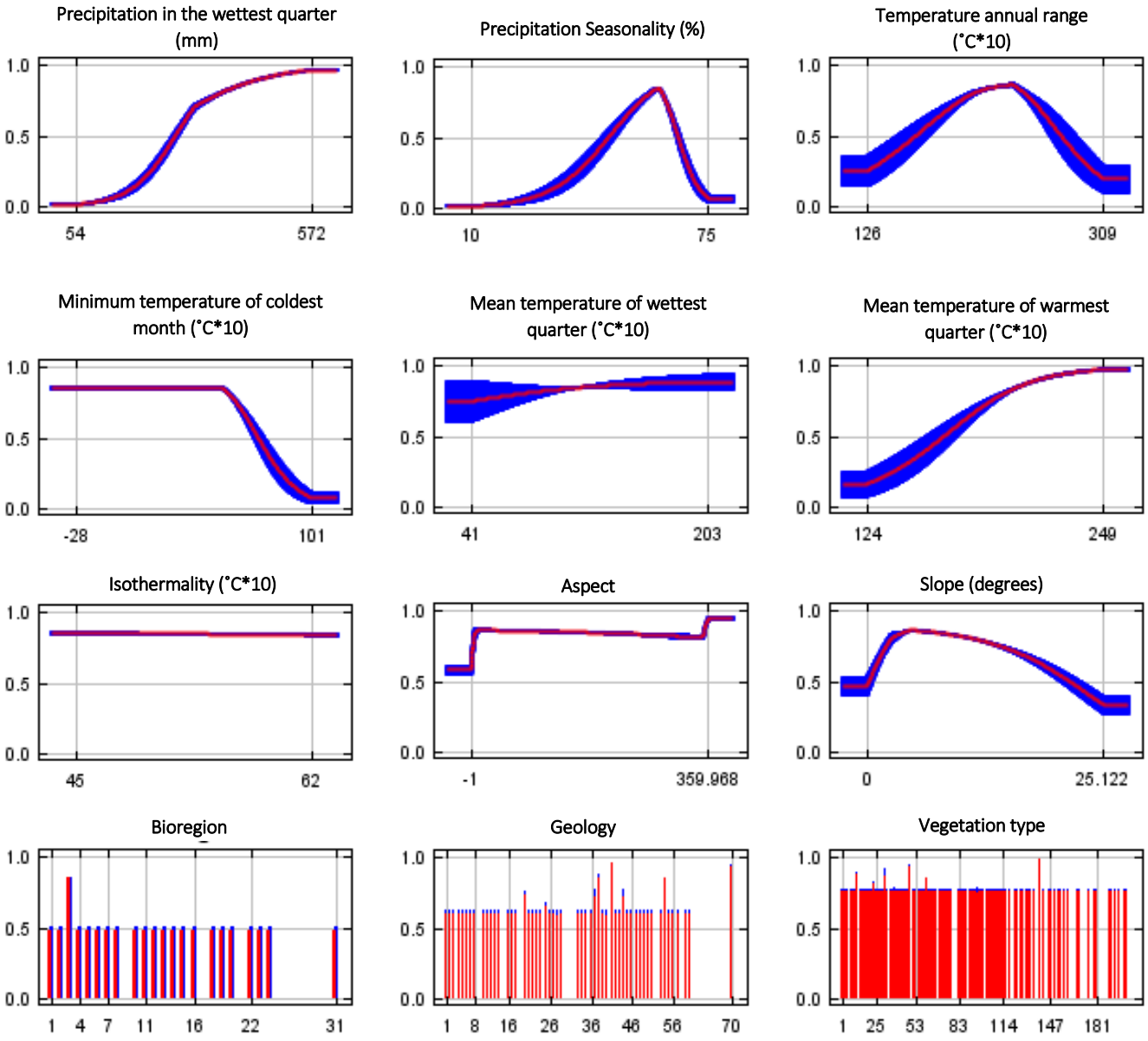

Figure 4: Ecological response curves for *Kumara plicatilis* showing the ranges of environmental conditions that are more suited for the species distribution. The x-axis represents the ranges of each of the variables across the study area and the y-axis presents the predicted suitability of the focus variable when all other variables are set to their average.

3.3 Current and future projected distribution ranges

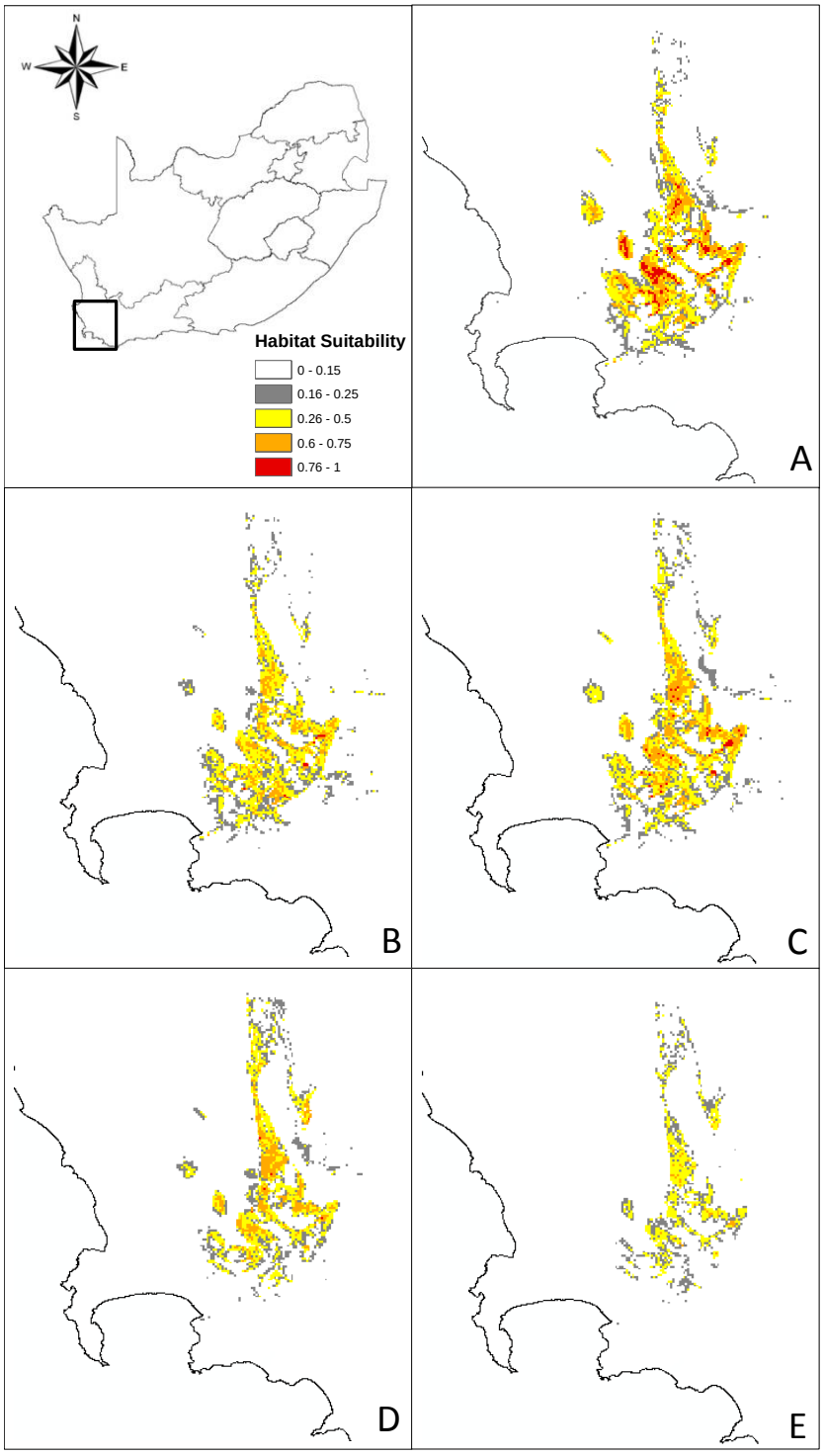

Figure 5: Distribution model projections of habitat suitability for *Kumara plicatilis* under A) current climatic conditions, B) RCP 2.6 climate conditions (for the year 2050), C) RCP 2.6 climate conditions (for the year 2070), D) RCP 8.5 climate conditions (for the year 2050) and, E) under RCP 8.5 climate conditions (for the year 2070). RCP 2.6 and RCP 8.5 represent CO_2 increases to 490 ppm and 1370 ppm and resultant temperature increases of between 0.3 °C to 1.7 °C and 2.6 °C to 4.9 °C above preindustrial levels by 2100 respectively (IPCC 2014).

Habitat suitability models for the future distribution range of the species (under different climate change scenarios) were developed using all occurrence points (i.e., dataset 1; Fig. 2 & Fig. 5). Under the current climatic conditions, there appears to be a significant amount of well-suited habitat areas available to the species (Fig. 5a). Projections of suitable habitat availability under future climate conditions are less optimistic (Fig. 5b - 5e). Areas with moderate (suitability > 0.5) and highly (suitability > 0.75) suitable habitats are projected to decrease as climate changes (Fig. 5, Table 3) with impacts on the species range increasing under the more hostile scenario (Fig. 5d & 5e). The influence of climatic shifts under the RCP 8.5 scenario are likely to worsen over time, whilst projections made under RCP 2.6 reflects more optimal conditions available to the species in 2070 as compared to 2050 (Fig. 5b & c). Nevertheless, a significant decline in the amount of highly suitable habitat (area in red) is projected under both scenarios in both the short and longer term (Fig. 5; Table 3).

Table 2: Projected habitat suitability of areas where 19 populations of *Kumara plicatilis* are known to occur (Cousins et al. 2014). Values of habitat suitability (ranging from low (0) to high (1)) are estimated for current and future climate conditions (under the IPCC's Reprentative Concentration Pathways trajectories, 2014) using the Maxent algorithm. Estimates of population sizes as well as altitude range is also given.

Population	**Estimated population size (number of individuals)**	**Altitudinal range (m)**	**Habitat Suitability as estimated by the Maxent models**				
			Current	RCP 2.6 (2050)	RCP 2.6 (2070)	RCP 8.5 (2050)	RCP 8.5 (2070)
Assegaaiboskloof	100 < n <500	387 – 474	0.83	0.81	0.80	0.54	0.43
Bosjemanskloof	100 < n <500	288 – 386	0.74	0.59	0.69	0.46	0.37
Du Toit's Kloof Krom River	1000 < n	462 – 632	0.80	0.58	0.67	0.62	0.40
Du Toit's Kloof Molenaars River	500 < n < 1000	372 – 501	0.27	0.13	0.23	0.17	0.09
Goudini Bardsberg	100 < n <500	481 – 521	0.74	0.43	0.60	0.57	0.29
Goudini Spa	500 < n < 1000	236 – 396	0.73	0.41	0.55	0.45	0.26
Jasons Hill	n < 50	337 – 373	0.53	0.25	0.33	0.31	0.19
Kliphoutkloof	1000 < n	213 – 340	0.66	0.30	0.48	0.36	0.21
La Motte	1000 < n	248 – 445	0.70	0.40	0.58	0.40	0.26
Skurweberg	1000 < n	414 – 565	0.51	0.28	0.37	0.23	0.13
Tulbagh Kleinpoort	1000 < n	867 – 944	0.19	0.11	0.18	0.25	0.21
Tulbagh Waterval	100 < n <500	192 – 226	0.50	0.30	0.39	0.44	0.13
Theewaterskloof	1000 < n	334 – 393	0.56	0.64	0.56	0.30	0.23
Voorsorg (Grootkloof)	n < 50	458 – 542	0.66	0.50	0.66	0.44	0.30
Voorsorg (Watervalskloof)	50 < n < 100	443 – 485	0.78	0.68	0.78	0.57	0.44
Wiesenhof Lookout	1000 < n	203 – 392	0.48	0.26	0.35	0.21	0.12
Windmuel	1000 < n	285 – 338	0.28	0.06	0.12	0.08	0.03
Windmuel Rhebokskloof	100 < n <500	579 – 634	0.61	0.27	0.42	0.27	0.19
Zachariashoek	1000 < n	608 – 830	0.58	0.39	0.47	0.37	0.22

With the sizeable changes in area (km^2) projected to be suitable under shifting climates (Fig. 5; Table 3), it is unsurprising that many of the known populations of *Kumara plicatilis* will be faced with increasingly unsuitable habitat conditions in the future (Table 2). The impact on the known current distribution of the species will again be most affected by the harsh climate conditions projected under RCP 8.5 for both the short and long terms with all populations above, projected to be exposed to unsuitable habitat by 2070 (Table 2). Habitats of several populations (more than five of the 19 presented above) are projected to remain suitable (suitability > 0.5) under climate conditions arising under RCP 2.6 in both the short and longer terms (Table 2).

Previous studies that model the effects of climate change on mountain plant species have shown projections of species moving up a mountain as climate changes force suitable conditions up the elevation gradient (Lenoir *et al*. 2008; Randin *et al.* 2009; Engler *et al.* 2011). Projections for *K. plicatilis* suggest that suitable habiat conditions will most likely persist around the same elevation range currently occupied by the species (i.e., < 1000 m a.s.l; Fig. 6). Nevertheless, in some areas, changing climates may see suitable distribution ranges shifting to higher altitudes, but typically not in excess of 1500 m a. s. l. (Fig. 6), whilst lower lying regions are projected to become less suitable most notably under the RCP 8.5 climate scenario (Fig.6).

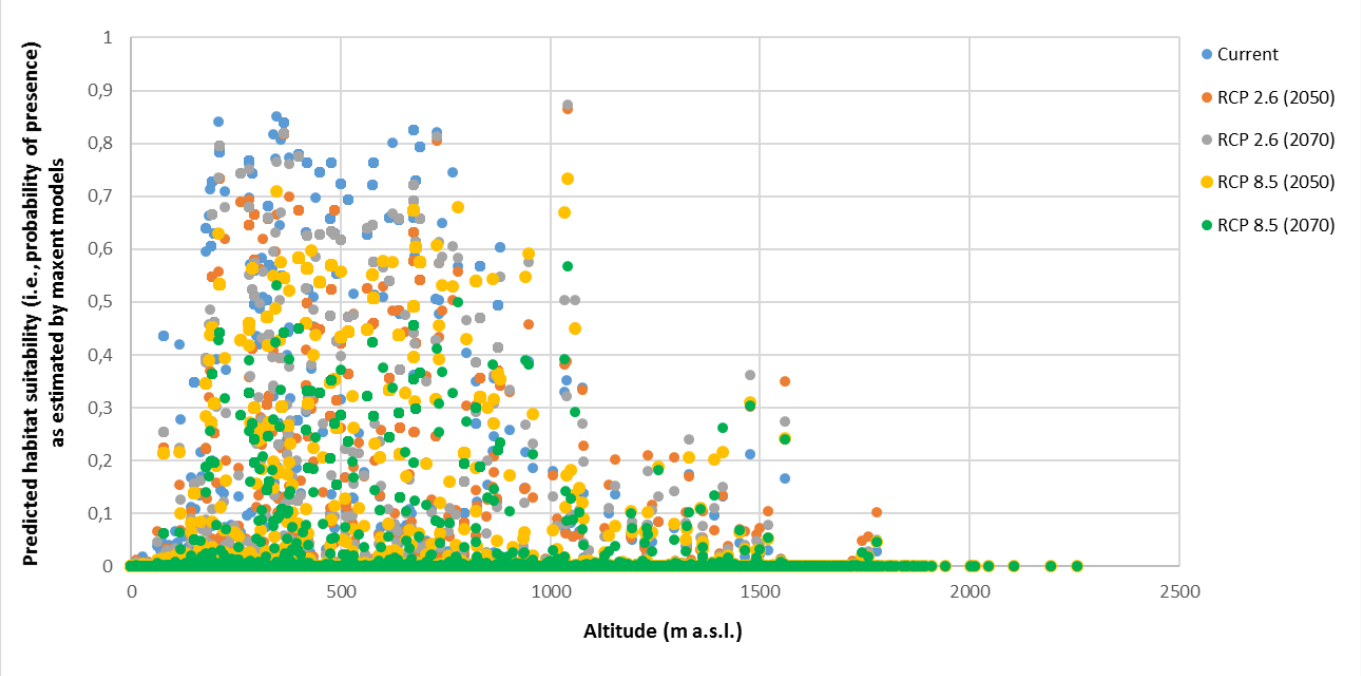

Figure 6: Scatter plot of *Kumara plicatilis* optimum altitudinal range (i.e., altitude values at maximum probability of presence) under different climate change scenarios. Shifts to slightly higher altitudinal ranges are projected for the species as climates and habitat suitability change. RCP 2.6 and RCP 8.5 represent CO_2 increases to 490 ppm and 1370 ppm and resultant temperature increases of between 0.3 °C to 1.7 °C and 2.6 °C to 4.9 °C above preindustrial levels by 2100 respectively (IPCC 2014).

3.4 Environmental niche characteristics

The results of the niche breadth assessment show that the species generally has a narrow niche breadth corresponding to the relatively concentrated distribution range of suitable habitat (Table 3, Fig. 2a). Whilst the niche breadth and area of habitat predicted to be suitable now and in the future under the RCP 2.6 scenario remains around the same range, both niche breadth and area are projected to decrease under the RCP 8.5 scenario in both the short and longer terms (Table 3, Fig. 7). Niche overlap results suggest low variability in the environmental space inhabited by *K. plicatilis* now and in the future under changing climates (Table 3, Fig. 7).

Table 3: Ecological niche comparisons between current and future projected distribution range of *Kumara plicatilis*. The future climate scenarios are based on the Representative Concentration Pathways (RCPs) that explore a range of plausible changes in climate due to anthropogenic activities and have been adopted by the IPCC in the fifth assessment report of 2014. RCP 2.6 and RCP 8.5 represent CO_2 increases to 490 ppm and 1370 ppm and resultant temperature increases of between 0.3 °C to 1.7 °C and 2.6 °C to 4.9 °C above preindustrial levels by 2100 respectively (IPCC 2014).

Ecological Niche Model (Fig. 5)	**Niche breadth**	**Area predicted suitable (out of ~129 000 km^2)$^+$**		**Niche comparison pairs**		**Niche Overlap (*D*)**	**Niche Similarity**		**Niche Equivalency**
		Suitability > 0.5	**Suitability > 0.75**	**1**	**2**		**1 → 2**	**2 → 1**	
5a	0.0224	893	409						
5b	0.0234	563	207	Current (2016)	RCP 2.6 (2050)	0.506	0.05941	0.11881	0.0198
5c	0.0231	740	319	Current (2016)	RCP 2.6 (2070)	0.512	0.15842	0.07921	0.0198
5d	0.0197	601	201	Current (2016)	RCP 8.5 (2050)	0.447	0.41584	0.13861	0.0198
5e	0.0181	327	0	Current (2016)	RCP 8.5 (2070)	0.346	0.75248	0.15842	0.0198

$^+$The area predicted as suitable corresponds to the model projections of habitat suitability across the study area after converting the Maxent outputs to presence binary maps

Measuring the environmental habitat properties rendered a PCA-env with the first axis loaded primarily by precipitation of the wettest quarter (bio_16) and bioregion along with several other variables including minimum temperature of the coldest month (bio_6), mean temperature of the wettest quarter (bio_8), slope, geology and precipitation seasonality (bio_15). This first axis accounted for 44.74% of variation in environmental conditions for the species across the study area (Fig. 7). The second axis explained 13.42% of

variation and was loaded by vegetation type, mean temperature of the warmest quarter (bio 10), temperature annual range (bio_7) and aspect (Fig. 7).

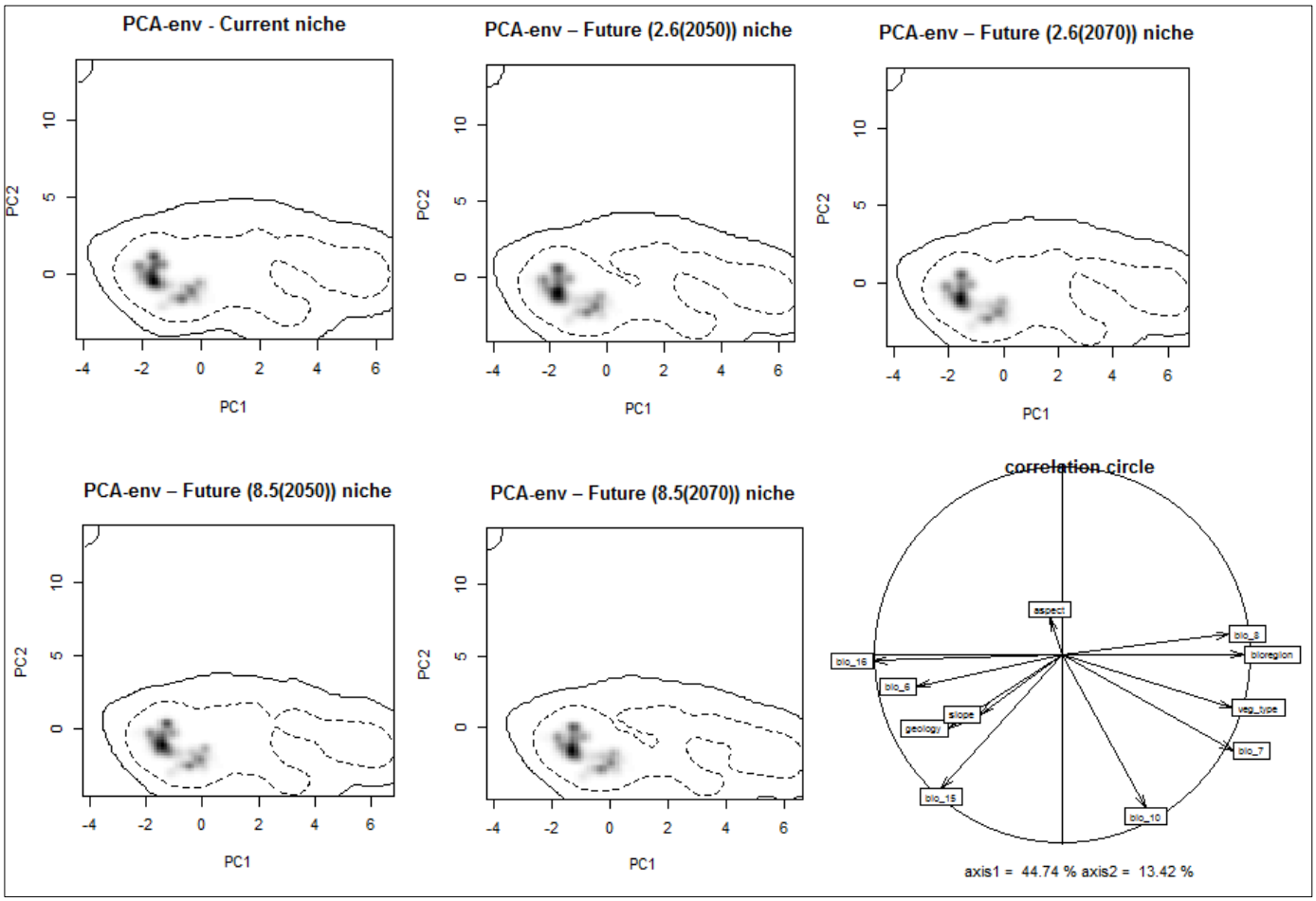

Figure 7: Environmental space patterns of *Kumara plicatilis* arising under current and future climate conditions using the principal component (PCA-env) analyses calibrated on the entire environmental space present in the study area (i.e. the Western Cape Province). The results of the PCA-env analyses represent the environmental space of the species along the two main axes of environmental conditions across the study area. The solid and dashed contour lines show 100% and 50% of the environment available to the species respectively, whilst the grey-black shading shows the density of occurrences by cell (black being the highest density). The correlation circle shows the contribution of variables to the loadings of the main axes of the PCA-env analyses and the percentage of inertia explained by each axis.
(Variable codes are explained in Table 1).

For each of the pairwise comparisons between the species environmental niche under current and future climate conditions, the null hypotheses for niche equivalency was rejected ($P < 0.05$), but owing to the conservatism of the test, the results do not necessarily indicate that niches are strongly opposing (Table 3). In addition to this, niche similarity tests upheld the null hypotheses of this statistic with each pairwise

comparison showing that niches are not significantly more similar or more different than expected by chance ($P > 0.05$). Results from the niche equivalency and similarity tests show that the niche inhabited by *K. plicatilis* currently, although not identical, is likely similar to the future environmental niche (Table 3). The species is therefore likely to not show signs of niche shifts, but rather niche stasis (Fig. 7; e.g., Glennon *et al.* 2014).

4. Discussion

4.1 Data quality and model performance

Spatial patterns of species occurrence and species abundance are important aspects of understanding species ecological requirements (Elith *et al.* 2006; Howard *et al.* 2014). Whilst presence data allows us to determine the environmental conditions that limit the distribution of a species, data on abundance provides an insight into the conditions that promote higher population growth of the species (Brown 1984). However, as in the case of species 'absence' data, abundance data are regrettably often lacking owing to the cost and difficulties accompanying the collection of these data across wide survey areas (Bradley *et al.* 2016). Nevertheless, estimates of abundance are often made at locations where species have been found (e.g., Cousins *et al*. 2014) and previous studies have shown that modeling abundance given presence-only data is possible (Pearce and Boyce 2006; Jingwa 2011; Bradley 2016). In the case of *Kumara plicatilis*, the results were consistent with the findings from a study that used presence only models to project abundances of invasive species across areas of the US (Bradley 2016). In effect, presence-only models based on known distributions were effective predictors of distribution but poor predictors of abundance whilst presence-only models based on abundance were poor predictors of distribution but effective predictors of abundance. As such, the overlap observed across certain areas projected to be highly suitable by the two models in this study, indicate the existence of areas that are not only likely to support species presence but are also likely to support high abundances of the species. The collection of field data available for the species has allowed for the generation of robust ecological distribution models for *Kumara plicatilis,* providing a good indication of the abiotic variables contributing to the overall species distribution, as well as the variables significant in promoting higher abundances of *K. plicatilis.*

4.2 Current distribution range and key environmental predictors of *Kumara plicatilis* habitat

Projected areas of suitable habitat (that could support both the distribution and high abundance of *Kumara plicatilis*) closely match the current patchy distribution of the species and are centered within the central southwestern fynbos region. Although areas outside of this central region (e.g., Table Mountain) have come up in the distribution maps, suitability in these extended ranges is low (suitability < 0.5). Whilst current known distributions of the species is not limited to single mountain ranges, projections made by models in this study confirms that the species exhibits signs of being a habitat specialist with a narrow overall distribution range (i.e., less than 1000 km^2 of land area is projected as having habitat suitability > 0.5

for the species) which is not uncommon for locally endemic species (Cowling *et al*. 1996; Cowling and Lombard 2002).

This distribution range along with the abundance of the species is constrained by several bioclimatic and biophysical variables. Rainfall appears to have a marked impact on the species spatial patterns. Models identified winter rainfall (precipitation in the wettest quarter) as an important variable influencing both the distribution and abundance of the species whilst precipitation seasonality (CV) was also highlighted as having an impact on the species distribution. These findings are highly plausible as these plants are found in areas with moderate to high rainfall, and a mean annual rainfall of 422 – 1940 mm (Cousins *et al.* 2014), which falls predominantly in the winter months (Manning and Goldblatt 2012). Populations also tend to decrease in abundance as they reach areas where rainfall is at the lower end of this mean annual range. In addition to high rainfall areas, the species appears to be tolerant of a wide range of temperatures, with highly suitable habitat being distributed in areas where temperatures drop to below freezing in the cold months, and are relatively warm (> 18 ˚C) during the warmest period of the year. Many aloe species are reasonably cold tolerant and some have adapted to survive temperatures lower than –7 ˚C (Cousins and Witkowski 2012). Suitable annual temperature ranges for both distribution and abundance are projected to be between 18 ˚C and 26 ˚C, although the long-term average monthly temperatures in areas of known species occurrence range between 14 ˚C and 18 ˚C (Cousins *et al.* 2014). These temperature ranges are typical for the inland areas of the fynbos where temperatures get hot during the summer, and mountain tops can become covered with snow in the winter (Bradshaw and Cowling 2014). Consistent winter rainfall allows the species to accumulate sufficient winter reserves to survive the hotter, drier summers (Cousins *et al*. 2014). Finally, the biophysical variables most important in constraining both the distribution and abundance of the species include geology and vegetation type with *K. plicatilis* preferring to grow among sandstone fynbos vegetation in sandstone derived soils. The species is less sensitive to slope and aspect with suitable habitat occurring across a wider range of slope faces and gradients.

The Mediterranean-type climate prevalent in the fynbos region is not only characterized by cool, wet winters and hot, dry summers, but is also largely subject to fire disturbances (Yates *et al.* 2010; Keeley *et al.* 2012). The fynbos vegetation is largely adapted to fire occurrence with a high percentage of plants displaying behaviours such as serotiny and obligate reseeding (Kraaij and van Wilgen 2014). A smaller proportion of plants that are more susceptible to fire, adopt other strategies such as growing in fire protected areas such as mountain gorges and rocky outcrops (Kraaij and van Wilgen 2014). *Kumara plicatilis* is known to adopt a 'dual fire survival strategy' (Cousins *et al.* 2015). The species possesses morphological traits (including thick corky barks and well protected apical meristems) that afford it the ability to 'tolerate' fires and, in addition, the species is also found growing in rocky outcrops where it essentially 'avoids' fires (Cousins *et al.* 2015). These rocky habitats are a particularly important aspect of

the species survival strategy with a previous study showing larger declines in plant density across populations growing amongst lower rock cover after natural fires had burned through the region (Cousins *et al*. 2015). The fire frequency variable included in the initial model runs yielded no impact on the projected habitat suitability for both the distribution and abundance of the species and was therefore excluded from the final results. This could be as a result of the scale applied to the model given that all variables included were measured at a fairly course scale (~1 km^2) and drivers such as fire could potentially be influencing the species distribution at a more localised scale. Alternatively, given that fire in the fynbos is both inevitable and necessary, the species could perhaps be well adapted to withstand areas of frequent fire occurrence and its distribution and abundance is possibly more affected by fire intensity (large, hot fires can destroy entire plants; Cousins and Witkowski 2012). This would explain why the species prefers growing in rocky outcrops where fuel loads may be less. Whilst not significant in delineating suitable habitat areas, high fire frequency is more likely to have an impact on post-fire population recovery with juvenile and surviving adult plants requiring sufficient time to recruit and recover respectively between fires (Cousins *et al*. 2015).

Accounting for fire intensity is more complex than drawing estimates of fire frequency. Fire intensity varies with the amount of fuel available per unit area as well as the amount of time it takes for the fuel to burn (Kraaij and van Wilgen 2014). Percent vegetation cover or biomass (i.e., fuel load) provides us with a measure of primary productivity which is closely linked to fire behaviour (Brown and Bevins 1986; Goldammer 1990; Bond and Keeley 2005; Goslar 2006). By incorporating NDVI (an estimate of vegetation cover) into the model, I attempted to obtain some confirmation that the species prefers to grow in areas with lower vegetation cover (i.e., in more rocky regions), where sporadic fires could occur but at low intensity due to the limited available biomass. The NDVI variable, apart from being highly correlated to several climate variables, yielded no influence on predicating habitat suitability (i.e. low percent contribution to the outcome) and was therefore also excluded from the final model. Values of NDVI are known to be less reliable over complex terrain and at higher altitudes (Box *et al.* 1989) and this could have had an influence on the resultant outcome.

Distribution models created for several fire-adapted Proteaceae species (in the fynbos) found that fire-related variables accounted for additional variation in distribution, which was not captured by climatic variables and thus increased the model performances (Tucker *et al*. 2012). Whilst the fire-related variables included in this study did not yield the same outcome, consideration of dynamic processes including natural disturbances, species interactions and dispersal ability remains an important part of studying species patterns (Wisz *et al.* 2013). Furthermore, incorporating these aspects into species distribution models provides a clearer understanding of the entirety of a species' ecology and can ultimately improve the

projections made by SDMs for species under abiotic conditions arising presently and in the future (Keith *et al.* 2008; Engler *et al.* 2009; Madani *et al.* 2015).

4.3 Future projected distribution range of the species under shifting climates

Climates are predicted to become hotter and drier across Mediterranean-type ecosystems (Yates *et al.* 2010; Altwegg *et al*. 2014) with potentially catastrophic impacts on the rich biodiversity occurring in these regions (Midgley *et al*. 2002). In the case of *Kumara plicatilis*, which is well adapted to a set of climatic conditions arising in the fynbos region, this study projects small-to-significant range contractions under the different climate change scenarios for various time frames and under various assumptions. Climate scenarios presented by RCP 2.6 offer the best-case scenario for conservative climate change, and under this scenario, 'liveable' range contractions are projected for the species. Conditions in the year 2050 however appear to be more unsuitable for the species than conditions arising in the year 2070, with larger areas of suitable habitat maintained under shifts associated with the latter scenario. This pattern is also manifested in the estimates of habitat suitability made across areas where populations are currently known to occur. Six out of 16 highly suitable populated areas are expected to remain suitable under the RCP 2.6 scenario by the year 2050, whilst nine of these 16 are projected to have suitable conditions under this scenario in 2070. These statistics only deteriorate under the worst-case climate scenario presented by RCP 8.5. Only three out of these 16 populated areas are expected to remain suitable by 2050, with this number decreasing to zero by 2070. Should the species be unable to withstand shifting climates (as is projected here) and colonize new areas of suitable habitat, extinction risk of several populations is likely to increase drastically, particularly in areas where movement and dispersal are limited (Engler *et al*. 2009).

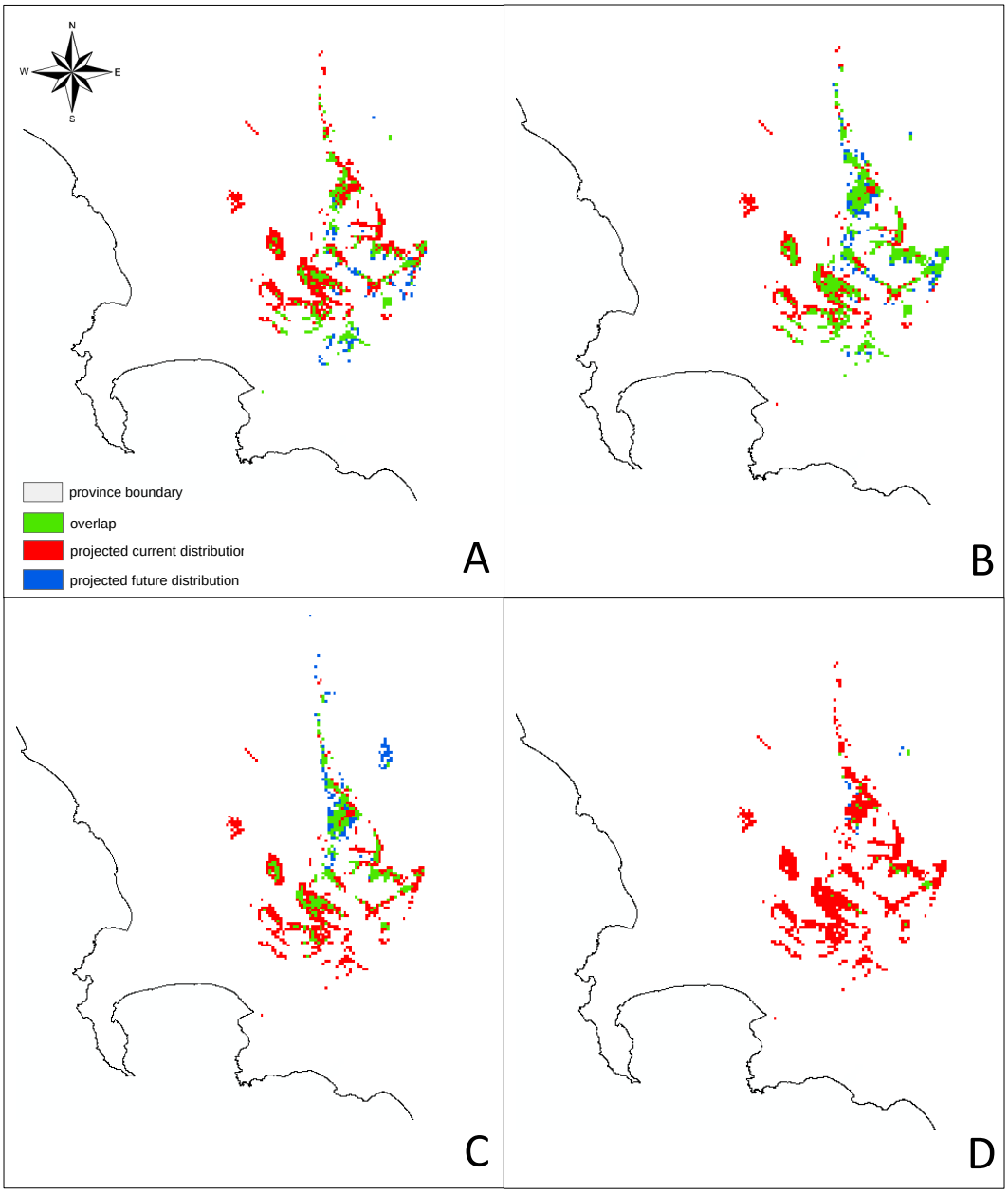

Figure 8: Overlap between current and future suitable habitat areas (suitability > 0.5) for *Kumara plicatilis* under different climate scenarios: A) RCP 2.6 for 2050, B) RCP 2.6 for 2070, C) RCP 8.5 for 2050 and D) RCP 8.5 for 2070.

Varying degrees of suitable habitat will remain available under the different scenarios, whilst new zones of suitability will also emerge between and around these available areas (Fig. 8). For the most part, range contractions will see suitable habitat become more concentrated toward the north and central regions of the current distribution range. Under the worst-case scenario, highly suitable (suitability > 0.75) range areas could experience contractions of up to 60% by 2050 and 100% by 2070, whilst moderately suitable habitat (suitability > 0.5) could decrease in area by 30% and 50% by 2050 and 2070 respectively. The projected outcomes under RCP 2.6 are a little more optimistic with contractions in highly suitable and moderately

suitable habitat expected to be around 40% and 50% by 2050, and around 15% and 20% by 2070 respectively. These shifts are most likely due to climate values falling outside of the species preferred range of suitable conditions (see Appendix IV for more information). Climates across the fynbos have for the most part remained relatively stable particularly in the montane areas of the western region (Altwegg *et al.* 2014). Slight changes in these conditions to which many species are adapted could explain the range contractions predicted in studies such as these. Winter rainfall as an example in this case, is expected to drop below 400 mm across the entire region under RCP 8.5 in 2070 accounting partly for the sharp decline in suitable habitat observed for this scenario. Whilst the species is able to tolerate a wider range of temperatures, cold winter temperatures (to which the species is accustomed) are predicted to increase above the current range and concurrent shifts in the distribution pattern of the species are expected.

Altitudinal shifts in distribution amongst montane plant species as a result of warming climates is not a new concept. Numerous studies have shown how species have, and most likely will, experience increases in the upper edges of their altitudinal range in order to escape rising temperatures (Lenoir *et al*. 2008; Randin *et al*. 2009; Dirnbock *et al*. 2010; Chen *et al.* 2011; Engler *et al.* 2011; Dullinger *et al.* 2012; Bentley 2015). Similar patterns are projected for *Kumara plicatilis,* where shifting climates will most likely see areas of suitable habitat conditions extending up the mountains towards a slightly higher elevation (between 1000 and 1300 m a.s.l.) than occupied and projected suitable now (between 200–950 m a.s.l.). This expected rise in the tree-line of the species accounts for the northward contractions (where there is higher altitude land) of the current range observed under shifting climates. Whilst the treeline of many mountain species are projected to continually increase upwards (Hickling *et al.* 2006; Chen *et al*. 2011), very high altitudes (> 1500 m) are projected to harbour unsuitable habitat conditions for *K. plicatilis* now and in the future which severely decreases the refuge space available to the species under changing climates. This resultant limitation on this mountain species aggravates its extinction risk particularly under the most severe climate change scenario.

Several studies on climate change effects have been conducted at both species and biome level across the fynbos and CFR (Midgley *et al.* 2002 & 2003; Hannah *et al.* 2005; Driver *et al.* 2012). Endemic plants and animals including species of proteas, birds and bees are predicted to experience a shift in their habitat to cooler areas at higher latitudes and higher altitudes (Midgley *et al.* 2003; Kuhlmann *et al*. 2012; Huntley and Barnard 2012). Furthermore, these species are all projected to experience a contraction in their current distribution ranges under different projections of climate change. Range contractions for plants species which have evolved under conditions that have promoted limited dispersal ability (i.e., climate stability, rugged topography and a variety of soil types) in the fynbos, increases the susceptibility of local populations to extinction (Ellis *et al.* 2014). Seed dispersal in *Kumara plicatilis* is estimated to be limited to short distances (about three times the canopy height of an adult plant; Cousins *et al*. 2013). Nonetheless, the

occurrence of several isolated populations patchily distributed on mountain ranges around more continuous populations suggest that the strong Cape winds have been able to disperse the winged seeds across much larger distances (Cousins *et al.* 2013). Dispersal capacity is an important aspect of plant survival, acting as a key determinant of whether the species will be able to reach the areas of habitat predicted to be suitable in the face of global climate change (Midgley *et al.* 2006; Randin *et al.* 2009). Selection against unfavourable traits over a short period of time resulting in rapid evolutionary change will also impact the successful establishment and survivability of species under situations of changing conditions (Pearson and Dawson 2003). Given that *K. plicatilis* is a long-lived and fairly slow-growing species with large populations consisting mainly of adult plants with low seed dispersal and low recruitment ((Cousins *et al.* 2013 & 2014); the species could face further challenges in being able to successfully undergo intergenerational selection and shifts in its tolerance range in time to adapt to changing climatic conditions.

4.4 Niche overlap, equivalency and similarity

Niche conservatism refers to the tendency of species to maintain ancestral ecological requirements (Harvey and Pagel 1991; Peterson *et al.* 1999; Wiens and Graham 2005). Several studies have demonstrated general and persistent niche conservatism in individual species as well as large biomes over long periods of time in spite of changes in climate and environmental conditions (Martınez-Meyer and Peterson 2006; Crisp *et al.* 2009; Romdal *et al.* 2012). The retention of climatic tolerances (i.e., climate niche conservatism) in particular, is one aspect of niche conservatism that has been known to limit the geographical ranges of species and clades and carries important consequences for conservation (Peterson *et al*. 1999; Wiens and Graham 2005; Crisp *et al.* 2009; Wiens *et al*. 2010). The statistical analysis used in this study to further interpret the change in spatial patterns observed under changing climates suggest that *Kumara plicatilis* is a species unlikely to experience measurable changes in environmental niche occupancy and therefore displays traits of niche conservatism. The test of niche similarity suggests that the species shares more environmental niche space now and in the future than randomly expected. The assessment of niche equivalency does however point out that the species environmental niche under present and future climate conditions are not exactly identical. However, it is important to note that the niche equivalency test is a test of strict identity, which means that it is extremely conservative; rarely do species exhibit identical niches (Warren *et al.* 2008). Consequently, these results are not contradictory, but instead suggest that the niche of the species currently and in the future encompass similar but not equivalent environmental conditions (Warren *et al.* 2008) and the test of niche similarity more importantly points out that the species

displays patterns of long-term stasis in its environmental and climate tolerances which would challenge its ability to survive shifting conditions.

These findings provide further context to the outcomes of the SDMs showing that future areas of suitable habitat are found in the same niche space as currently occupied by the species. In this context, the decrease in available suitable habitat projected under scenarios of climate change make sense as the species climatic niche is narrow and this limits its ability to change its geographic distribution i.e., to shift to, and inhabit new areas with different climates outside of its current distribution. Authors who describe the niche conservatism concept often link the idea to evolutionary patterns and process. Whilst some literature proposes that climatic niche conservatism is a key factor in initially isolating populations and driving large-scale patterns of divergent evolution (Wiens 2004; Rangel *et al*. 2007; Romdal *et al*. 2012), other studies conclude that a lack of niche conservatism across large heterogeneous areas is what results in high levels of species richness (Martinez-Cabrera *et al.* 2012). In the case of *Kumara plicatilis* it is possible that the sharp climatic gradients arising in the Cape Floristic Region following the initial transition to a Mediterranean climate (around > 8 million years ago) resulted in a burst of speciation (Goldblatt 1978; Linder 2003) after which climatic stability (along with other factors such as topographic heterogeneity, geology, fire etc. (Cowling and Lombard 2002; Ellis *et al*. 2014; Verboom *et al.* 2015)) increased the persistence of new species and resulted in many well adapted species maintaining traits of their ancestral climatic niches. This display of niche conservatism means that unsuitable conditions such as those arising under estimates of global climate change can limit the geographic distribution of the species and have notable influences on its conservation status. It is most likely due to niche conservatism that we see the distribution patterns above emerging under different scenarios of climate change distribution models. Whilst the analysis used in this study presents robust ways to measure niche differences between or within species at a given time or over a period of time respectively (Broennimann *et al.* 2011), the outcomes of this research would benefit from future field work confirming the idea that *Kumara plicatilis* will remain constrained within its current environmental niche space even as climates change.

4.5 Considerations for conservation and limitations to the study

With impacts of population growth and anthropogenic climate change slowly being realized around the world (Rosenzweig *et al.* 2008; Butchart *et al.* 2010; Seto *et al.* 2012; IPCC 2014), understanding potential threats to vital species and ecosystems becomes increasingly necessary (Chapin *et al*. 2000). Modeling the distribution of species under estimates of probable climate change provides an initial approximation of the possible impacts of shifting climates on biodiversity and, is a useful means of

integrating future conditions into conservation practise (Pearson and Dawson 2003; Wiens *et al.* 2009). These results should however, be interpreted cautiously with due consideration of the assumptions, limitations, and uncertainties underlying these models (Pearson and Dawson 2003, Thuiller 2004; Wiens *et al.* 2009; Araujo and Peterson 2012).

Modeling responses of individual species to impacts of global change is often more reliable than modeling impacts on entire assemblages but all projections nevertheless rest on assumptions and are underpinned by limitations not unlike the ones present in the study. Firstly, the models above do not account for the biotic factors that could influence the distribution and survival of the species at a local scale such as landscape processes (e.g., fire), species interactions and dispersal capacity. These biotic interactions and their dynamics influence the species response to climate and have important implications on predicting future distributions of species habitat (Keith *et al.* 2008; Brook *et al.* 2009; Wisz *et al.* 2013). Furthermore, by not accounting for these biotic processes, we have effectively modeled the species environmental niche (with climate and biophysical factors) but have not effectively described its ecological niche (which includes the set of biotic conditions in addition to the abiotic conditions where a species can persist; Hutchinson 1957; Holt 2009). Whilst many SDMs often do not account for these biotic processes, there are a number of methods being developed to allow for their incorporation (Keith *et al.* 2008; Brook *et al.* 2009; Pagel and Schurr 2012; Wisz *et al.* 2013). It would be good for example, to include a more fine scale fire frequency or intensity variable in the initial run and then use a simulated fire variable, showing increased intensity or frequency under different climate scenarios for the projected runs (Reside *et al.* 2012). However, these methods and required data were beyond the scope of this study.

The second limitation to SDMs in this study is the uncertainty attached to Global Climate Models (Randall *et al.* 2007; Wiens *et al.* 2009; Flato *et al.* 2013). GCMs are the best currently available tools for simulating global future climate scenarios but there are variations within and amongst alternate climate models (Beaumont *et al.* 2008) which can result in differential outcomes for distributions trained on different GCMs (Pienaar *et al*. 2015). Furthermore, the climate in the CFR is influenced by both large scale atmospheric and more locally-derived oceanic processes and to better understand climate change in this region requires a sound working knowledge of how the regional drivers of climate variability will be affected by climate change (Altwegg *et al.* 2014). Whilst this type of understanding might be absent from GCMs, Regional Climate Models (RCMs) such as the ones available from AfriClim (Platts *et al*. 2014; https://www.york.ac.uk/) offers more robust regional assessments of expected climate change for local areas and where spatial heterogeneity is high e.g., in mountainous areas (Guisan and Thullier 2005; Platts *et al.* 2014). The resources currently available from these sites are however limited and do not encompass all four of the IPCCs (2014) climate change scenarios and could not be used in this study. Another

consideration for SDMs aimed at projecting future distributions of species is that of the climate variables included in the models. Climate variables are highly correlated and using them in climate change studies often requires you to use one or two highly correlated variables. It is important to note that whilst arbitrary inclusion or exclusion of correlated variables is likely to have a marginal effect on the current range projections, future distributions may vary considerably based on the climate parameters included or excluded from the model (Braunisch *et al.* 2013). It is therefore of utmost importance to select variables for which we have a good degree of certainty that they are important towards understanding the species habitat requirements, particularly if model outcomes are intended for conservation decisions (Braunisch *et al.* 2013).

Finally, there are the almost opposing assumptions that (a) the species will be able to migrate to available areas of suitable habitat, and (b) the species will not be able to adapt to conditions prevailing under climate change. Whilst the latter assumption may be more plausible seeing as the species displays climatic niche conservatism, the former assumption could under-estimate the vulnerability of the species to shifting climates. If the species is unable to overcome dispersal barriers (such as competition) or, if prevailing conditions do not allow for long distance dispersal and germination, the species could face local population extinctions particularly in areas where climate changes are projected to be highly unsuitable. *Aloe dichotoma*, a tree aloe endemic to the Namib desert region, has experienced high mortality rates in warm areas closer to the equator, whilst populations closer to the poles showed signs of population growth albeit with a limited expansion in range towards cooler areas (Foden *et al.* 2007). The authors attributed these patterns to climate change and limited dispersal ability deducing that the geographical distribution of the species was being progressively squeezed between areas of its critical climate between a zone of range contraction (where areas were exceeding critical climate limits), and a zone of lagging range expansion (owing to poor dispersal). This means that whilst the species was declining in numbers under unsuitable conditions, it was also unable to expand populations into new regions due to its sessile nature and poor dispersal ability (Foden *et al*. 2007). Recent research has since supported future impacts of climate change on the species (Guo *et al.* 2016), although some researchers have attributed the observed mortalities to small-scale spatial heterogeneity and life history characteristics noting importantly, that in order to fully understand impacts of climate change on longer lived species, studies need to take place over much longer periods of time (Jack *et al.* 2016). These findings nevertheless highlight the importance of including dynamic processes such as demographics, microhabitat and dispersal ability into distribution models.

SDMs constructed on projections of future climates offer only an insight into potential changes in the spatial patterns of *Kumara plicatilis* across the central southwestern fynbos region based on the best available information at hand, and whilst assumptions and limitations add to the uncertainty of the models,

documenting these reservations can help inform appropriate conservation action. Exposure to climate change is in no way the ultimate determinant of probable impacts on a species or population. Factors including the sensitivity (i.e., degree to which a species or population is dependent on the prevailing climate) and adaptability (i.e., the capacity of a species or population to cope with climate change by either surviving *in situ* or by shifting to more suitable regions) are equally important in the assessment of species vulnerability (Dawson *et al.* 2011; Foden *et al.* 2016). Whilst *Kumara plicatilis* does not currently face immediate threats of human disturbance, invasive species or habitat degradation, climate change has the potential to impact the conservation status of the species. The species is a habitat specialist inhabiting and maintaining a unique environmental niche space that could influence the species sensitivity and adaptability to new climate conditions. Whilst niche conservatism may have influenced the success of the species up until now, projections of severe climate change is likely to see the species lose a large percentage of suitable habitat which may be accompanied by the loss of several populations. This phenomenon will severely increase the vulnerability of *K. plicatilis* to extinction. Nevertheless, the results from the SDMs provide opportunities to identify critical habitat areas where translocation projects may be successful and necessary (Guisan *et al.* 2013). Germination and long-term seed storage studies (*see* Cousins *et al.* 2013) would also benefit the species along with plans for *ex-situ* conservation in the event of severe climate changes.

Conclusion

This study used distribution modeling and comparative niche indices to successfully identify suitable habitats for *Kumara plicatilis* as well as infer distributions for the species under current and future climate conditions. The results provide insight into the species climatic requirements and future conservation standing. The outcomes of this study suggest that climate change will have a limited to severe impact on the suitability of habitat for the species under the 'best-case' and 'worst-case' climate change scenarios respectively. Identifying and measuring areas of suitable climatic habitat allows us to understand patterns of species distribution that can be used in pro-active conservation initiatives when uncertainties associated with model outcomes are well accounted for. Further field surveys and ground-truthing will nevertheless be useful in varying the model outcomes. These outcomes shed light on the importance of using novel scientific techniques for the conservation of wildlife species.

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APPENDIX I

Table A: List of environmental (climate and biophysical) variables initially considered for the Maxent models.

	Variable	**Code**	**Source**
1	Annual Mean Temperature	Bio_1	http://www.worldclim.org (Hijmans et al. 2005)
2	Mean Diurnal Range	bio_2	
3	Isothermality	bio_3	
4	Temperature Seasonality	bio_4	
5	Max Temperature of Warmest Month	bio_5	
6	Min Temperature of Coldest Month	bio_6	
7	Temperature Annual Range	bio_7	
8	Mean Temperature of Wettest Quarter	bio_8	
9	Mean Temperature of Driest Quarter	bio_9	
10	Mean Temperature of Warmest Quarter	bio_10	
11	Mean Temperature of Coldest Quarter	bio_11	
12	Annual Precipitation	bio_12	
13	Precipitation of Wettest Month	bio_13	
14	Precipitation of Driest Month	bio_14	
15	Precipitation of Seasonality (CoVar)	bio_15	
16	Precipitation of Wettest Quarter	bio_16	
17	Precipitation of Driest Quarter	bio_17	
18	Precipitation of Warmest Quarter	bio_18	
19	Precipitation of Coldest Quarter	bio_19	
20	Elevation	elevation	http://www.worldclim.org
21	Aspect	aspect	
22	Slope	slope	
23	Geology	geology	GCSRI departments, Wits
24	Bioregion	bioregion	Mucina *et al*. 2006
25	Vegetation type	veg_type	Mucina *et al*. 2006
26	Normalised Difference Vegetation Index	NDVI	https://earthdata.nasa.gov/
27	Fire Frequency	Fire_freq	https://earthdata.nasa.gov/

Table B: Correlation matrix generated using ENM toolbox highlighting the highly-correlated variables (Pearson correlation coefficients (>|0.7|)

	aspect	bio_1.a	bio_2.as	bio_3.	bio_4.a	bio_5.a	bio_6.a	bio_7.as	bio_8.a	bio_9.	bio_10	bio_11	bio_12	bio_13	bio_14	bio_15	bio_16	bio_17	bio_18.	bio_19	bioregi	elevati	fire_fr	geolog	ndvi.as	slope	veg_typ
aspect	1	0.0292	-0.0129	0.0226	-0.0181	0.0110	0.0390	-0.0184	-0.0130	0.0282	0.0187	0.0339	0.0055	0.0188	-0.0198	0.0405	0.0202	-0.0178	-0.0203	0.0224	-0.0210	-0.0345	0.0090	0.0162	0.0227	-0.0075	-0.004
bio_1.asc	1	1	0.0513	0.1708	-0.0675	0.6328	0.6417	-0.0040	0.1792	0.5395	0.8863	0.8757	-0.296	-0.232	-0.317	0.2928	-0.231	-0.3296	-0.4008	-0.115	-0.0815	-0.7856	-0.077	0.0987	-0.072	-0.4867	0.1502
bio_2.asc	1	1	1	0.0330	0.8473	0.7699	-0.684	0.9620	0.3715	-0.223	0.4355	-0.370	-0.763	-0.663	-0.606	0.0765	-0.676	-0.6121	-0.4374	-0.688	0.6336	0.4485	-0.279	-0.322	-0.768	-0.1080	0.5682
bio_3.asc	1	1	1	1	-0.467	-0.053	0.3030	-0.235	-0.058	0.2077	-0.065	0.3630	-0.054	-0.144	0.0836	-0.023	-0.127	0.0865	-0.029	-0.044	0.1962	-0.271	-0.049	0.4052	0.1005	0.0826	-0.008
bio_4.asc	1	1	1	1	1	0.6938	-0.745	0.9520	0.2664	-0.256	0.4001	-0.538	-0.618	-0.463	-0.601	0.1606	-0.481	-0.5996	-0.3888	-0.532	0.4652	0.5577	-0.197	-0.448	-0.717	-0.1064	0.4706
bio_5.asc	1	1	1	1	1	1	-0.143	0.7572	0.3200	0.1820	0.9012	0.1998	-0.733	-0.564	-0.724	0.3536	-0.574	-0.7296	-0.6268	-0.519	0.3994	-0.102	-0.222	-0.208	-0.638	-0.3776	0.5114
bio_6.asc	1	1	1	1	1	1	1	-0.754	-0.255	0.6154	0.2462	0.9066	0.3567	0.3455	0.1848	0.2387	0.3641	0.1874	-0.020	0.4757	-0.453	-0.887	0.1661	0.4411	0.5334	-0.1862	-0.326
bio_7.asc	1	1	1	1	1	1	1	1	0.3807	-0.285	0.4348	-0.465	-0.721	-0.602	-0.602	0.0764	-0.620	-0.6073	-0.4019	-0.658	0.5641	0.5178	-0.257	-0.429	-0.772	-0.1274	0.5543
bio_8.asc	1	1	1	1	1	1	1	1	1	-0.629	0.2914	0.0032	-0.375	-0.465	-0.004	-0.397	-0.505	-0.0624	0.2166	-0.649	0.2718	0.1794	-0.253	-0.486	-0.405	-0.3328	0.4369
bio_9.asc	1	1	1	1	1	1	1	1	1	1	0.3716	0.5934	0.0596	0.1541	-0.215	0.4115	0.1860	-0.1745	-0.4955	0.4124	-0.308	-0.709	0.1399	0.4646	0.2730	-0.0578	-0.284
bio_10.asc	1	1	1	1	1	1	1	1	1	1	1	0.5559	-0.548	-0.418	-0.562	0.3415	-0.425	-0.5721	-0.5365	-0.346	0.1384	-0.458	-0.160	-0.121	-0.388	-0.4945	0.3587
bio_11.asc	1	1	1	1	1	1	1	1	1	1	1	1	0.0610	0.0457	0.0213	0.1827	0.0549	0.0124	-0.1537	0.1785	-0.301	-0.934	0.0382	0.3055	0.3001	-0.3510	-0.110
bio_12.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	0.9115	0.7788	-0.141	0.9122	0.7938	0.6557	0.8521	-0.550	-0.161	0.3462	0.2097	0.7758	0.3300	-0.567
bio_13.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.4717	0.2264	0.9947	0.4875	0.3679	0.9428	-0.484	-0.163	0.3840	0.2365	0.6482	0.3117	-0.483
bio_14.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.668	0.4619	0.9924	0.9120	0.3776	-0.425	-0.041	0.1465	0.0251	0.6747	0.2409	-0.457
bio_15.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.2336	-0.6496	-0.6464	0.2885	0.1634	-0.183	0.1140	0.2722	-0.157	-0.0559	0.1229
bio_16.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.4801	0.3425	0.9608	-0.493	-0.184	0.3943	0.2681	0.6573	0.3225	-0.498
bio_17.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.9042	0.4045	-0.429	-0.043	0.1603	0.0534	0.6883	0.2561	-0.482
bio_18.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.1686	-0.212	0.2150	0.0729	-0.152	0.4947	0.1771	-0.258
bio_19.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.552	-0.348	0.4038	0.3845	0.6753	0.3148	-0.560
bioregion.as	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.4567	-0.229	-0.133	-0.582	-0.0690	0.7191
elevation.as	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.126	-0.344	-0.411	0.2854	0.2670
fire_freq.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.1526	0.3323	0.1441	-0.293
geology.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.3441	0.2023	-0.246
ndvi.asc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.2783	-0.601
slope	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.315
veg_type.as	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

APPENDIX II

MODELS USING DATASET 1 (All occurrence points)

1) **Model with all variables**

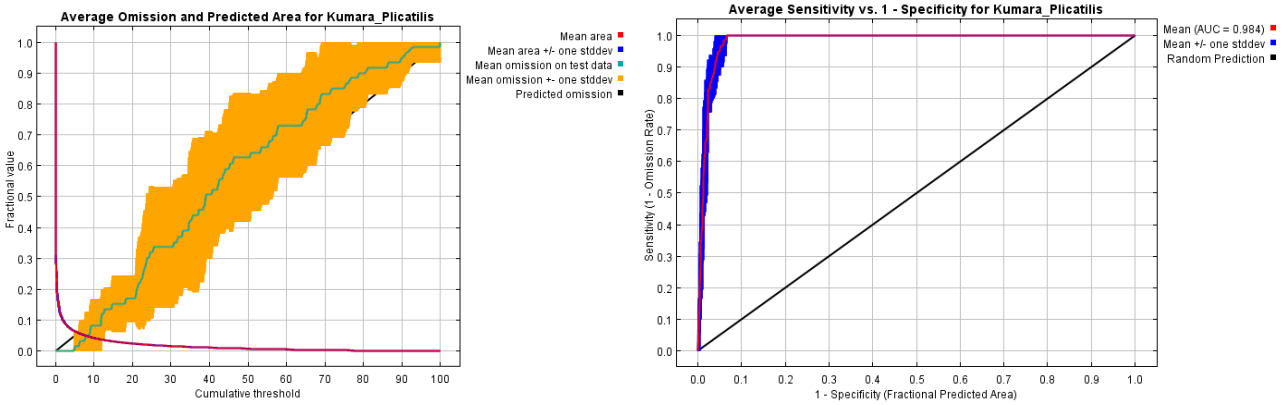

Figure A: (i) The test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs and (ii) the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. The average test AUC for the replicate runs is 0.984, and the standard deviation is 0.003.

Variable	Percent contribution	Permutation importance
bio_16	37.1	27.7
bioregion	28.8	7.7
veg_type	5.8	4.8
geology	5.7	3.9
bio_7	5.4	3.3
bio_5	4.5	3
slope	2.9	3
bio_15	2.2	23
bio_19	1.8	0
bio_13	1.2	0
bio_2	1	0.5
elevation	0.8	0
bio_12	0.8	0.9
aspect	0.5	0.7
bio_6	0.5	9.6
bio_4	0.3	5.2
ndvi	0.2	2
bio_1	0.2	0.7
fire_frequency	0.1	0.1
bio_10	0.1	2.8
evi	0.1	0.4
bio_17	0	0
bio_9	0	0.4
bio_8	0	0
bio_3	0	0
bio_11	0	0
bio_18	0	0
bio_14	0	0

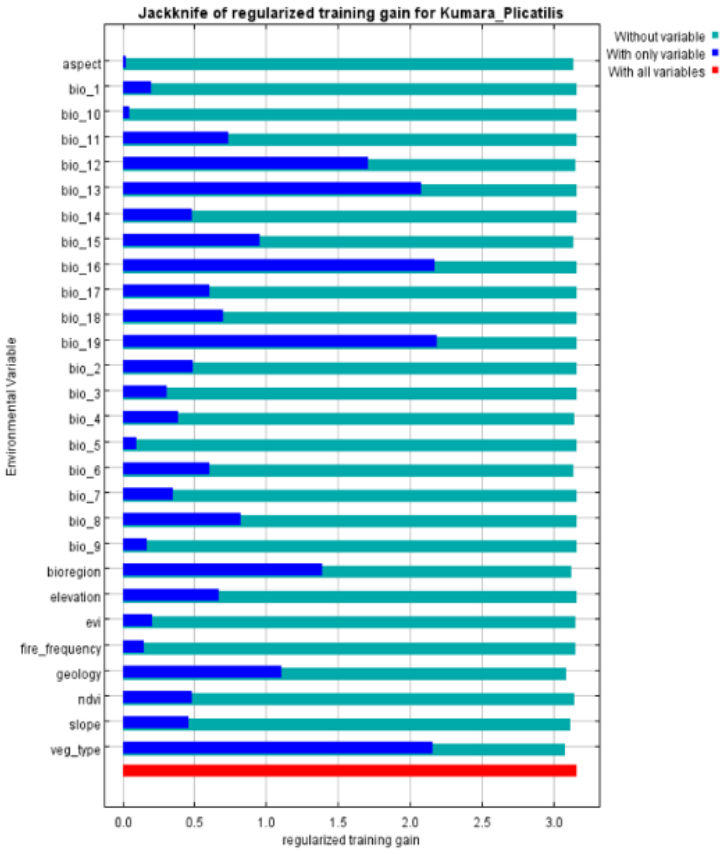

Figure B: (i) Table giving the estimates of relative contributions of the environmental variables to the Maxent model, and (ii) the results of the jackknife test of variable importance.

2) **Final model after removal of correlated variables and additional stepwise removal of least contributing variables (with no impact on the model gain)**

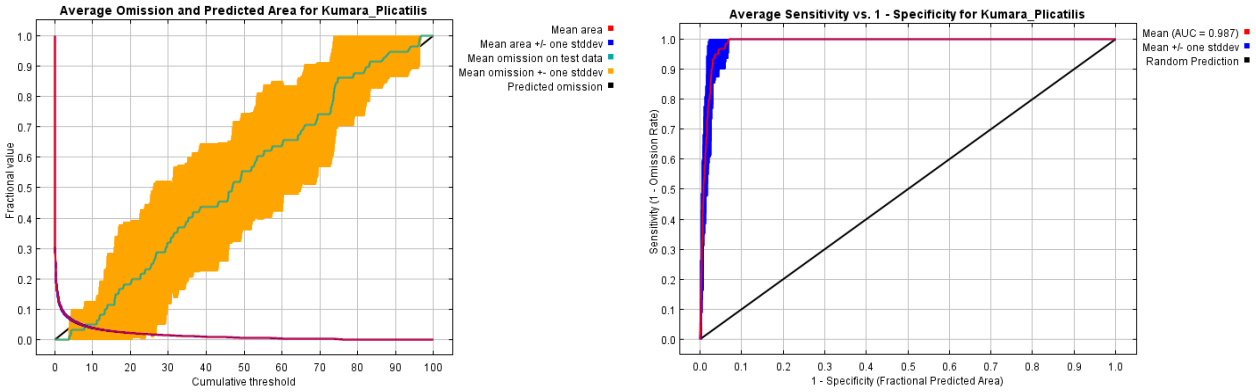

Figure C: (i) The test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs and (ii) the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. The average test AUC for the replicate runs is 0.987, and the standard deviation is 0.006.

APPENDIX III

MODELS USING DATASET 2 (Occurrence points with known high abundance)

1) **Model with all variables**

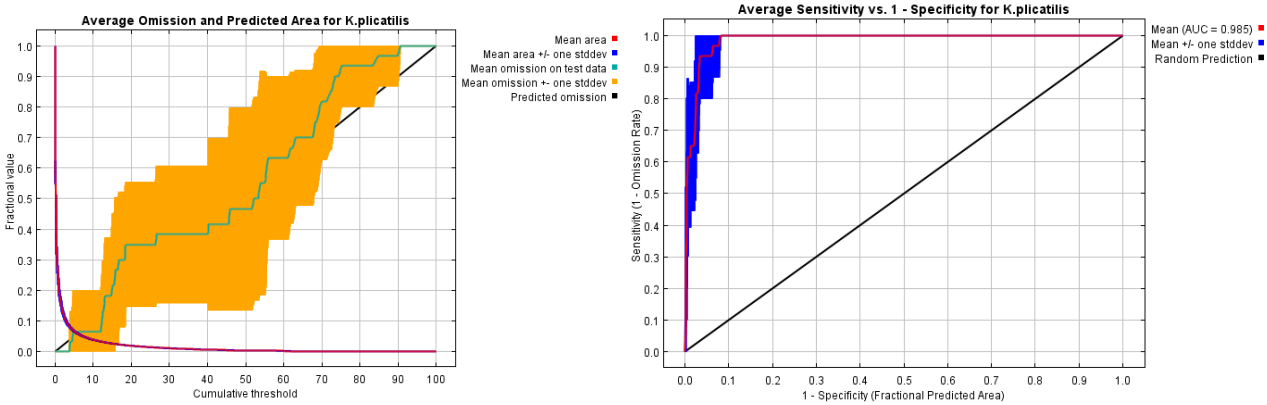

Figure D: (i) The test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs and (ii) the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. The average test AUC for the replicate runs is 0.985, and the standard deviation is 0.008.

Variable	Percent contribution	Permutation importance
bio_16	50	37.7
veg_type	14.9	10.4
geology	8.4	10.1
bioregion	7.3	0
bio_7	6.1	12.1
bio_13	4.2	0
bio_19	2.3	0
aspect	2.2	9.1
bio_12	2.2	0
bio_4	0.6	8.8
bio_2	0.4	2.9
slope	0.3	0.4
fire_frequency	0.3	0.1
elevation	0.2	0.4
bio_3	0.1	2.5
bio_15	0.1	5.2
ndvi	0.1	0.3
bio_5	0	0
evi	0	0
bio_9	0	0
bio_8	0	0
bio_6	0	0
bio_18	0	0
bio_17	0	0
bio_14	0	0
bio_11	0	0
bio_10	0	0
bio_1	0	0

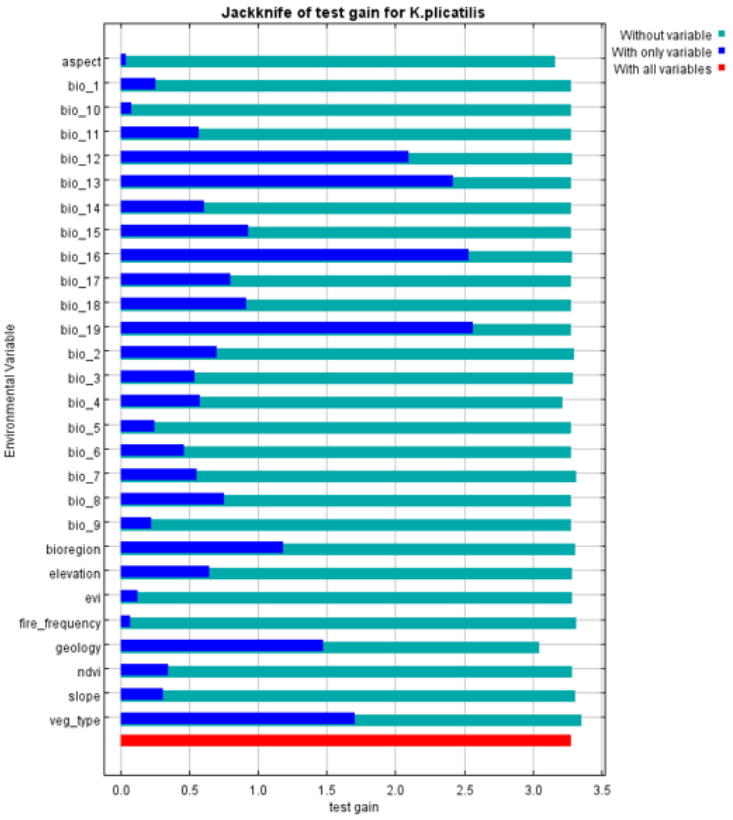

Figure E: (i) Table giving the estimates of relative contributions of the environmental variables to the Maxent model, and (ii) the results of the jackknife test of variable importance.

2) **Final model after removal of correlated variables and additional stepwise removal of least contributing variables (with no impact on the model gain)**

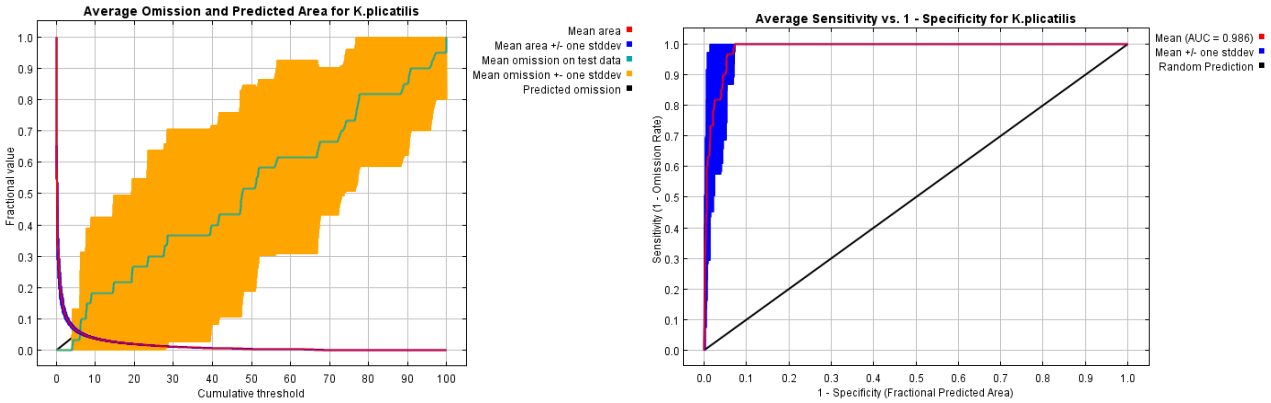

Figure F: (i) The test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs and (ii) the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. The average test AUC for the replicate runs is 0.986, and the standard deviation is 0.012.

APPENDIX IV

Table B: Range of values (minimum and maximum) for ecologically significant environmental variables influencing the distribution of *Kumara plicatilis.*

Climate Scenario	**Range of values (minimum and maximum) for ecologically significant environmental variables**					
	Minimum temperature of coldest month in ˚C (bio_6)	Temperature annual range in ˚C (bio_7)	Mean temperature of wettest quarter in ˚C (bio_8)	Mean temperature of warmest quarter in ˚C (bio_10)	Precipitation seasonality (CV) (bio_15)	Precipitation in the wettest quarter in mm (bio_16)
Current Conditions	-3.7 - 9.9	13.6 – 32.2	5.3 – 23.2	12.8 – 25.6	10% - 75%	40 – 484 mm
RCP 2.6 (in 2050)	-2.4 – 11.1	13.9 – 32.5	5.9 – 24.9	14.2 – 27.1	13% - 76%	40 – 509mm
RCP 2.6 (in 2070)	-2.1 – 11.1	13.7 – 32.3	6 - 25	14.4 – 27.2	8% - 78%	35 – 473mm
RCP 8.5 (in 2050)	-1.1 – 11.9	13.8 – 32.4	7.1 - 26	14.9 – 28.2	9% - 78%	34 – 440mm
RCP 8.5 (in 2070)	0 – 12.5	13.7 – 32.3	7.7 – 27.1	15.8 – 29.2	12% - 77%	28 – 396mm