Assessing the Feasibility of Assisted Colonisation to Reduce Climate Change Extinction Risk for Western Cape Proteaceae

By

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Abstract

Anthropogenic climate change may be testing certain species' abilities to adapt via range migration, or natural selection *in situ*. Particularly vulnerable species have restricted ranges and limited dispersal capabilities – characteristics of many endemic species found in the Cape Floristic Region (CFR). Many have evolved anti-telechory, including several Proteaceae species, and may thus require active conservation interventions to ensure their future persistence in the wild. Assisted Colonisation (AC) is a conservation strategy aimed at reducing species' climate change-induced extinction risk, but no detailed assessments exist of the feasibility of assisted colonisation in the CFR context.

By combining Species Distribution Modelling (SDM) outputs for 191 Proteaceae species under future climate scenarios, with selected species traits and land-use maps, this study developed a hierarchical screening approach to identify potential assisted colonisation candidates in the CFR. Using projections over shorter time periods allowed for more potential assisted colonisation candidates to be identified and using life-history traits in conjunction with spatial projections shifted the prioritisation of some assisted colonisation candidates. Thirty-one potential assisted colonisation candidates were identified and subset into three types: Sustained intervention, Short-term intervention, and Mitigation dependent candidates, indicating different degrees of active intervention. The Mitigation dependent candidate group highlighted the potential for future global emissions reductions to reduce extinction risk for several assisted colonisation candidate species projected to become highly vulnerable after 2040. Vulnerable species not suitable for assisted colonisation were also identified.

Some implicit assumptions behind assisted colonisation implementation were explored using field measurements on selected populations of *Protea compacta,* a species historically planted and harvested for the cut flower industry. *P. compacta* allowed exploration of ecological performance differences across a range of environmental suitability levels. *P. compacta* populations were targeted in sites defined by species distribution models (SDMs) as having high bioclimatic suitability in 'core' range sites, supporting naturally established populations, and sites of 'marginal' bioclimatic suitability, occupied by artificially introduced populations. The latter represents a pragmatic assisted colonisation approach – establishing populations in marginal sites that are projected to become more suitable with progressive climate change. Microhabitat buffering against low suitability in a marginal site was also explored.

Measurements unexpectedly showed individuals in marginal sites had higher growth and flowering rates, but higher disease susceptibility. Additionally, the densely populated core sites showed significantly more monopodial branching, and sympodial branching in marginal sites, suggesting that the relaxation of strong intraspecific competition in marginal sites may compensate for lower population densities, supporting population establishment, and thus favouring the practical implementation of assisted colonisation. This pattern was confirmed by a finer-scale study at a marginal site, where high population densities found in wetter microhabitats showed growth and flowering responses similar to those in core populations. This supports the idea that purposeful microhabitat choices may buffer marginal unsuitability and increase likelihood of successful assisted colonisation implementation. This work has allowed for a novel assessment of the feasibility of assisted colonisation in the CFR, but assessment of unintended consequences and generalising to more species and systems is necessary to further establish a basis for considering assisted colonisation implementation.

Opsomming

Bewyse oor klimaatsverandering dui daarop dat die koers daarvan die koers kan oorskry waarteen sekere spesies kan migreer of *in situ* aanpas. Spesies met beperkte reekse en verspreidingsvermoë is veral kwesbaar, soos baie van die endemiese spesies in die Kaapse Floristiek Streek (KFS). Baie spesies in hierdie streek het kortafstrand verspreiding ontwikkel, insluitend baie Proteaceae. Hierdie spesies benodig dalk meer aktiewe bewaringsintervensies om hul toekomstige voortbestaan in die natuur te verseker. Hulp Kolonisering (HK) as a 'n bewaringstrategie kan dalk die risiko van uitwissing verminder, maar daar is geen gedetailleerde beoordelings van die uitvoerbaarheid van HK in die konteks van die KFS nie. Deur die kombinasie van Spesie Verspreidings Modelle (SVM) met spesie-eienskappe en landgebruikskaarte, het hierdie studie 191 Proteaceae beoordeel as potensiële HK-kandidate om die toepasbaarheid van die gebruik van HK in die KFS te beoordeel. 31 potensiële kandidate was geïdentifiseer en in drie soorte gekategoriseer: Volgehoude ingryping kandidate, Kort-termyn ingryping kandidate, en versagtende afhanklike kandidate. Kwesbare spesies was ook geïdentifiseer vir alternatiewe ingryping. Dit is belangrik om te verstaan dat populasie-dinamika kennis nodig is vir die praktiese toepassing van HK. Meeste van huidige HK-gebiede het eers onlangs geskik geword en daarom is dit belangrik om die lewensvatbaarheid van die gebruik van marginale gebiede te beoordeel. *Protea compacta*-groei- en reproduksieprestasie was in twee kern- en twee marginale gebiede ondersoek. Mikrohabitatte was ook binne een marginale gebied getoets om te bepaal of dit ongeskiktheid kan verreken. Dit was gevind dat marginale gebiede goed gepresteer in verhouding tot kerngebiede. Hoë oorlewing as gevolg van die hoë geskiktheid van kerngebiede het gelei tot 'n hoë intraspesifieke kompetisie. Dit het gelei tot laer reproduksietempo's en minimale vertakking (as gevolg van hoër intraspesifieke digtheid). Marginale populasies het dalk laer oorlewings gewys as saailinge, en dus laer intraspesifieke kompetiesie. Hierdie populasies het egter meer blomme geproduseer en komplekse vertakkings vertoon. Individue in sypels het soortgelyke neigings as kern-populasies getoon. Hierdie studie het dus bevind dat sekere mikrohabitatte die kernpopulasieprestasie binne 'n marginale gebied naboots. Die kombinasie van modellering en meganistiese benaderings het 'n voorlopige positiewe beoordeling van die potensiaal vir HK-toepassing in die konteks van die KFS anngedui.

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the Middle elevation sub-site with all individuals measured showing Witches Broom, compared to Low and High sub-sites. The High elevation sub-site had the lowest rates of Witches' Broom compared to the other two sub-sites.

Abbreviations

IUCN	International Union for Conservation of Nature
AC	Assisted Colonisation
CFR	Cape Floristic Region
GCM	General Circulation Model
SDM	Species Distribution Model
IPCC	Intergovernmental Panel on Climate Change
SPARC	Spatial Planning in Response to Climate Change
RCP	Representative Concentration Pathway
AUC	Area Under the ROC Curve
DF	Degrees of Freedom
PA	Protected Areas
IQR	Inter-Quartile Range
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model

1 Chapter 1: Literature review

1.1 General Introduction

In the past few decades, anthropogenic impacts on species and ecosystems have increased exponentially due to human activity (IPBES, 2019). While habitat fragmentation and ecosystem degradation have long been identified as the main current drivers of global floral and faunal biodiversity loss (Sala *et al*., 2000; Barnosky *et al*., 2011; Foden *et al*., 2013), climate change is emerging as a major threat at least over the course of the 21st century (Parmesan, 2006; Leadley *et al*., 2010; Loss *et al*., 2010). Current extinction rates are estimated to be anywhere between 1000 and 10 000 times the natural 'background' rate (IPBES, 2019). Africa is thought to be especially vulnerable to climate change, with the observed rate of temperature change roughly double the global average (Archer *et al*., 2018), and a projected continuation of a similar trend over the next two to three decades even with substantial mitigation efforts (Yates *et al*., 2010; Osborn & Jones, 2014; Davis *et al*., 2017).

Several extensive reviews of species responses to observed climate change, many located in the Northern Hemisphere, have found that species follow a general trend of shifting their ranges polewards and upwards in elevation in response, mainly to warming trends (Parmesan *et al*., 1999; Parmesan & Yohe, 2003; Christmas *et al*., 2016). In the Southern Hemisphere, a less extensive set of observations of ecosystem response has begun providing support for this general conclusion (Sintayehu, 2018). However, in regions of high species richness and endemism, there may be limited potential for species to achieve the extent of range shifts required (e.g., Midgley *et al*., 2002; Midgley *et al*., 2003), especially given the change in land-use trends towards high rates of land conversion (Bomhard & Midgley, 2006; IUCN, 2013; Mantyka-Pringle *et al*., 2015).

Plant populations are known to respond to climate change by adapting in place, undergoing shifts in geographic range (sometimes accompanied by isolation, vicariance, and disruptive selection), or declining and ultimately being locally extirpated (Davis & Shaw, 2001; Vitt *et al*., 2010; Higgins *et al*., 2012). Traditional conservation methods have been geared towards supporting *in situ* adaptive capacity (e.g., Hannah *et al*., 2002), but more recently have begun considering more interventionist approaches, including assisting the migration of species as bioclimatic conditions suitable for them are displaced from their current ranges (von Maltitz *et al*., 2004 – see Figure 2; Prober *et al*., 2019). Habitat loss and fragmentation present

significant barriers to the natural migration of plants, and this challenge has been met by planning for increased connectivity of patches via corridors or networks (Williams *et al*., 2005; Phillips *et al*., 2018) to allow for some species to migrate into more suitable habitats. However, given recent analyses of the potential velocity of climate-induced ecological change (Williams *et al*., 2014; Burrows *et al*., 2014; Prober *et al*., 2019), there is already evidence that suggests that the rate of climate change is exceeding certain species' abilities to move via migration or adapt *in situ* (Williams *et al*., 2005; Heller & Zavaleta, 2009; IPCC, 2014).

With climate change and biodiversity loss increasing rapidly around the world, conservationists have begun considering more interventionist ways to mitigate species extinction risk (Hoegh-Guldberg *et al*., 2008; Schwartz & Martin, 2013; Lunt *et al*., 2013). One of these more interventionist conservation methods is reintroductions, most commonly for animal species, which aims to re-establish historical ranges of species by releasing captive bred or translocating wild individuals into areas that were once part of their range (Rondeau, 2001; Wilmers *et al*., 2003; Seddon *et al*., 2007; e.g., Toone & Wallace, 1994). This is useful for species that have suffered extirpations of subpopulations in areas of historical range that remain environmentally suitable, and where the threat responsible has been mitigated. However, many species are projected to undergo range shifts into novel areas but due to poor dispersal capabilities and natural/anthropogenic barriers, are unable to traverse large distances to these newly suitable areas (Renton *et al*., 2011). Such species are likely to face extinction without more active intervention.

Typically, the intervention for plant species at high risk of extirpation or extinction is to conserve individuals through *ex situ* conservation methods - in cultivation and/or in the form of seeds collected and preserved in seed banks (Liu *et al*., 2020). Maintaining populations in cultivation and seed banks are thought to be more cost effective than *in situ* conservation (Li & Prichard, 2009), however, *in situ* conservation allows for large amounts of genetic and ecosystem diversity, while maintaining important biotic interactions and ecosystem function (Wolf, 1999; Zegeye, 2016). This suggests that conservation strategies like Assisted Colonisation (AC) could play an important role in reducing climate change extinction risk for species with restricted ranges and limited dispersal. Assisted colonisation aims to translocate populations beyond their historic ranges into their future projected ranges (potential range) to mitigate biodiversity loss caused by anthropogenic climate change (Hough-Guldberg *et al*., 2008; Hewitt *et al*., 2011). There are many terms used to describe this process, with slight

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variation in definition. These include assisted translocation, assisted migration and managed relocations, but for the purpose of this study, the term assisted colonisation (Hough-Guldberg *et al*., 2008) is used with the aforementioned definition.

Assisted colonisation has seen an increase in theoretical development for conservation and has seen some early testing and implementation in the past decade (e.g., van der Veken *et al*., 2012). Assisted colonisation is widely discussed in the conservation literature but mostly with respect to the ethics, methodology and legality (Prober *et al*., 2019), with few studies reflecting successful application. Willis *et al*. (2009) were able to successfully establish two butterfly species beyond their current range but within their potential range, in Northern England. Results showed expansion of both these butterfly populations in their respective recipient sites, which addressed the climate lag experienced by these species.

In the Cape Floristic Region (CFR) of South Africa, Slingsby *et al*. (2017) identified that Fynbos plant communities are also experiencing a climatic lag. Adults have been found to be more resilient to temperature increases than seedlings and juveniles, and since fynbos is a fire driven system, this leads to punctuated shifts in community composition associated with fires, as the seedlings of resilient adults fail to establish in novel climate conditions. This suggests that the impacts of recent anthropogenic climate change are yet to be realised and adds importance to the potential for assisted colonisation to facilitate plant species adaptation by range adjustment.

Most literature on assisted colonisation reflects work focused in the Northern Hemisphere, and is widely debated in that context (see Ricciardi & Simberloff, 2009). However, there is little to no exploration of how assisted colonisation of plants may perform in the African context, specifically the South African context with its hyper-diverse ecosystems. The Cape Floristic Region (CFR) has been identified as a biodiversity hotspot with over 9000 species, many with limited dispersal capabilities (Goldblatt & Manning, 2002), limited range sizes (Enquist *et al*., 2019), and challenges of ecosystem fragmentation due to land-use (Bomhard *et al*., 2005), and thus could potentially benefit from assisted colonisation.

Paleo-ecological records show that the CFR acted as a refugium during the Miocene and Pliocene epochs, and the prolonged climatic stability during the Pleistocene allowed for many of the fynbos clades to radiate to the extent to which they have (Cowling & Lombard, 2002). The relative climatic stability in the Cape, especially since the beginning of the Quaternary, means that many species may be vulnerable to climatic changes due to niche specialisation

(Valente et. al., 2009; Mokhatla *et al*., 2015), including the evolution of anti-telechory (short-range seed dispersal), which limits the potential for range shifts (see Midgley *et al*., 2006).

Biodiversity in the CFR is also severely threatened by habitat loss and invasive plants, with over 30% loss of natural habitat due to agricultural practices and urbanisation (Rouget *et al*., 2003; Sarmento *et al*., 2013). The Fynbos Biome is one of the most invaded biomes in South Africa (Richardson & van Wilgen, 2004; Mostert *et al*., 2017; van Wilgen *et al.* 2020), which has had significant impacts on species assemblages and ecosystem functioning and is considered one of the largest threats to plant species after habitat loss (Richardson *et al*., 1997; Higgins *et al*., 1999; van Wilgen *et al*., 2016; Slingsby *et al*., 2017). This has led to a fragmented landscape, further limiting dispersal and gene flow (Heller & Zavaleta, 2008).

With increases in minimum and maximum temperatures and aridity in the Greater CFR (Kruger & Shongwe, 2004; Jones *et al*., 2012; Altwegg *et al*., 2014; Osborn & Jones, 2014), there are already signs of species in the CFR adversely affected by such rapid changes. Milne (2014) has found that the Cape rock-jumper, an endemic bird species, is particularly unable to cope with temperatures higher than 31.2 °C without suffering severe evaporative water loss. Thus, increased temperature in the CFR is expected to result in significant range contractions for the Cape rock-jumper, and the species has consequently been uplisted by the IUCN from 'Near threatened' to 'Vulnerable' (Lee & Barnard, 2016). Similarly, the germination and establishment phase for many Fynbos Proteaceae is highly sensitive to drought (Altwegg *et al*., 2014). *Protea* seedlings that were transplanted into more xeric conditions than found within their natural habitats, had higher mortality rates (Agenbag, 2006; Lechmere-Oertel & Cowling, 2001), which suggests a strong bioclimatic threshold existing at the arid edge of their distributional range (Altwegg *et al*., 2014).

With evidence of species in the CFR showing early signs of climate change-induced stress, it seems very likely that further anthropogenic climate change in the CFR will only exacerbate biodiversity loss (van Wilgen *et al*., 2016; Davis *et al*., 2017). Unlike many parts of Africa, there is high agreement between General Circulation Model (GCM) projections for rainfall reduction and warming in the winter rainfall regions of the Cape (IPCC, 2007; IPCC, 2014). Multiple models project that the CFR could experience increased temperatures (0.3-2.5°C by 2050, relative to 1985-2006 averages), greater frequency of hot days (Stocker *et al*., 2013*b*), increased aridity and frequency of extreme weather events, including drought (Davis *et al*., 2017; Archer *et al*., 2018). These climatic projections, overlaid on the ongoing anthropogenic

impacts such as invasive plants and habitat loss, present significant challenges for the conservation of endemic biodiversity in the CFR.

Species Distribution Modelling (SDM) has allowed conservation efforts to move from reactive conservation strategies to increasingly proactive strategies (Pereira *et al*., 2010), which can play an important role in planning and implementing targeted interventions such as *ex situ* efforts, and assisted colonisation. SDMs allow for the overall vulnerability of a multitude of species to climate change to be investigated. However, it is widely acknowledged that SDMs have limitations and rely on an array of assumptions (Thuiller *et al*., 2008; Higgins *et al*., 2012; Briscoe *et al*., 2019). Thuiller *et al*. (2008) highlights that SDMs fail to account for the migration of populations, and the changes in range dynamics at the leading and trailing edges of species distributions. Midgley *et al*. (2010) developed a dynamic implementation of an SDM approach to account for these dynamics, but this approach is dependent on a large number of assumptions (Fourcade *et al*., 2014), and is thus more useful as a heuristic versus a predictive model. The current lack of coherent understanding of range dynamics and the factors governing the limits of species distributions (Gaston, 2009; Kerr, 2020), represents a significant barrier to implementing strategies such as AC with confidence.

In broad terms, niche theory provides a conceptual framework that can inform the implementation of AC. Niche theory defines the realised niche as the environmental space in which the species is observed to occur, and the fundamental niche as the potential range that is potentially environmentally suitable for the species (Vandermeer, 1972; Jackson & Overpeck, 2000; Chase, 2011). Dispersal limitation is one of the mechanisms that may prevent a species from occupying its fundamental niche, as shown by Schurr *et al*. (2007), who found that wind-dispersed Proteaceae more closely filled their fundamental niche than ant-dispersed Proteaceae. If this is the case, AC may provide the opportunity for threatened species to colonise unfilled areas of range (recipient sites) that may be currently marginal in bioclimatic suitability but is projected to become more suitable as climate change progresses. The application of SDMs is expected to help identify such areas, and how they may shift geographically over time (see Midgley *et al*., 2006), thus potentially providing a series of 'steppingstones' for population establishment.

Figure 1.1 provides a simplified diagrammatic example of a niche shift in geographic space, with the shaded areas in (b) and (c) representing important areas to examine as potential

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recipient sites since they contain currently intra-limital range over the relevant time periods despite representing the 'leading edge' for the species range. Therefore, beyond highlighting target recipient sites, understanding the growth and reproductive performance of a population in core, and marginal sites is of particular interest. Marginal sites that are predicted to become more suitable are particularly important when considering the successful implementation of AC, as they might provide the highest probability of successful establishment with a minimum additional risk. However, the feasibility of using marginal range sites for this purpose is unclear. Investigating the differences in species performance in core and marginal sites is expected to improve understanding of range dynamics and inform the efficacy of AC implementation.
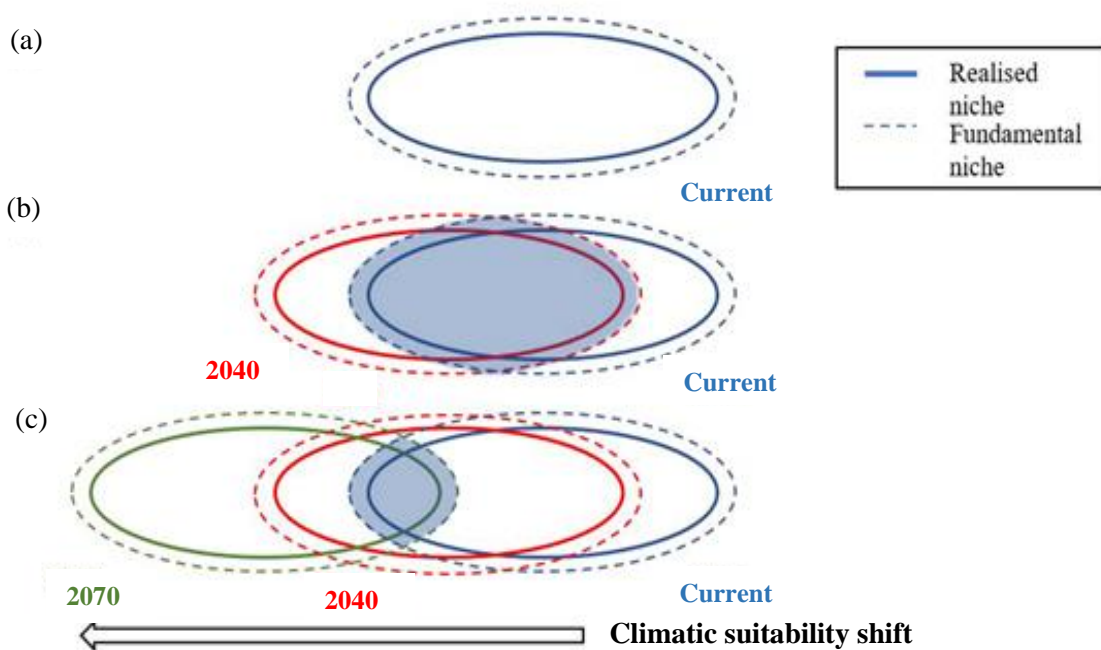
Figure 1.1 Theoretical model of how fundamental and realised niches move over time. The shaded overlap seen in (b) and (c) show areas of interest as potential donor and recipient sites for assisted colonisation candidates at the range leading-edge, since it contains theoretically intra-limital habitats from both a fundamental and realised niche perspective for the relevant time periods.

While SDM and other modelling techniques have increased in predictive power and resolution over time, they remain relevant at fairly coarse spatial scales. Topographic and habitat heterogeneity at smaller scales might represent a powerful additional consideration when implementing AC in a potential recipient site, as individual plants are likely to experience a broader range of potential microclimatic conditions than identified at the scale of the SDMs (Pincebourde *et al*., 2016). In fact, climate heterogeneity within a landscape can

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be found to be incredibly complex, where microclimates can magnify or buffer the effects of climate change (Woods *et al*., 2015). Differences in slopes, vegetation cover and underlying surface composition in a landscape are known to attenuate solar radiation differently (Sears *et al*., 2011; Ashcroft *et al*., 2012; Pincebourde *et al*., 2016). This means that finer scale recipient site choice likely plays an important role in the success of a translocation, especially in marginal sites predicted to become more suitable. Therefore, testing differences in climatic landscape heterogeneity can provide interesting possibilities into microhabitat choice potentially offsetting marginal site unsuitability. The combination of modelling and a mechanistic approach is expected to have higher accuracy in helping determine the practical feasibility of assisted colonisation.

This study thus seeks to inform potential conservation action in the CFR by using SDM approaches to classify selected Proteaceae into groups of species that can naturally adapt, that require *ex situ* conservation, and those that might persist under field conditions if provided with AC. Further, an associated field study to assess the efficacy of establishing populations of an exemplar species in two such marginal sites and two core sites is undertaken.

1.2   Study Species

The Proteaceae represent an iconic component of the Fynbos vegetation in the CFR, comprising 14 genera and around 400 species with extremely well documented distributions from the Protea Atlas Project (Cowling & Lamont, 1998; Rebelo, 2001), and with Species Distribution Models (SDMs) available from Spatial Planning in Response to Climate Change project (SPARC). Many Proteaceae species are known for their short-distance dispersal traits and associated limitations in establishing new populations over long distances (Midgley *et al*., 2002; Shurr *et al*., 2007). Garcia *et al*. (2014) highlight the importance of including species traits when assessing their vulnerability to climate change. The availability of extensive life-history traits for over 300 Proteaeceae (Rebelo & Foden, *unpublished*) can be used to better inform migration ability and likelihood of species establishment. Some 86% of Proteaceae species are reseeders, which makes it more likely that intervention will be needed since reseeder populations are known to experience extreme fire-related population fluctuations (Rebelo, 2001; Bomhard *et al.*, 2005). Proteaceae also play a crucial role in water, carbon and nutrient cycling, as well as in providing resources for various bird, rodent

and ant pollinators and herbivores (Collins & Rebelo, 1987; Cowling & Holmes, 1992). Finally, Proteaceae is world-renowned, with many species used in the international cut flower trade (Turpie *et al*., 2003). Assisted colonisation may provide the practical potential to mitigate biodiversity loss and the theoretical opportunity to investigate range dynamics in the CFR. Thus, the extensive life-history traits and distributional knowledge available coupled with vulnerability to climate change, make Proteaceae a highly suitable study subject for assisted colonisation in the CFR.

1.3   Risks of AC in the Fynbos Biome

As previously mentioned, assisted colonisation has largely been discussed in the literature, especially regarding the potential risks (see McLachlan *et al*., 2007; Riccardi & Simberloff, 2009; Hewitt, 2011). While many risks and considerations have been highlighted, the main considerations relevant to this study are the risk of invasion by the candidate and the risk of hybridisation, including issues of hybrid vigour and outbreeding depression.

Mueller & Hellmann (2008) found that plants moved intra-continentally had the lowest likelihood of becoming invasive compared to other taxa. Therefore, when using assisted colonisation for certain taxonomic groups, the lower risk of intracontinental invasion and dispersal constraints of most plants, could support the case for using assisted colonisation (Mueller & Hellmann, 2008). Certain traits have been identified to increase a species' risk of invasibility (Rejmánek & Richardson, 1996; Catford *et al.* 2012).These include fast generation time, high dispersal capabilities, small seed size and high propagule pressure (Jeschke *et al*., 2012; Moodley *et al*., 2014). Moodley *et al*. (2014) found that out of the 402 Proteaceae species introduced worldwide, only eight have become invasive, all of which are Australian natives. Australian plants such as *Banksii* and *Hakea* have been highly invasive in South Africa, however, there have not been cases of South African Proteaceae being invasive in Australia and this is thought to be due to longer interims between fires (Moodley *et al*., 2014).

Hybridisation and introgression are two other major concerns when considering assisted colonisation and is particularly relevant in the context of the CFR. Hybridisation potential and hybrid fitness is difficult to predict since gene pool mixing can simultaneously have deleterious and beneficial genetic outcomes (Edmands *et al*., 2004). Hybridisation has been

known to be more frequent between recently divergent taxa (Mallet, 2005). Proteaceae in the CFR show high species turnover on a small spatial scale (Valente *et al*., 2009), which may mean that allopatric species may not have evolved distinct reproductive barriers. The relatively recent divergence of the CFR means that hybridisation is quite common and/or likely (Visser, 2005). Croxford *et al*. (2001), found that closely related *Leucadendron* species were easily crossed, however species with larger distance between their phylogenetic positions showed stronger evidence of prezygotic hybridisation barriers. MacQueen & Potts (2018) were able to show that the allopatric species *Protea eximia* and *Protea susannae* readily hybridise among many more documented *Protea* hybrisations (Rebelo, 2005).

This raises concerns around the potential occurrence of both outbreeding depression and hybrid vigour. A study conducted by Edmands *et al*. (2004) supported the prediction that outbreeding depression is a temporary phenomenon, with incompatible gene interactions being rapidly purged through natural selection (Templeton, 1986). Todesco *et al*. (2016) indicate in their analysis that extinction risk from hybridisation is more likely in vertebrates than plants and outbreeding depressions do not persist if there is a single immigration event, and those immigrants have locally adapted alleles. This may not always be the case but does raise interesting questions about the long-term viability of populations and the role of local provenance in assisted colonisation.

Weeks *et al*. (2011) argue that outbreeding depression is likely to be over-emphasised in the literature. Nowadays there are clear predicted risk factors for strong outbreeding depression such as taxonomic status, fixed chromosome differences, historical isolation, the environments of the source/recipient populations, the degree of adaptive differentiation among source and recipient populations, and rates of environmental change that populations are likely to experience (Burbidge *et al*., 2011). These factors also indicate population fitness and evolutionary resilience, giving insight into whether gene flow could improve fitness through a genetic rescue effect (Madsen *et al*., 2004). Therefore, risk of outbreeding depression should be contrasted with ability to increase genetic diversity (Burbidge *et al*., 2011).

Interestingly, differences in Proteaceae genotypes also led to differing viability of cross-bred individuals (Croxford *et al*., 2001). *Leucadendron laureolum* pollen created no seed with one genotype of *Leucadendron salignum* but produced a viable seed with another *L. salignum* genotype (Croxford *et al*., 2001). Proteaceae thus do contain species that readily hybridise,

but translocation of Proteaceae in South Africa in the past has been done without knowledge of possible introgression. Hybridisation is a complex issue that requires extreme caution when considering translocating species, especially in the context of the CFR where species turnover is extremely high over relatively small geographical areas.

Other challenges to implementing assisted colonisation are financial and logistical in nature. Implementation projects can become expensive and extend over long periods of time (Gallagher *et al*., 2015). However, with proper scientific backing, funding and long-term monitoring can be properly planned and increase the success and viability of assisted colonisations (McLachlan *et al*., 2007).

1.4   Rationale, Key Questions and Hypotheses

Despite the risks which have been identified above which need careful consideration, assisted colonisation still demonstrates strong potential as a conservation strategy. The CFR, a region with exceptional biodiversity, has been shown to be highly threatened by climate change, with anthropogenic impacts projected to worsen into the future. Conservationists are at a critical point where more active roles in conservation are needed to mitigate biodiversity loss. Traditional conservation strategies have focused on supporting the natural capacity of ecosystems and while this is important, given the expected velocity of climate change, more active and hands-on strategies may be needed. Prober *et al*. (2019) highlights in their meta-analysis that more active conservation strategies, termed "climate-targeted interventions", are often disregarded due to contradictions with traditional conservation ideals. There is a trade-off between maintaining the wildness of nature with minimal human intervention and the climate-targeted interventions that are inherently more hands-on (Thomas, 2011). With the rate of global change, society and conservationists may be forced to redefine how we value nature and maintain core elements of wildness despite having more active intervention strategies.

Without intervention, many CFR species may be at risk of extirpation or even extinction and the Proteaceae provide a well-researched and documented exemplar group for testing the feasibility of assisted colonisation in the CFR context. Furthermore, studying the factors that influence species range dynamics can provide important information for establishment in potential recipient sites and how this choice may relate to the range limitations of a species

based on their realised and fundamental niche limits. This study seeks to provide a thorough evaluation of the feasibility of several important aspects of assisted colonisation, with the broader objective of reducing extinction risk in Proteaceae. I pursue this by integrating ecological theory and climate change predictions to identify candidates for AC using SDM-based spatial metrics (Hällfors *et al*., 2017), and examine the performance of a focal *Protea* species in climatically core and marginal (informed by SDM suitability scores) parts of its range.

The following aims, central questions and hypotheses are addressed in my data chapters.

Chapter 2: Identifying Suitable Candidate Species in the Proteaceae for Future Assisted Colonisation Adaptation Responses

Aim: To identify suitable Proteaceae candidate species and potential recipient sites for implementation of AC by using a systematic approach, based on SDM modelling, relevant Proteaceae trait data and cross-checking of feasibility of recipient sites with current land-use maps.

Central questions:

- How many species were found to be appropriate AC candidates?
- Of the Proteaceae species for which AC was found to be an unsuitable intervention strategy, what proportion of species were classified as likely persisters (low future vulnerability), potential persisters (intermediate future vulnerability) and non-persisters (high future vulnerability), and how many are appropriate AC candidates?
- Does evaluating Proteaceae species using shorter timescales result in more potential AC candidates being identified?
- To what extent does the inclusion of life-history traits shift prioritisation of potential AC candidates?
- To what extent do current land-use practices, including protected areas, affect the feasibility of potential AC candidates?

Hypotheses:

- A substantive fraction of Proteaceae will qualify as potential AC candidates due to both a need for range translocation and the potential for such a range translocation.

- The consideration of finer time scales will provide greater numbers of candidates for AC.
- The inclusion of life-history traits will shift prioritisation of a proportion of species with AC potential.

Chapter 3: Growth and Reproductive Performance of *P. compacta* in Marginal and Core Populations

Aim: (i) To compare the performance of *P. compacta* in sites of high climatic suitability (i.e., well within their historical range) with those that were planted and established in marginally suitable areas (i.e., at the margin of their historical range) and (ii) to assess whether microhabitats present in marginal sites can buffer overall site unsuitability.

Central questions:

- How much does the growth and reproductive performance of *P. compacta* individuals differ between populations growing in core and marginal bioclimatic conditions?
- Are there differences in microclimatic conditions, growth, reproduction and disease susceptibility found in *P. compacta* individuals in differing microhabitats in marginal sites?

Hypotheses:

- Individuals in *P. compacta* populations growing in areas with optimal projected climatic suitability will have higher growth and flowerhead production, and lower disease susceptibility.
- The growth and flowerhead production of individuals in a range of microhabitats in a marginal site will reflect differences in bioclimatic suitability at these finer scales.

This dissertation comprises four chapters, with chapters two and three as data chapters and one and four as a literature review and synthesis, respectively. The structure of data chapters two and three include introductions with key concepts discussed in this chapter, which may result in some repetition, and the references cited in this dissertation have been combined into a single reference list and appended after Chapter 4.

2 Chapter 2: Identifying Suitable Candidate Species in the Proteaceae for Future Assisted Colonisation Adaptation Responses

2.1 Abstract

Traditional conservation strategies are geared towards building the adaptive capacity of species in the wild, but for species that have limited dispersal capabilities and restricted ranges, there are already signs that the velocity of climate change may be exceeding their ability to adapt *in situ* or to track their preferred bioclimatic conditions via range migration. Such species are likely to become extinct without targeted intervention. Assisted colonisation (AC) has long been suggested as a response aimed at assisting species to shift their distributions to increase the chances of persistence within their future projected suitable range. Assisted colonisation may be most valuable in biodiversity hotspots, which are characterised by range restricted species with limited dispersal capacity. The CFR is a hyper-diverse region with high numbers of endemic species, many of which have been identified as vulnerable to projected anthropogenic climate change, however, a detailed assessment of the potential of AC in the context of the CFR has not yet been done. A hierarchical analysis using a combination of SDM-based spatial metrics, species life-history traits and current land-use maps was conducted to test if AC would be a potential intervention strategy for 191 Proteaceae species. The analysis highlighted 31 suitable AC candidates, 14 of which would require Sustained intervention up to 2070 at least, 7 that would require Short-term intervention (over the next three decades), and 11 for whom successful intervention beyond 2040 is dependent on aggressive climate change mitigation efforts. Furthermore, AC was found to be an unsuitable intervention strategy for the majority of Proteaceae species. These species were evaluated and classified as likely persisters, potential persisters and non-persisters depending on their relative range loss and gain over time. Some 79-126 non-persisters were identified (depending on the time period) as requiring alternative intervention were, while 45-57 likely persisters were identified to require no targeted intervention for climate change adaptation beyond the maintenance of the current protected area networks. Candidates range shifts identified over a single 6-decade period (current-2070) versus two successive 3-decade periods (current-2040 and 2040-2070) revealed significantly more species classified as highly vulnerable in the current-2070 period. This demonstrates the importance of timely action to reduce the extinction risk of several species. AC appears, based on these theoretical criteria, to be a possible conservation strategy for some Proteaceae.

2.2   Introduction

In the past few decades, anthropogenic impacts on species and ecosystems have increased exponentially due to human activity (IPBES, 2019). Climate change, land fragmentation and habitat degradation have been identified as the main current and future drivers of global floral and faunal biodiversity loss at least over the course of the 21st century (Bellard *et al*., 2012). The observed rate of temperature change in Africa has been found to be roughly double the global average, making Africa particularly vulnerable (Archer *et al*., 2018). A similar trend is projected to continue over the next two to three decades even with substantial mitigation efforts (Davis *et al*., 2017). However, with aggressive mitigation responses, the likelihood of stabilising global temperature below the 2°C increase greatly improves (IPCC, 2018), and the reversal of some anthropogenic impacts may be possible by the end of this century.

Plant populations are known to respond to climate change by adapting, migrating, or declining and ultimately being locally extirpated (Vitt *et al*., 2010). Traditional conservation methods are geared towards building adaptive capacity in the wild or aiding the natural migration of species through habitat connectivity and corridors (e.g., Hannah *et al*., 2002; Williams *et al*., 2005). However, recent analyses of the potential velocity of climate induced ecological change (Williams *et al*., 2014; Prober *et al*., 2019) suggests that there is already evidence for the rate of climate change exceeding certain species' abilities to shift their ranges or adapt *in situ* (IPCC, 2014). Many species are predicted to experience range shifts into novel areas as previously unsuitable areas become more suitable, however, many may be unable to traverse large distances to these newly suitable areas due to limited dispersal capabilities and natural or anthropogenic barriers (Renton *et al*., 2010; Thomas, 2011). Such species are likely to face extinction in the wild without more active intervention.

Slingsby *et al*. (2017) identified that Fynbos plant communities are experiencing a climatic lag. Adults have been found to be more resilient to temperature increases than seedlings and juveniles. Because Fynbos is a fire driven system, the variation in resilience between juveniles and adults leads to punctuated shifts in community composition, as the seedlings of resilient adults fail to establish in novel climatic conditions. Furthermore, many Proteaceae species are considered vulnerable due to their restricted ranges and limited dispersal capabilities, which makes natural migration into newly suitable areas unlikely (Schurr *et al*., 2007). Assisted colonisation (AC) could therefore play an important role in addressing the climatic lags that Fynbos species may be experiencing.

AC aims to translocate populations beyond their historic ranges into their future predicted ranges to reduce biodiversity loss caused by anthropogenic climate change (Hough-Guldberg *et al*., 2008; Hewitt *et al*., 2011). With almost no focus on AC in the context of South African flora, there are virtually no systematic analysis of how AC could help in reducing climate change induced extinction risk, especially for species restricted by range and dispersal. Therefore, this chapter aims to take the first step in assessing the feasibility of AC in reducing climate change extinction risk of CFR flora by attempting to characterise range shifts of 191 selected Proteaceae species in South Africa. Proteaceae distribution models under current and future projected climate scenarios were used and combined with species life-history traits. Candidates were subsequently identified based on their need and potential for assisted colonisation, and the use of current land-use maps allowed for a practical evaluation of potential AC candidate recipient sites in the CFR context.

Aims, key questions, and hypotheses

Aim: To identify suitable Proteaceae candidate species and potential recipient sites for implementation of AC by using a systematic approach, based on SDM modelling, relevant Proteaceae trait data and cross-checking of feasibility of recipient sites with current land-use maps.

Central questions:

- How many species were found to be appropriate AC candidates?
- Of the Proteaceae species for which AC was found to be an unsuitable intervention strategy, what proportion of species were classified as likely persisters (low future vulnerability), potential persisters (intermediate future vulnerability) and non-persisters (high future vulnerability), and how many are appropriate AC candidates?
- Does evaluating Proteaceae species using shorter timescales result in more potential AC candidates being identified?
- To what extent does the inclusion of life-history traits shift prioritisation of potential AC candidates?
- To what extent do current land-use practices, including protected areas, affect the feasibility of potential AC candidates?

Hypotheses:

- A substantive fraction of Proteaceae will qualify as potential AC candidates due to both a need for range translocation and the potential for such a range translocation.
- The consideration of finer time scales will provide greater numbers of candidates for AC.
- The inclusion of life-history traits will shift prioritisation of a proportion of species with AC potential.

2.3   Methodology

2.3.1   Study area and species

The Cape Floristic Region (CFR) is known for its extremely high levels of species diversity and endemism, supporting over 9000 species in an area of 90 000km^2 (Hobbs *et al*., 1995; Goldblatt & Manning, 2002, Goldblatt *et al*., 2005; Allsopp *et al*., 2014). (). The climate in the Western Cape is predominantly Mediterranean with winter-rainfall in the West, grading to all-season rainfall in the East. A combination of soil type heterogeneity, elevation variability, and a relatively stable climatic history over the Pleistocene are all factors thought to contribute to the high species richness and local- and landscape-scale species turnover observed in a relatively small spatial scale (Linder 2001; Linder, 2003).

The dominant biome of the CFR, the Fynbos Biome, has island-like characteristics, in that it is largely restricted to dystrophic, nutrient poor, sandstone-derived sandy soils (Mucina & Rutherford, 2006). Many plant lineages have evolved anti-telechorous (short distance) dispersal mechanisms that are linked to wildfire cues (Bond & Midgley, 1995). While many plant groups are well studied in the CFR, the family Proteaceae are one of the most intensively mapped taxa globally, due to decades of targeted efforts of the Protea Atlas Project and database. This foundational work provides a virtually unparalleled resource for the study of climate limits to plant distributions using niche-based modelling approaches, and the exploration of conservation strategies under anthropogenic climate change.

The Fynbos Biome is also characterised by co-dominance of small trees, shrubs, and graminoid forms, with geophytes an important component (Rebelo *et al*., 2006). Three main taxa are accepted as defining Fynbos, namely Proteaceae, Ericaceae, and Restionaceae. The Proteaceae is the largest family in the CFR with almost 400 species (Goldblatt *et al*., 2005). As a dominant life form in the CFR, and world-renowned in horticultural terms, this taxon carries a large symbolic value for South Africans (Turpie, 2003). Since most of the CFR is

found in the Western Cape, I have chosen the Western Cape as the target area of my study and the Proteaceae as the subject taxon to focus my modelling and analysis efforts. My study includes 191 well-studied Proteaceae species which occur across 12 of the 14 Proteaceae genera (see Appendix A for full species list), comprising species that had sufficient data density and geographic range to permit the application of species distribution model techniques. Species distribution data was only used if more than 10 unique presence records were available (Hernandez *et al*., 2006).

2.3.2   SPARC species distribution models and projected habitat shift

Species distribution models (SDMs) use locality data of species occurrence with spatially continuous environmental data layers (generally climatic data, but in this case also by broad soil-type data) to model the environmental niche of a species of interest (Vitt *et al*., 2010, Higgins *et al*., 2012). The 191 Proteaceae SDMs used in this study were obtained from the GEF-funded Spatial Planning for Area Conservation under Climate Change (SPARC) project. The following methodology outlined by Roehrdanz *et al*. (2019), was used to create the 191 Proteaceae SDMs – for more detail methodology and reasoning for modelling decisions, see Roehrdanz *et al.* (2019):

Climate variables used to construct SDMs were selected from the standard WorldClim dataset, downscaled to 30-year norms from 1960 to 1990. Proteaceae distribution maps were based on data compiled in the mid-2000 by Protea Atlas. For the purpose of this study, rounding to the closest decade, Proteaceae distribution maps were classified as representative of 2010. These distributions are widely referred to as the current distribution, therefore from here-on it will be referred to as 'current'. De Marco & Nóbrega (2018) found that eliminating closely correlated environmental variables and using fewer, more relevant environmental variables increases the reliability and statistical power of SDM predictions (Braunisch *et al*., 2013). Therefore, the WorldClim (version 1.4) data used (WorldClim, n.d.) in the SPARC generated SDMs included the following six environmental variables:

1.   Mean annual temperature (BIO1)
2.   Mean diurnal temperature range (BIO2)
3.   Seasonality of temperature (BIO4)
4.   Minimum temperature of the coldest month (BIO6)
5.   Mean annual precipitation (BIO12)

6. Seasonality of precipitation (BIO15)

Soil variables were included as soil-type and substrate play an important role in Fynbos species occurrence (Cramer *et al.,* 2014). Soil data were obtained from Soilgrids (Soilgrids, n.d.).

The variables included were:

1. Depth to bedrock
2. pH
3. Clay proportion
4. Silt proportion
5. Bulk density

The environmental data used had 30 arc second resolution (roughly ~1km^2 resolution at South African latitude).

SDMs for the 191 Proteaceae species were used to project changes in environmental niche space using five different general circulation model projections (ncar_ccsm4, cnrm_cm5, gfdl_cm3, mohc_hadgem2_es and mpi-esm-lr). The use of five climate model outputs accounts, to some degree, for uncertainty or bias of individual model projections (Stohlgren *et al.,* 2010). The Representative Concentration Pathway (RCP) used was the 8.5 Watts/m^2 forcing (RCP 8.5), which reflects a high fossil fuel use trajectory driving greenhouse gas emissions (Riahi *et al*., 2011). The modelling tool Maxent was applied following Merow *et al*. (2013) and Merow *et al*. (2014), to produce relatively less complex models to avoid model overfitting. Thirty percent of occurrence records were reserved for model performance testing.

The projections of SDM environmental niche space at 3 time-frames (current, 2040 and 2070) were used to determine the velocity of environmental change for the 191 species in roughly 30-year intervals. Projected occurrences for the 2040 and 2070 time-frames were generated using an AUC-defined probability of occurrence, which resulted in a suitability score ranging between 0 and 1. This suitability score was binned at 0.5 to create a binary outcome (0 or 1). Jarnevich *et al*. (2015) states that the application of the model output should guide the threshold set. Therefore the 0.5 threshold method was used as it provides relatively conservative model outputs, which is favoured in the context of assisted colonisation feasibility testing as higher model confidence of range shifts is needed. Therefore, occurrences were attributed and ascribed 1 if a data point had at least a 0.5 (or

50%) suitability score (probability of occurring) and data points with a suitability score less than 0.5 (or 50%) were ascribed 0 and set as absent (McPherson *et al.*, 2004; Jiménez-Valverde & Lobo, 2007). The area of all the presence points can be summed to represent a potential range size for each model at each time frame. For a full description of the methods and modelling decisions, see Roehrdanz *et al.* (2019).

2.3.3   Identifying AC candidate species
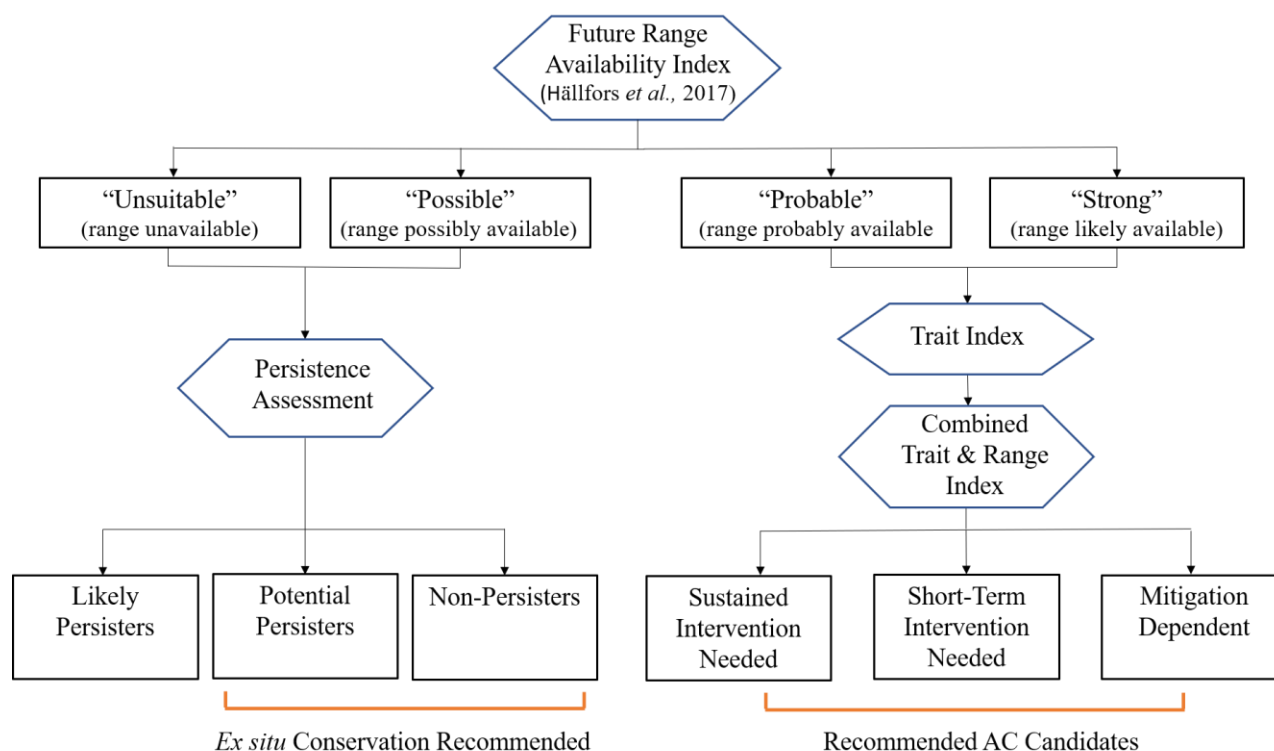
Figure 2.1. A diagram depicting the hierarchical approach used to identify AC candidates. Blue hexagons indicate processes while black rectangles indicate classification outcomes. The Hällfors *et al.* (2017), assisted translocation index was used to classify the 191 Proteaceae species into four categories, namely Strong, Probable, Possible and Unsuitable candidates. For species identified as unsuitable and possible, AC was not recommended as a suitable strategy. These species' ability to persist was assessed and were classified into three groups: (1) 'Non-persisters', which have large reductions in their range and little to no future range gain; (2) 'Potential persisters', are species with a high enough need to warrant monitoring; and finally, (3) 'Likely persisters', which suffer little range loss in the future and are regarded as having low extinction risk. Strong and probable candidates were used in a trait analysis to assess their establishment ability. Trait and Hällfors *et al.* (2017) indices are combined to create a final "AC-Suitability index", from which the remaining strong candidates are identified as the recommended AC candidates. These candidates are subset into three groups: (1) 'Sustained intervention' candidates, including those that are strong candidates in the current-2040 and 2040-2070 timesteps; (2) 'Short-term intervention' candidates, which are strong candidates in 2040, however do not need further intervention in 2040-2070; and lastly, (3) 'Mitigation dependent' candidates are strong candidates from current-2040 but become vulnerable due to significant projected range loss from 2040-2070, however, with successful mitigation efforts, these candidates would likely become Sustained or Short-term intervention candidates.

2.3.3.1   Quantifying range shifts over time

All statistical analyses were carried out using R (version 4.0.3; R Core Team, 2013), and graphics were produced using either *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2020) R packages or Excel (version 2101). Species range extents were limited to the extent of the target study area, the Western Cape. A loop function was created to automate range shift quantification, due to the large amount of data. The spatial range shifts of the 191 species, each containing five general circulation models, were compared at the three time-frames (current-2040, 2040-2070 and current-2070). For each species, overall range size, persistence (present:present), loss (present:absent) and gain (absent:present) was calculated for each of the five general circulation models. Outputs were expressed as percentage cover in the Western Cape. These outputs were then averaged to generate an 'ensemble-like' mean across all model predictions. Outputs were collated into an Excel '.csv' file. Percentages were then converted to km^2 to calculate AC metrics.

Calculating AC spatial metrics

Hällfors *et al*. (2017), developed an index that uses range shift data to quantify a species' need and potential for assisted translocation (or colonisation). The need for translocation (T_N) is determined by how much range a species has lost between time periods (Eq. 1), and the potential for translocation (T_P) is determined by how much new suitable range is created between time periods (Eq. 2). T_N and T_P are then used to calculate an index value which indicates how suitable assisted translocation/assisted colonisation is as an intervention strategy for a species ($I_{AM,t}$; Eq. 3).

Equation 1: $M_{Need,t} = \dfrac{A_{original} - A_{reminant,t}}{A_{original}}$

Equation 2: $M_{Potential,t} = \dfrac{A_{New,t}}{A_{New,t} + A_{Original}}$

Equation 3: $I_{AM,t} = \sqrt{M_{Potential,t} \times M_{Need,t}}$

Hällfors *et al*. (2017), created index thresholds for classifying the suitability of AC for a species. It is based on Thomas *et al*.'s (2011) minimum definition of a species threatened by climate change, which is 1% loss of range per decade. Range loss rates of 4% and 7.5% per decade were used as middle and upper index thresholds (See Eq. 4 - 7; see Hällfors *et al*.,

2017, for further explanation). This resulted in three categories to describe the suitability of AC for a given species: (1) strong candidates, (2) probable candidates and (3) possible candidates. Species with an index lower than the possible candidate threshold were regarded as unsuitable for AC in this study. Thresholds were calculated using the equations below.

Equation 4: $A_{Reminant,t} = A_{Original} (1 - P_{Loss})^t$

Equation 5: $M_{Need,t} = 1 - (1 - P_{Loss})^t$

Equation 6: $A_{New,t} = A_{Original} [(1 + P_{Gain})^t - 1]$

Equation 7: $M_{Potential,t} = \dfrac{(1+P_{Gain})^t - 1}{(1+P_{Gain})^t + (1-P_{Loss})^t - 1}$

Time *t* is determined by the number of decades in the time period in question. In the case of current-2040 and 2040-2070, *t* = 3. Therefore, the thresholds for current-2040 and 2040-2070 are as follows:

- Unsuitable < 0.17
- 0.17 < Possible < 0.34
- 0.34 < Probable < 0.46
- Strong > 0.46

In the current-2070 time period, *t* = 6 decades, therefore the thresholds for current-2070 are as follows:

- Unsuitable < 0.24
- 0.24 < Possible < 0.46
- 0.46 < Probable < 0.61
- Strong > 0.61

A 2-sided Chi-squared test was conducted in R using the *chisq_test* function in the *rstatix* R package (Kassambara, 2020) to assess if there was a significant difference between the timescale used and the number of strong and probable AC candidates that were found.

2.3.3.2   Assessing Possible and Unsuitable Candidate's Persistence

Species classified into the possible and unsuitable categories contained both highly vulnerable species (high need) and species that had low risk (low need). The index thresholds outlined by Hällfors *et al*. (2017) were augmented to identify species in need of *ex situ* intervention (Non-persisters), those that need monitoring (Potential persisters) and those that do not need targeted intervention (Likely persisters). Classification were as follows:

- *For current-2040 and 2040-2070*

  - Non-persisters = need > 0.46

  - Potential persisters = need $0.34 < x < 0.46$

  - Likely persisters = need < 0.34

- *For current-2070*

  - Non-persisters = need > 0.61

  - Potential persisters = need $0.46 < x < 0.61$

  - Likely persisters = need < 0.46

A 2-sided Chi-Squared test (performed as described above) was used to test if there was a significant difference between the timescale used and the number of vulnerable species that were identified. The null hypothesis was that all time periods had an equal number of Likely persisters, Potential persisters and Non-persisters.

2.3.3.3   Species traits

Incorporating species traits allows for more realistic predictions of how species may perform in their novel ranges. Strong and probable candidates identified using the Hällfors *et al*. (2017) index was used in a trait-based analysis with the intention of adjusting the raw area-based scores to reflect a candidate's ability to establish post-translocation. Following Foden *et al*. (2013), traits that reflected useful establishment and adaptive capacity in species were incorporated to assess if AC candidates would be suitable. Species trait data used contains 366 Proteaceae species that were manually collected by Foden and Rebelo (*unpublished*). Trait data was used to form three main categories: (1) Rarity, (2) Dispersal ability and (3) Establishment ability. A total of seven traits were used, each having a binary outcome, with 1

and 0 indicating the presence or absence of a beneficial trait, respectively. The traits were classified as follows:

1. <u>Rarity</u>: To account for the size and density of a species' range.

    a. **Range size** (in either 2040 or 2070 depending on the time-period in question). The median range size of all 366 documented Proteaceae was used as a threshold with range sizes >2080km^2 being awarded 1 and less than 2080km^2 ascribed zero.

    b. **Population size** (current) was calculated using the median estimated population size of all 366 Proteaceae species of 95 000. If the species' population size >95 000 it was awarded 1 and if it was less, it was ascribed 0.

2. <u>Dispersal ability</u>: Dispersal ability is used to assess species' ability to colonise new range.

    a. **Dispersal mechanism:** Species with long distance dispersal (wind) mechanisms were awarded 1 and species with local dispersal characteristics (passive seed drop with no apparent telechory mechanism such as pappus or wings, and ant or mammal dispersal) were ascribed 0.

    b. **Number of vegetation types in which species occur:** Species occurring in five or more vegetation types were considered generalists and awarded 1 and those occurring in or fewer vegetation types received 0.

    c. **Fire reproductive strategy:** Species that were reseeders are deemed advantageous in translocations relative to resprouters due to generation time and greater seed production. Reseeders were therefore awarded 1, and resprouters, 0. Species with dual strategies were awarded 1.

3. <u>Establishment</u>: This indicates the ability of a species to establish and persist.

    a. **Age to 50% Flowering** (in years): Species that reached 50% flowering (i.e., time taken for 50% of the population to reach flowering) by five or less years were awarded 1 and more than five were awarded zero.

    b. **Seed production** (per annum): Production of >667 seeds per annum was ascribed 1 and less than 667 ascribed 0.

For each species, the trait scores were summed and divided by 7 to derive a trait index (I_{Trait}) score.

2.3.3.4 Overall AC-Suitability Index (I_{AC})

To create an overall AC-suitability index, the range index using the Hällfors *et al*. (2017) equations, and the trait index (I_{Trait}) were combined using the following equation:

$$I_{AC} = \sqrt{I_{AM} \times I_{Trait}}$$

Species' AC-suitability index (I_{AC}) was compared to their previous range index (I_{AM}). Using the same thresholds previously outlined; strong or probable candidates were reclassified if their I_{Trait} increased or decreased their overall classification. Therefore, species were uplisted or downlisted accordingly.

The adjusted list of strong candidates from current-2040, 2040-2070 and current-2070 were compiled. Three outcomes were expected:

1. 'Sustained intervention': Species that were strong candidates for current-2040 and remain strong candidates in 2040-2070.
2. 'Short-term intervention: Species that were strong candidates in current-2040 and became possible or unsuitable candidates in 2040-2070, with a low vulnerability i.e., Likely persisters.
3. 'Mitigation dependent': Species that were strong candidates for current-2040 but became vulnerable in 2040-2070 (i.e., Non-persisters). If mitigation efforts are successful in the future, these species would become Sustained or Short-term intervention candidates. Species with a range $< 200km^2$ in 2040 or 2070 were also included in this group.

2.3.4 Characterising Species Range Shifts using SDMs and Land-use Maps

Further investigation was needed into the feasibility of potential recipient sites for AC candidates. The SDMs of identified candidates were combined using an ensemble approach (Araujo & New, 2007). For each of the species, stricter threshold for presence/absence were set where 3 out of the 5 (0.6 threshold) general circulation models (GCMs) had to show congruence for an occurrence to be marked giving a higher reliability of occurrence being present (Jarnevich *et al*, 2015). No occurrence was awarded if a data point only had 2 or less models noting an occurrence (Figure 2.2). This is an extremely conservative prediction since each of the general circulation models were already set to a threshold of 0.5. This strategy is

used to increase reliability of noting occurrences, since in practice, project funding is usually limited, and higher reliability would be needed. The 2018 National Land-cover map was obtained from the Environment, Forestry and Fisheries Department and had a resolution of $20m^2$, which was upscaled to match the $1km^2$ SDM resolution (Environment, Forestry and Fisheries Department, n.d.). The National land-cover map was overlaid with candidate species' SDMs in QGIS (version 3.10.14 with GRASS 7.8.5) to investigate the feasibility of target recipient sites. For each species, the range overlap between all three-time periods (current, 2040 and 2070) was identified, where possible. Measuring tools such as "Measure Area", "Raster Calculator", and processing tools such as "GRASS: r.report" were used to investigate potential recipient sites, occurrences in protected areas and current land-use.
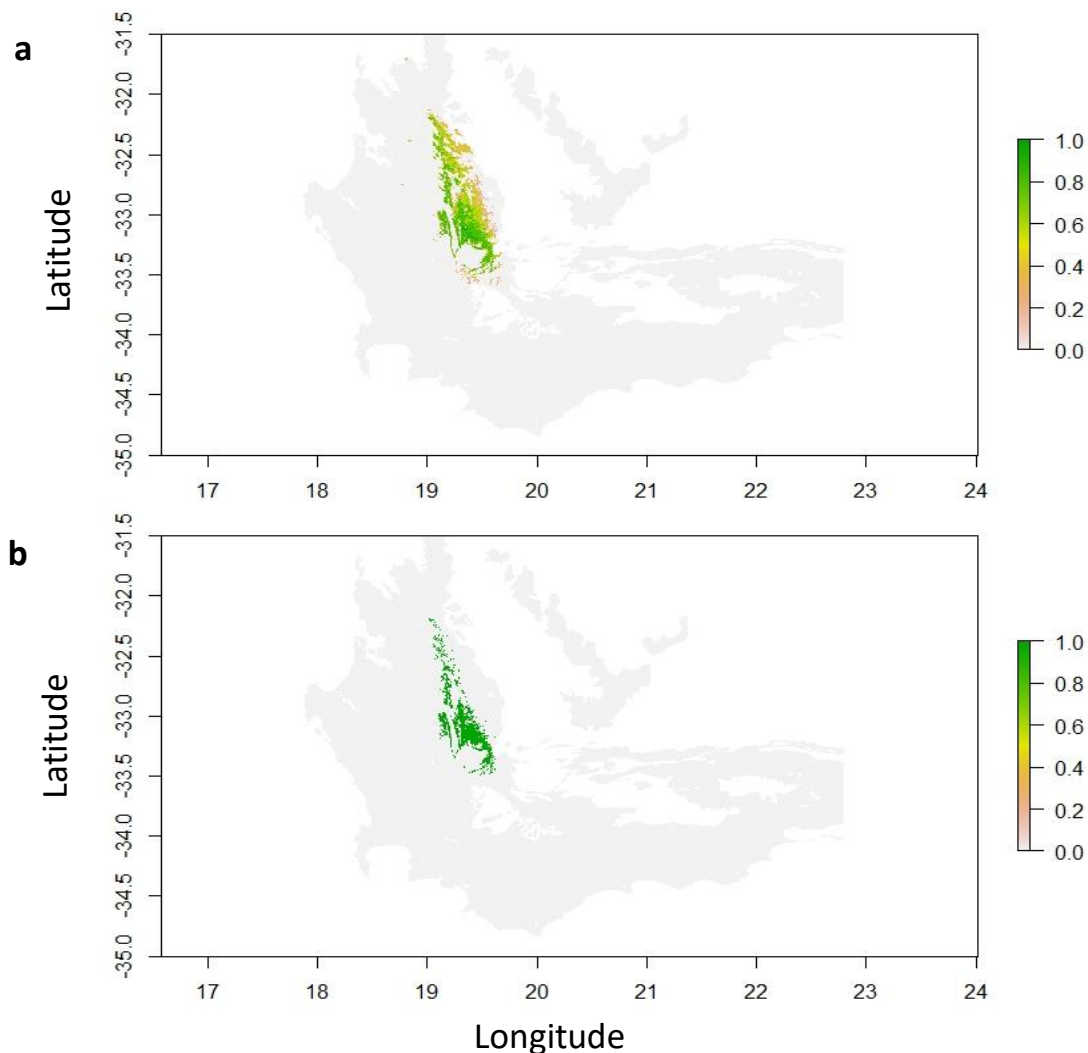
Figure 2.2. Example of how the model ensemble (average of five models) was combined to create a binary map. In (a), the ensemble of SDMs creates an averaged map of occurrence with green indicating all models project an occurrence for that data point, and with yellow, orange and white indicating decreasing agreement among models. In (b), only occurrences with 0.6 or more (at least 3 out of 5 models agree) are used.

2.4   Results

In this section, I present first the overall results of applying the Hällfors *et al*. (2017) framework for assessing the need and the potential for assisted colonisation by quantifying species range shifts over three time steps, namely current-2070, current-2040, and 2040-2070 (see Figure 2.2). As stated in the methods, subsetting the single current-2070 analysis into two shorter time steps of 30 years allows a more explicit understanding of the potential role for targeted interventions. Following this, results of the Hällfors *et al*. (2017) classification are presented using the SDM-based spatial metrics. This allows for the identification of "strong" and "probable" AC candidates, where life-history traits are then incorporated into their classification. The result is an adjusted classification (named AC suitability index) of Proteaceae candidates which incorporates their spatial projections with their ecology. Additionally, "possible" and "unsuitable" species were identified, for which assisted colonisation was not found to be an appropriate intervention. An assessment of their ability to persist was conducted on these species to differentiate between those that did not need AC because they had low vulnerability and are likely to persist, and species that did not need AC because they were highly vulnerable and *ex situ* conservation would be more appropriate.

2.4.1   AC Candidate Identification

2.4.1.1   Classifying Species Using the Hällfors *et al*., (2017) Range Index (I$_{AM}$)

Need for translocation versus Potential for translocation

When correlating range shift potential (relative future range gain) with range shift need (relative current range lost) using the current-2070 time-step (Figure 2.3*a*), a significant negative relationship ($F = 368.3$, df = 189 and $p < 0.001$) was found, with the linear regression explaining almost 66% of the variance ($R^2 = - 0.659$). However, when similar analyses were conducted for subsequent 30-year time periods (Figure 2.3*b* and 2.3*c*), the relationship weakened successively, with a weaker significant negative relationship found between need and potential in current-2040 ($F = 41.29$, df = 189 and $p < 0.001$, explaining only 18% of the variance) and for 2040-2070 ($F = 11.15$, df = 189 and $p < 0.01$, explaining only 5% of the variance). In other words, there was a weaker correlation coefficient between the need and potential of shorter time periods (correlation coefficient = - 0.423 and - 0.236, respectively), relative to the single time step (correlation coefficient = - 0.81). These indices suggest a greater number of species had both a larger need and larger potential in the current-2070 time period compared to the two shorter time periods.
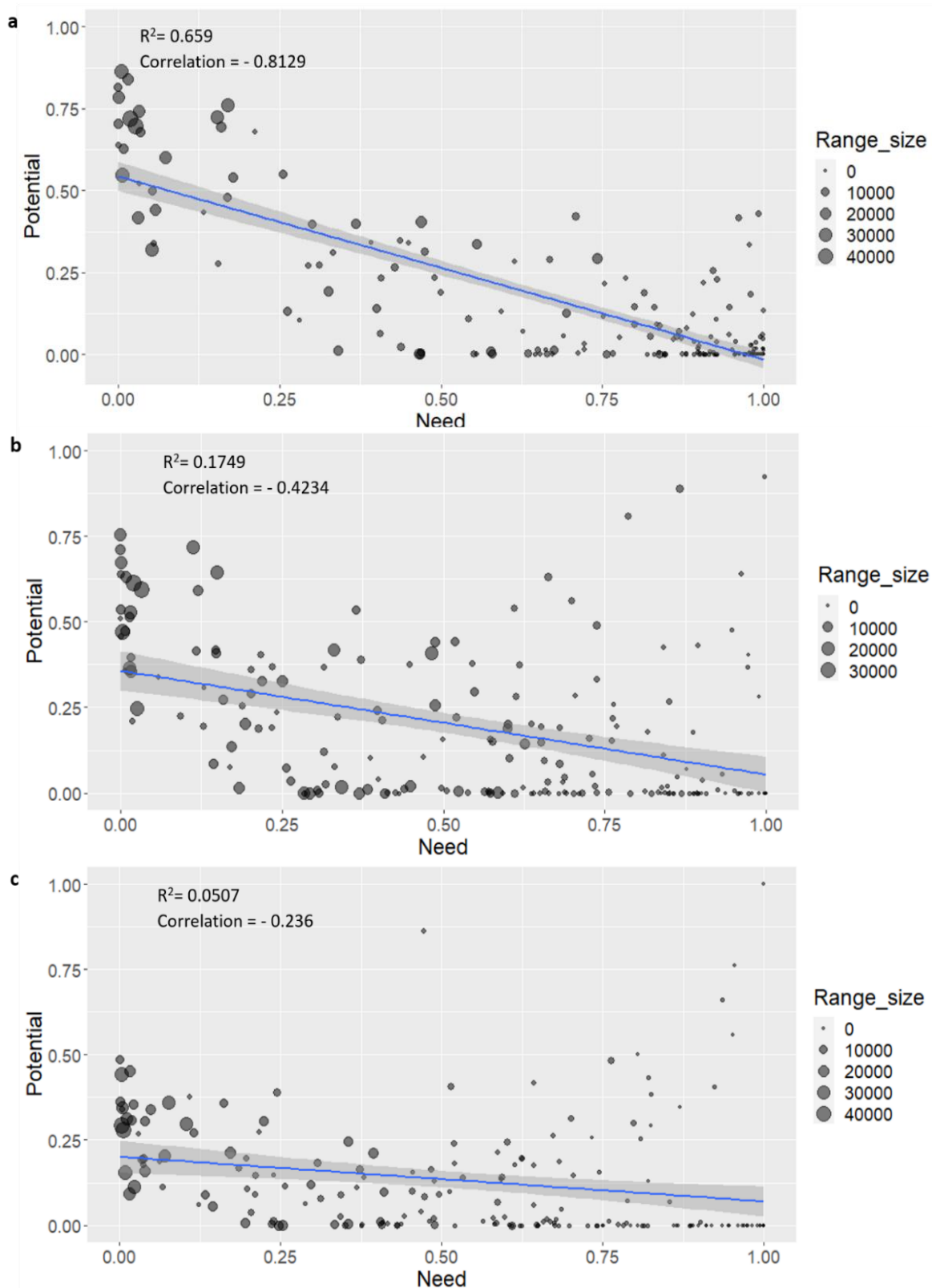
Figure 2.3 Correlation between the need and potential for assisted colonisation of 191 Proteaceae species in the Cape Floristic Region, South Africa for three time-steps: (a) *Current to 2070,* (b) *Current to 2040* and (c) *2040 to 2070*. Data point size indicates initial range size (in km^2) for each species. Corresponding R^2 and correlation coefficient are reported on the graphs. R^2 refers to the amount for variance explained, and the correlation coefficient indicates the strength of the relationship between need and potential.

Strong and Probable AC Candidates

The current-2070 time period (figure 2.4*a*) yielded the fewest strong and probable AC candidates. A 2-sided Chi-squared test was used to assess if using a longer timeframe resulted in less strong and probable AC candidates (6-decade versus two 3-decades). The test showed that the current-2070 time period had significantly less ($X^2 = 26.378$, df = 2, $p < 0.001$) probable and strong candidates than was expected to occur (the null hypothesis assumes that there are an equal number of candidates in each time period). Current-2040 (Figure 2.*4b*) had significantly more strong and probable AC candidates than expected, with 19 strong and 23 probable candidates and the 2040-2070 (Figure 2.4*c*) time period had no difference between expected and observed number of probable and possible candidates. Since the threshold calculation is based on 6-decades, the accumulated velocity of climate change between the time periods is expectedly higher, resulting in a potentially large differential between species' current and projected future ranges. Only two species were classified as strong candidates and four as probable candidates in the current-2070 time period (see Table 2.1). This time period also had the most species classified as unsuitable, with assisted colonisation found to be an unsuitable conservation strategy for 138 of the 191 species.

Table 2.1 The 191 Proteaceae species classified into strong, probable, possible and unsuitable categories for each projected time period, calculated using the Hällfors *et al*. (2017) equations.

Time period	Classification			
	Strong	**Probable**	**Possible**	**Unsuitable**
Current to 2070	2	4	47	138
Current to 2040	19	23	41	108
2040 to 2070	15	11	42	123

Several species were identified as strong or probable candidates in more than one time-step, therefore across all time-steps, 50 different species were identified as strong (*n* = 27) or probable (*n* = 23) AC candidates. These 50 strong and probable candidates were used in the trait analysis (see Appendix B for list of strong and probable AC candidates).
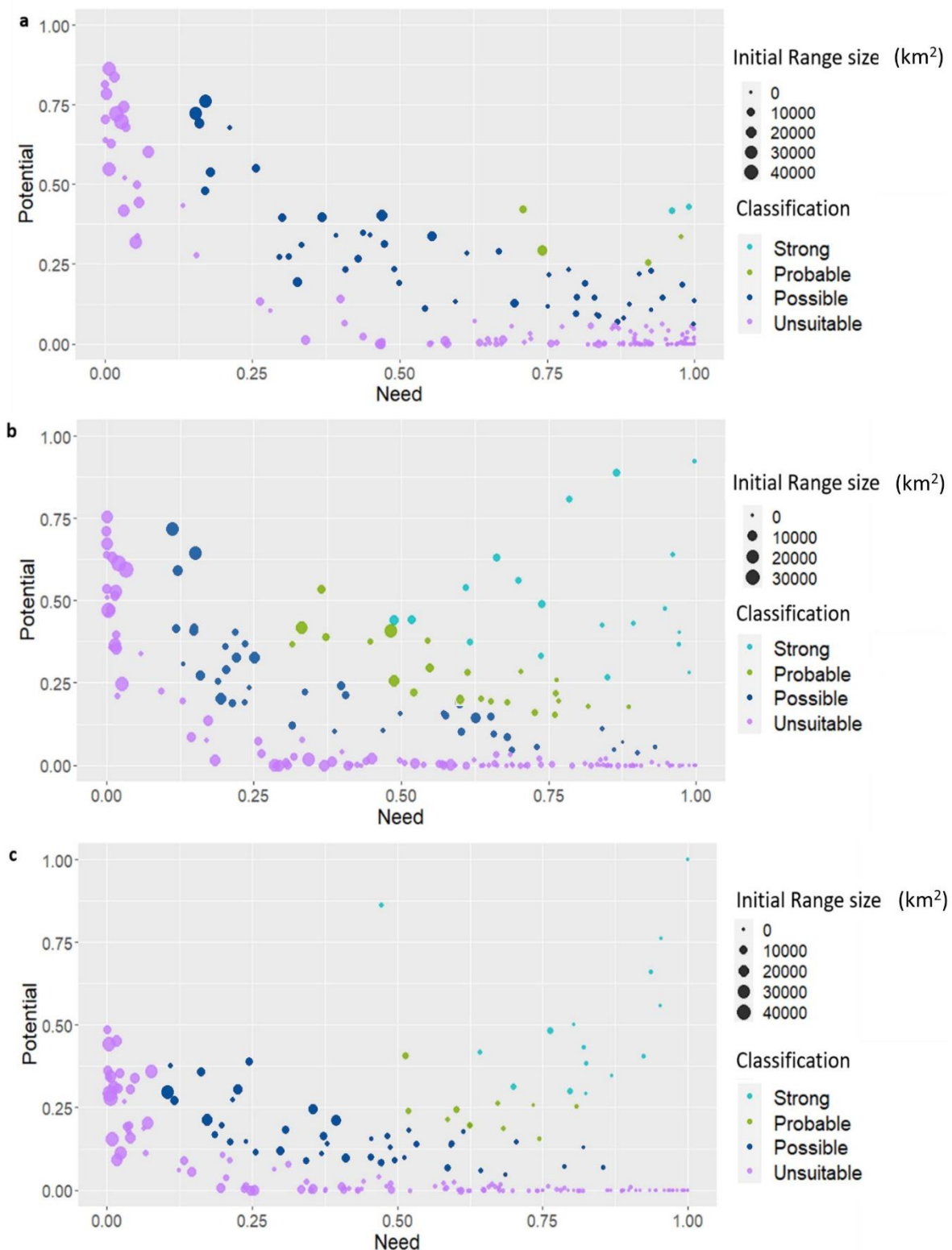
Figure 2.4. Graphs show the 191 species classified into four groups depending on their Hällfors *et al.* (2017) index score and threshold cut-offs for need and potential for AC. This was done for three time-steps:(a) *Current to 2070,* (b) *Current to 2040* and (c) *2040 to 2070*. Strong candidates are indicated in light blue, Probable in green, Possible in dark blue and Unsuitable candidates in purple. The size of the data points indicates the initial range size (in km²) of each species.

2.4.1.2 Persistence of Possible and Unsuitable Candidates

Possible and Unsuitable Candidates

Assisted colonisation was taken to be an unsuitable strategy for species classified as possible and unsuitable, however, this group comprised species with low need (low vulnerability) and species with high need (vulnerable). Therefore, to distinguish these groups and assess species' ability to persist, possible and unsuitable candidates were assessed using the augmented vulnerability thresholds to identify which species were 'likely persisters' (do not need intervention *in situ* intervention) or 'potential persisters' (species that may need monitoring), and which are 'non-persisters' (likely *ex situ* conservation; Figure 2.5). A 2-sided Chi-squared test revealed that there were significantly more non-persisters, and fewer likely persisters found in the current-2070 time step ($X^2 = 12.73$, df = 4, $p < 0.05$). The current-2040 and 2040-2070 time periods, both had fewer than expected non-persisters ($n = 78$ and 86, respectively, Table 2.2) and more likely persisters ($n = 60$ and 59, respectively).

Table 2.2 Summary of the vulnerability of Proteaceae species in the possible and unsuitable candidate groups in three time-steps: Current to 2040, current to 2070 and 2040 to 2070.

Time-step	Vulnerability		
	Non-Persisters	**Potential Persisters**	**Likely Persisters**
Current to 2070	126	14	45
Current to 2040	79	13	57
2040 to 2070	54	22	89

Across the three time periods, there were more 'non-persisters' than 'likely persisters' identified and would likely need an alternative targeted intervention to AC (Figure 2.6, also see Appendix C, for species list). Their vulnerability is due to their relatively high loss of range (need) and lack of future environmentally suitable range gain (potential). Between current and 2040, there were 79 species identified as 'non-persisters'. Out of these species, 34 were predicted to have a range less than 500km^2 by 2040, with five of those predicted to have a range less than 10km^2.

Figure 2.5 The vulnerability of Proteaceae species in the possible and unsuitable categories for three time-steps:(a) *Current to 2070,* (b) *Current to 2040* and (c) *2040 to 2070.* Data point size indicates the initial range size (in km^2) for each species. Species marked in blue are Likely persisters given their low need and species in black are Potential persisters due to their intermediate need and are recommended for monitoring. Lastly, the species in green are Non-persisters which have high need and low potential. These are recommended for *ex situ* conservation.

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Figure 2.6 A graphic comparison of the number of Proteaceae species classified into 'Likely persisters', 'Potential persisters' and 'Non-persisters' according to the time-step in which they occur (current-2070, current-2040 or 2040-2070). Current-2070 shows a significantly higher proportion of Non-persisters compared to current-2040 and 2040-2070 ($p < 0.05$).

2.4.1.3 Trait Index (I$_{Trait}$)

Only 3 of the 50 strong and probable AC candidates selected for the trait analysis possessed all 7 traits that were defined as favourable traits, namely, *L. modestum*, *L. teretifolium and P. repens* (trait index = 1, Figure 2.7). *Serruria leipoldtii* was the only species to have only one favourable trait (trait index = 0.14, Figure 2.7), and only in the current-2070 time-step. The trait index for *S. leipoldtii* in the current to 2040 time-step had two favourable traits since its range size in 2040 was above the 500km^2 threshold, assumed to be demonstrative of an adequate range size. Across all species and time periods, the average and median number of favourable traits for all species was four ($\overline{X} = {}^4/_7$ or trait index = 0.57). Age (in years) to 50% flowering was found to be the most common favourable trait, with 96% of strong and probable candidates having a maturity time less than five years (Figure 2.8). The rarest favourable trait was dispersal mechanism with only 22% of strong and probable candidates having a long-distance dispersal mechanism (i.e., wind).
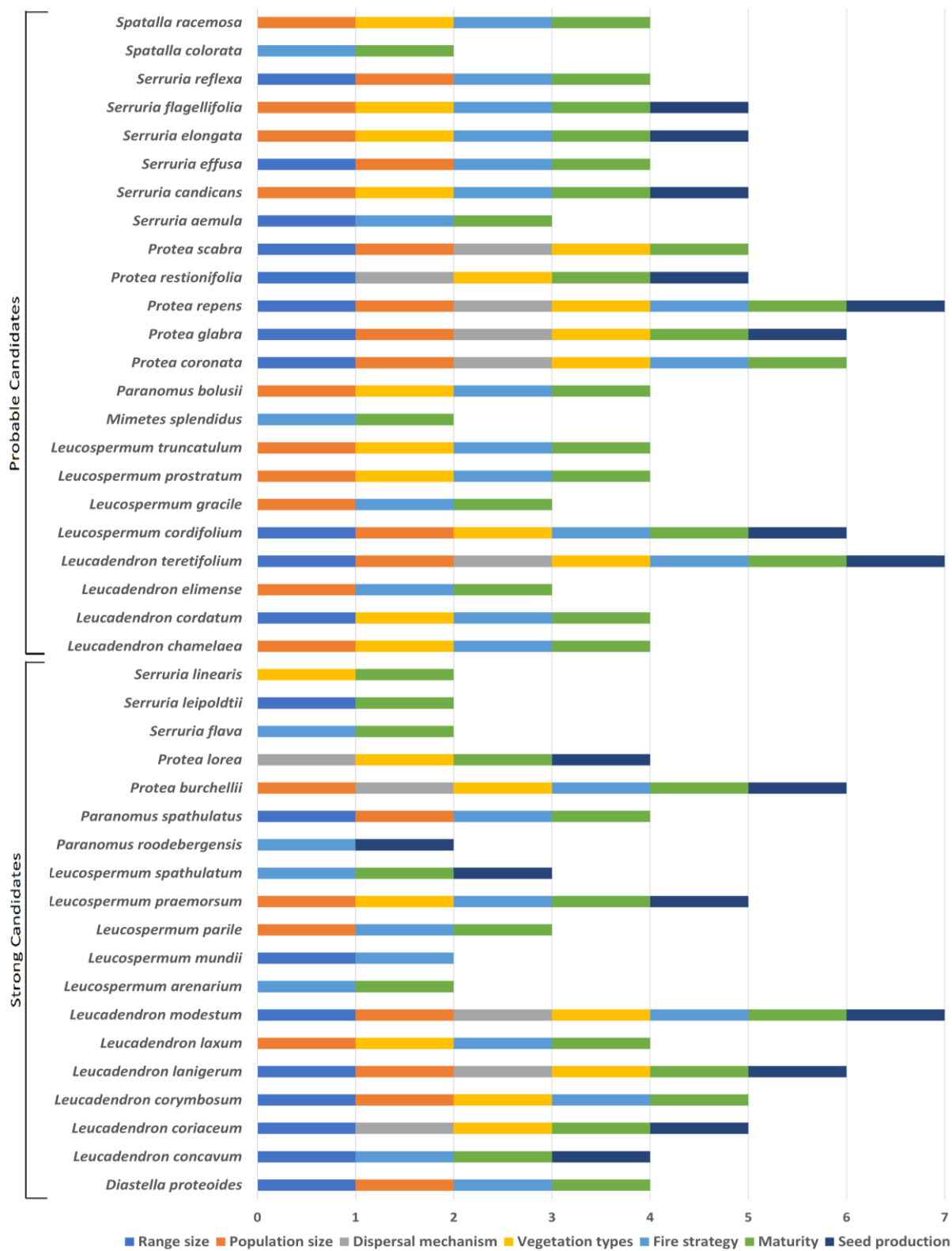
Figure 2.7 Stacked bar chart showing how many of the seven favourable traits (0-7) strong and probable candidates have. The colour of the bars represents different traits and if a species had the corresponding favourable trait, the trait was noted as present and the respective colour bar is shown.
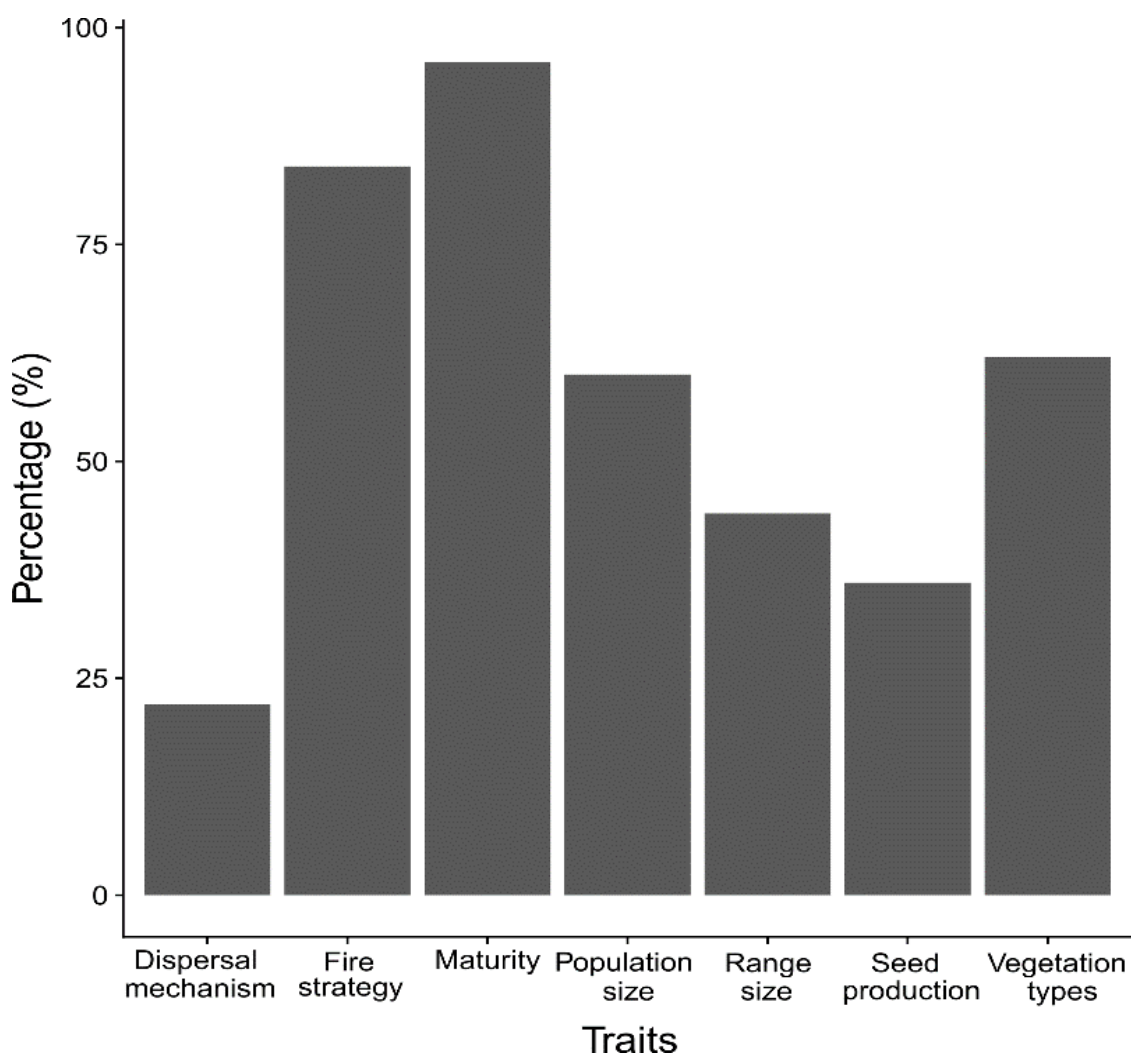
Figure 2.8 Bar chart showing the frequency (%) of each of the seven life-history traits in strong and probable candidates. The most common trait found was a favourable age to maturity (four or less years to 50% flowering), with 96% of candidates possessing this trait. The rarest favourable trait was long distance dispersal, with only 22% of candidates possessing it.

2.4.1.4   Overall AC-Suitability Index (I$_{AC}$)

The addition of the trait index to the Hällfors *et al*. (2017) range index changed the classification of several species, resulting in some species being uplisted and some species being downlisted in some time steps. In the current-2040 time-step, 12 species were uplisted from probable candidates to strong candidates due to their high trait index (Figure 2.9*b*). No species were downlisted in this time-step. In the 2040-2070 time-step, two species previously classified as probable candidates were uplisted to strong candidates (Figure 2.9*c*). However, two probable species were downlisted to possible candidates due to their unfavourable traits

and resultant low trait index. In the current to 2070 time-step, one probable candidate was uplisted to a strong candidate and one probable candidate was downlisted to a possible candidate (Figure 2.9*a*).
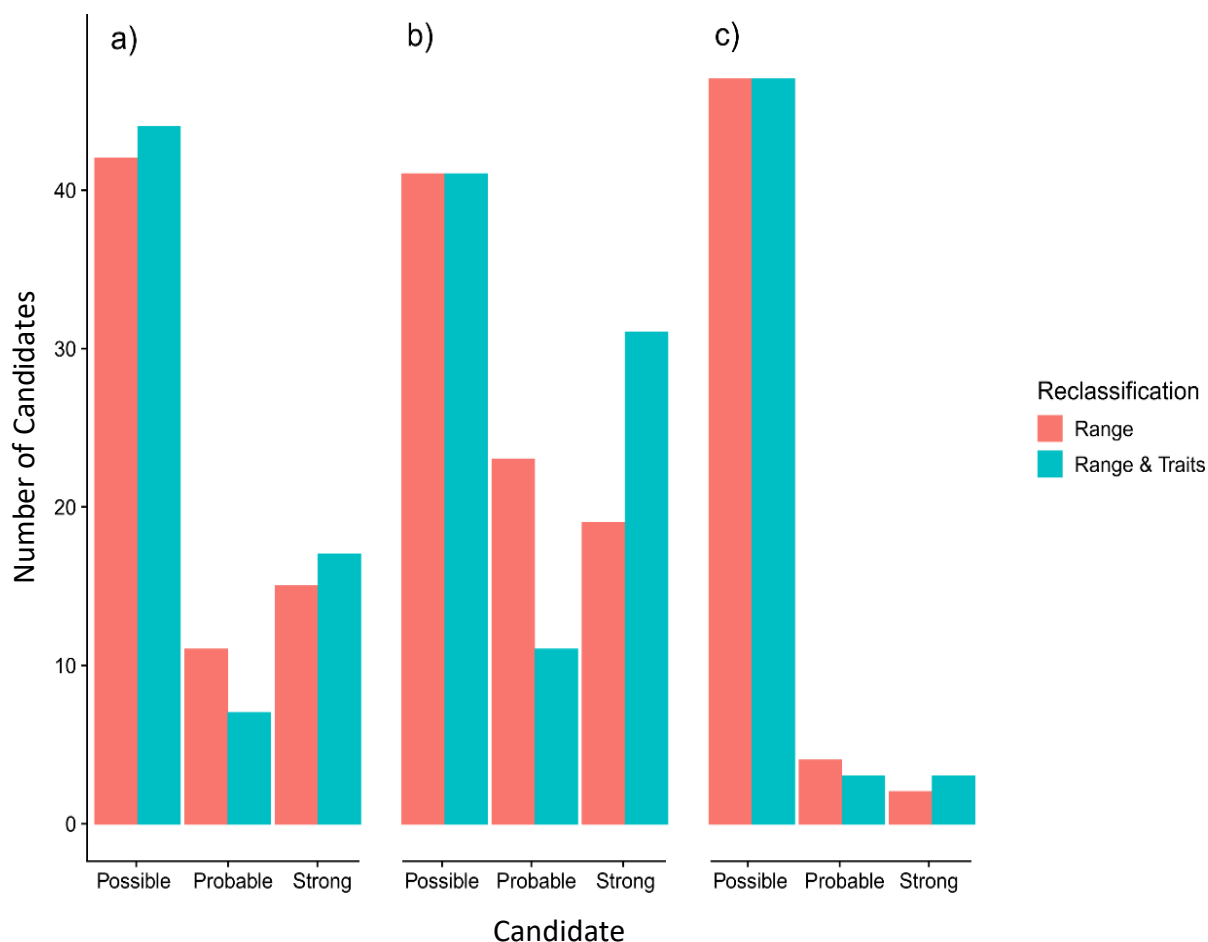
Figure 2.9 Graphs showing how many strong and probable candidates were uplisted or downlisted after their trait index was incorporated into their existing range index. This was done for three time-steps (a) *Current to 2070,* (b) *Current to 2040* and (c) *2040 to 2070.*

The remaining strong candidates classified using the AC-Suitability index (I_{AC}) in the current-2040 time-step, were compared to their classifications and vulnerability in the 2040-2070 time-step, which produced three outcomes (Table 2.3):

1. 14 species that were strong candidates in current to 2040 and remained strong candidates in 2040 to 2070. These species were classified as 'Sustained intervention candidates.

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2. 7 species that were strong candidates in current to 2040 and by 2040 to 2070 these species became 'Likely persisters' and would likely not require AC past 2040. These species were classified as 'Short-term intervention candidates.

3. 10 species that were strong candidates in current-2040, but suffered significant range loss post 2040, becoming Non-persisters in the 2040-2070 time-step. These species were classified as 'Mitigation dependent candidates' since successful mitigation efforts could result in these species graduating to Sustained or Short-term intervention candidates under aggressive global mitigation scenarios.

Table 2.3 The 31 Final Proteaceae AC candidate species subset into three groups: Sustained intervention, Short-term intervention and Mitigation dependent. Sustained intervention species were strong candidates in current-2040 and 2040-2070, which means intervention will likely need to be sustained over both time periods. Short-term intervention candidates were strong candidates in current-2040 but become 'likely persisters' in 2040-2070, therefore intervention is likely only needed in the first time period. Mitigation dependent candidates were strong candidates in current-2040 but become 'non-persisters' in 2040-2070, putting them at high risk. However, if aggressive mitigation action is taken, these species could graduate to Sustained or Short-term intervention species. Species with '*' are species that have a range size of less than 200km by 2040 or 2070.

Sustained intervention candidates	Short-term intervention candidates	Mitigation dependent candidates
Diastella proteoides	*Leucospermum prostratum*	*Leucadendron laxum**
Leucadendron concavum	*Paranomus bolusii*	*Leucospermum spathulatum**
Leucadendron coriaceum	*Protea coronata*	*Paranomus spathulatus*
Leucadendron corymbosum	*Protea repens*	*Serruria leipoldtii*
Leucadendron lanigerum	*Protea restionifolia*	*Leucospermum cordifolium*
Leucadendron modestum	*Serruria flagellifolia*	*Leucospermum praemorsum**
Leucadendron teretifolium	*Serruria reflexa*	*Leucospermum truncatulum*
Leucospermum arenarium		*Serruria candicans*
Protea burchellii		*Serruria effusa*
Protea glabra		*Leucospermum parile**
Protea lorea		
Protea scabra		
Serruria elongata		
Serruria linearis		

*Range <200km^2

2.4.2 Range shift characterisation based on SDMs and land-use maps

2.4.2.1 Sustained Intervention Candidates

There were 14 species identified in this category. According to the IUCN red list, two are 'Critically Endangered', six are 'Endangered', three Near Threatened', two 'Vulnerable' and one is of 'Least Concern' (Driver *et al.*, 2009). Species in this category followed a general trend of range contraction with higher altitude regions projected to become environmentally suitable over time (need $\bar{X} = 0.697$, potential $\bar{X} = 0.29$ and trait index $\bar{X} = 0.673$). This kind of shift means that most of the candidates had future range in Protected Areas (PA) since most mountainous regions in the Cape are protected areas *de facto*. *L. coriaceum* and *L. modestum* were the only species that had range overlap between the three time-steps and had no current or projected range (in any time-period) occurring in a protected area. They are low-lying species and since *L. coriaceum* occurs predominantly in renosterveld and *L. modestum* is prevalent in the highly transformed Elim Ferricrete Fynbos, these species occur in habitats that are predominantly unprotected.

Where possible, potential recipient sites for candidates were chosen in PAs, where species had projected environmental suitability overlap in all time periods. There were five species (*L. corymbosum, L. lanigerum, L. teretifolium, P. glabra* and *S. elongata*) with areas that were suitable from current-2070 and occurred in a PA. The size of suitability overlap varied from 52km^2 to 2071km^2, with the overlapping areas usually somewhat fragmented.

There were six species that had no predicted suitability overlap from current to 2070. However, there was a variation in the degree of separation. *L. burchelli* was found to have no direct overlap of suitability from current to 2070, however, the areas of projected range suitability for each time period were adjacent, with an inter-centroid distance of 14km between current range to 2070 predicted range. The range overlap of *L. lanigerum* was found to be located largely in areas transformed by intensive agriculture. While a potential site was located 5km between the current and projected 2070 range for this species, a mountain ridge separated the two ranges. *P. arenarium*, listed as critically endangered, was found to suffer a complete loss of current suitability but was projected to have environmentally suitable range 140km (inter-centroid distance) away from its current known suitable range.

There were six species with local (short) dispersal mechanisms and eight with regional (long) dispersal mechanisms. *P. lorea* was excluded from this calculation since it is an outlier and explained further on. There was a significant difference found between species' dispersal mechanism and the number of vegetation types they occurred in ($p < 0.001$; Figure 2.10). Furthermore, a linear regression (correlation coefficient = - 0.596) found that species which occurred in more vegetation types were found to have significantly shorter inter-centroid distances (distance between current range centroid and 2070 centroid), whereas species occurring in fewer vegetation types had larger inter-centroid distances ($F = 4.853$, df = 13, $p < 0.05$; Figure 2.11) When comparing the dispersal mechanism of species with no suitable range overlap between the three time periods, 4 out of those 5 species had local (short) dispersal. The only long-distance dispersal species that had no overlap between the three time periods was *P. burchelli* and as previously mentioned, its range suitability over time appeared to shift successively, needing to migrate only 14km by 2070, while the mean inter-centroid distance local dispersers had to migrate, was 89km to reach 2070 projected suitability.

Figure 2.10 Boxplot showing the difference between local and regional dispersal of Sustained candidates and the amount of vegetation types in which they occur in. Regional dispersal are species with long-distance dispersal and local dispersal are species with short dispersal distances. Sustained intervention candidates with long-distance dispersal were found to occur in significantly more vegetation types than short-distance dispersers. Significance is reported on the graph ($p < 0.001$).

Figure 2.11 Scatterplot with regression lines showing the relationship between Sustained intervention species' inter-centroid distance (distance between range centroids in current and 2070) and the number of vegetation types that species occurs in. Regional dispersal (blue) are species with long distance dispersal and local dispersal (red) are species with short dispersal distances. Species which occurred in fewer vegetation types had higher inter-centroid distances and species which occurred in more vegetation types showed smaller inter-centroid distances.

L. concavum is currently known to have two populations with an area of occupancy ~54km^2 and is listed as endangered by IUCN red list (Driver *et al.*, 2009). It is predicted to disappear from its current range and gain ~72km south of its current range. Although *L. concavum* is limited to one vegetation type (Cedarberg sandstone fynbos), the recipient site also has Cedarberg sandstone as a vegetation type. However, a 7.86km^2 patch 10km from the edge of its current suitability was predicted to be suitable from 2040 to 2070. This is much closer, but the area is not in a protected area and is relatively small.

P. glabra is currently listed as of 'Least Concern' by IUCN and is known to be widespread with minimal threats. However, when this species was mapped, there was almost a total reduction in range suitability by 2070. This could be due to the strict model threshold set for occurrence, but even so, it indicates that there is a lack of congruence between models for *P. glabra*'s projected range. *P. lorea* is an outlier candidate with its projected suitability in 2070 occurring 26km away from its current centroid.

All species mentioned above have attributes that make them favourable AC candidates, however, there are other attributes which make the success of a candidate complex. Having future range overlap with PAs is one such attribute. The five species mentioned with suitability in PAs from current to 2070 are considered likely to succeed. The two species that do not occur in PAs are considered difficult cases since their potential recipient sites appear to occur on private land, therefore stewardship interventions, for example, may be needed to preserve these species. The five local dispersal species with no suitability overlap and higher inter-centroid distances are considered more complex cases which need to undergo hybridisation potential analyses.

2.4.2.2 Short-term Intervention Candidates

Species in this group were not found to have a high extinction risk, with six of the seven species retaining substantial range overlap between current and 2070 (need $\bar{X} = 0.439$, potential $\bar{X} = 0.149$ and trait index $\bar{X} = 0.735$). However, four of these six species were projected to lose large parts of their low-lying ranges between current and 2040, potentially resulting in a severe loss of genetic diversity of these species (*L. prostratum, P. bolusii, P. coronata* and *S. reflexa*). In 2040-2070, there was a larger retention of range overlap, with species ranges during this time period remaining relatively stable. Interestingly, *P. restionifolia* (which has most of its range on low mountain slopes), was the only species predicted to gain range in low-lying areas. The only species that shows large range contraction and minimal overlap is *S. flagellifolia,* which showed a potential recipient site 13km from its current suitable range for the current-2040 time period. Overall, this group was found to represent species that were not in ultimately at risk of extinction, but for whom Short-term AC interventions could possibly contribute to limiting loss of genetic diversity (extirpation).

2.4.2.3 Mitigation Dependent Candidates

Species in this group were promising strong AC candidates in current-2040, however these species' ranges are projected to decrease substantially between 2040 and 2070 and have minimal range gain projected in that time (need $\bar{X} = 0.625$, potential $\bar{X} = 0.0996$ and trait index $\bar{X} = 0.571$). Four species suffered either a complete current range loss or a range under 200km^2. *S. leipoldtii* showed the highest potential for AC in this group, however its large reduction in range by 2070 and unfavourable traits (only 2 out of the 7 favourable traits

present), makes it a candidate with substantial vulnerability. Overall, candidates in this subset are characterised by high extinction risk due to substantial reductions in range size in 2040 to 2070, however, if aggressive mitigation action is taken, these species would be able to become Sustained or Short-term intervention candidates.

Summary of candidate groups

Each of the strong candidate sub-categories described above can be differentiated to an extent sufficient for broad conservation planning purposes. The Sustained intervention sub-category comprises candidates that most closely fit the definition of AC candidates as they are commonly described. In other words, they are species that are projected to have large range loss (high need), with sufficient projected future range gain (high potential) in novel areas. However, even within this group, the degree of range shift required varied. Short-term intervention species showed no significant immediate extinction risk but did show substantial loss of regions (local extirpation). Therefore, these species are at risk of losing genetic diversity at the meta-population level, however, also show relatively stable ranges between 2040 and 2070, making intervention likely Short-term. Mitigation dependent species show high extinction risk in 2040 to 2070 time period, with four species showing complete or almost complete loss of range by 2070. This combined with unfavourable traits, such as limited dispersal and limited range gain (potential), make the persistence of this group in the wild is clearly dependent on successful climate change mitigation efforts in order to be considered viable candidates.

2.5   Discussion

This chapter addresses the initial steps required for conceiving, designing, and implementing a targeted conservation strategy for range restricted species at risk of climate change extirpation. It is widely accepted that some proportion of species are likely to become extirpated under future climate change scenarios unless there is sufficient climatically suitable range available for them in the future (Midgley *et al*. 2006), and their dispersal constraints can be overcome (IPCC, 2014). This chapter uses current and two future projections (2040 and 2070) to quantify the projected range shifts of 191 Proteaceae species (as a model species) to understand if AC could be applicable in a hyper-diverse region such as the Cape Floristic Region (CFR). This is done by first applying a framework developed by

Hällfors *et al*. (2017), that defines both the need and the potential for AC using SDM-based spatial metrics which quantify species' projected geographic range shifts and then was expanded further by incorporating key sensitivity and establishment traits that necessitate consideration in addition to using spatially based metrics as suggested and contextualised by Foden *et al*. (2013) and Pacifici *et al.* (2015; 2017). This chapter therefore sought to assess the proportion of Proteaceae species that would be suitable candidates for assisted colonisation. Additionally, through the process of identifying candidates, a number of species were identified as unsuitable for AC however, requiring more immediate alternative intervention.

The implementation of the Hällfors *et al.* (2017) allowed the 191 species to be divided into three main groups of AC candidates (Strong, Probable and Possible). In this study, AC was assumed to be an unsuitable intervention strategy for species in the possible and unsuitable. This was either due to their extremely high vulnerability (Non-persisters) or low vulnerability (Likely Persisters). Previous work by von Maltitz *et al*. (2006), also using Proteaceae as an exemplar species, identified four vulnerability categories. These were defined as "Persisters": Species that retained sufficient range under climate change; "Obligatory dispersers": Species losing most or all current range but were projected to gain new range and would be able to migrate into these areas without intervention if they were autonomous dispersers or have to be moved artificially to newly climatically suitable areas if they were unable to do so autonomously (i.e., facilitated dispersers). "Range expanders" were species that retained most of their current range but additionally was able to expand their range into newly suitable areas. Lastly, "No hopers" were species that suffered large loss of their current range and had limited or no projected future range. The application of the Hällfors *et al*. (2017), framework represents a refinement and advancement on the categorisations of von Maltitz *et al*. (2006), and this analysis reveals that the category "Range Expanders" is likely rare, and that a binary approach to autonomous and facilitated dispersers ignores several considerations that are addressed in this chapter.

Overall, 31 potential AC candidates were identified amongst the 191 Proteaceae analysed, which were further subset into three more distinguished groups: Sustained intervention, Short-term intervention, and Mitigation dependent candidates. While most AC candidates were found to have short-dispersal capabilities, some possessed long-dispersal capabilities. This finding challenges the "autonomous disperser" category suggested by von Maltitz *et al.* (2006) and deviates from the notion that only Proteaceae with limited dispersal would be

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identified as strong AC candidates. For several long-distance dispersal species, the rate and extent of climate change was still found to be sufficient to warrant AC interventions. The possession of long-distance dispersal capabilities was however, still found to be the rarest trait among probable and strong candidates, with only 22% having this favourable trait. Dispersal distance was positively associated with high seed production rate, the second rarest trait, which is expected since species with short seed dispersal usually produce fewer seeds (Leishman *et al*., 2000). Therefore, short distance dispersal species are additionally vulnerable in the context of implementing AC.

The Sustained intervention candidate group had six short-distance dispersers and eight long-distance dispersers. Short dispersers were found to occur in fewer vegetation types (indicating substrate and habitat type specialisation) and long-distance dispersers were found in more vegetation types (generalists in terms of substrate and habitat type). Midgley *et al*. (2006) found in their climate predictions that long distance dispersers suffered large range contractions whereas short dispersers showed much less significant range contraction. They suggested that this could be due to short dispersal species being constrained more to occupying core ranges whereas long dispersers occupy marginal sites that might become unsuitable as climate change progresses.

Paleo-ecological records show that the CFR has long acted as a refugium from environmental change (Linder, 2001; Linder, 2003). This has allowed for many fynbos clades to radiate and to the extent in which they have (Cowling & Lombard, 2002; Schnitzler *et al*., 2011). The relative climatic stability in the Cape is at least partly implicated in why there are many specialised species (Valente *et. al*., 2009; Mokhatla *et al*., 2015). In this study, a significant relationship was found between the habitat specificity of a species and the distance in the displacement of range centroids by 2070. Short dispersers showed significantly higher centroid displacement distances than long dispersers. While refugia allowed for short-dispersal species to remain stable over the millennia, anthropogenic climate change may exceed the ability of these refugia to buffer environmental change/extremes (Midgley & Bond, 2015), resulting in potential local to global extinction in these highly vulnerable species. This analysis identified a large fraction of species in this most vulnerable group.

One of the most significant barriers to implementing assisted colonisation is the risk of hybridisation, especially in the CFR context (Rebelo, 2005; MacQueen & Potts, 2018). Since many Proteaceae species are isolated by geographical barriers, they are found to hybridise

readily since they lack reproductive barriers (Croxford *et al*., 2001; Visser, 2005). It is assumed that the larger the distance over which AC is implemented, the bigger becomes this risk (Mueller & Hellmann, 2008). Therefore, species most at risk of hybridisation amongst the candidates identified are *S. linearis, L. arenarium, L. concavum* and *D. proteoides*. These species are projected on average to require range shifts of up to 89km by 2070. Their large centroid displacement distance and lack of current suitability overlap increases their risk of hybridisation, and other novel community-level interactions in the novel range areas. However, many AC candidates did not require such extensive range extension, and either had environmentally suitable overlap of all three time periods or novel range gained was adjacent to its current range. Though this study stresses the importance of assessing hybridisation risk, it was not able to meaningfully quantify the hybridisation risk of candidates, therefore before AC can fully be seen as feasible for a candidate, it is critical that a thorough genetic investigation with rigorous testing is conducted.

The Mitigation dependent group was an interesting new phenomenon to emerge in this study, and highlights that the persistence of several species in the wild likely relies on what climate mitigation action currently underway. The Mitigation dependent category had the lowest average of potential range gain and the lowest average trait index, exacerbating their level of vulnerability. All species in this category had short dispersal capabilities which aligns with the hypothesis that species that are most vulnerable have limited dispersal (Foden *et al*., 2013). They were found to have a high extinction risk with a few species projected to completely lose their range. However, if mitigation efforts can slow the rate of climate change, these species may persist beyond mid-century (Loarie *et al*., 2009). Warren *et al*. (2013), predicted that without mitigation, species are likely to lose more than 50% of their current climatic range, however, if emissions peak in 2030, this loss could be reduced by as much as 40%. Moreover, the relationship found between species' need and potential for AC implementation indicates that acting on shorter timescales would reduce the extinction risk of many species. The identification of 11 Mitigation dependent candidates highlights the importance of timeous action.

Protea lorea was an outlier candidate amongst those identified as 'Sustained intervention', with a 2070 range centroid 264km from its current range centroid. Inspection of this species revealed that there are fewer than 12 known locations of known occurrence, thus a lack of data may have led to this outcome. *Protea restionifolia*, a Short-term Intervention species, was the only species to show range expansion into low-lying areas which are known to

support a non-Fynbos vegetation (Renosterveld) type, and which is also highly transformed by agricultural land-use. This is an interesting projection since according to the SANBI redlist, *P. restionifolia*'s preferred vegetation type (either renosterveld or fynbos) is unknown (Rebelo *et al*., 2011). This projection emphasises that renosterveld may be more suitable for some Proteaceae as climate change progresses, it they are able to tolerate the heavier shale-derived soils.

Protea glabra was listed by the IUCN as 'Least Concern' (Rebelo *et al*., 2011), but comparison of SDMs and land-use maps indicates a large reduction of range by 2070 for this species. This reduction may be due to an overly stringent suitability threshold in the ensemble SDM used for land-use exploration since range shift calculations showed *P. glabra* retained enough overlap between current and projected 2070 range size ($>200km^2$). Instances where an apparent lack of congruence between models for species would require further investigation.

Species distribution models (SDMs) are widely used in conservation planning and management and are particularly useful in the context of climate change, however, it is important to recognise the various caveats of using this method. SDMs rely on many assumptions, notably, the assumption that adequate sampling has taken place across important environmental gradients and that the included environmental variables capture the distributional constraints of a given species. There are also various abiotic factors that SDMs do not account for which are important considerations when looking at the candidacy of a species. These include genetic diversity, dispersal ability, competing species, adaptations, and evolution (Jarnevich *et al*., 2015). The 191 Proteaceae SDMs obtained from SPARC used various techniques to reduce inaccuracies of the models as much as possible. This included using an ensemble of five models (Stohlgren *et al.*, 2010), highly correlated environmental variables were eliminated (Braunisch *et al*., 2013) and a strict threshold of 0.5 was used to decrease potential of false positives. Species traits were also incorporated to included potential influential factors that were not accounted for in the modelling (Foden *et al*., 2013). However, when species distributions are forecast over time and space, assumptions are made, and, to some extent, uncertainty is introduced. This is important to keep in mind as the highlighted AC candidates found in this chapter would need further on-the-ground assessing to further validate their candidacy.

The Hällfors *et al*. (2017) equations were developed to assess risks to a species, while this study used it to assess multiple species simultaneously. This has resulted in direct comparison of multiple species with large differences in their initial range sizes. The range shift index calculations are based on relative loss and gain to allow for general comparison, potentially concealing important information about differences in species' absolute vulnerability versus their relative vulnerability. To compensate for this, initial range size was used as a trait variable, but without heavier weighting, this may be an aspect worth revisiting. Pacifici *et al*. (2015), note that one of the drawbacks of trait-based vulnerability analyses is that species' specific trait thresholds are usually unknown and necessitates arbitrary, relative selections of thresholds (e.g., higher or lower extinction risk). This is true in this case, where in the absence of known thresholds, logical inferences were used which may not be definitive, however provided important insight. It is also noted that an extensive database of Proteaceae traits was available for this study, and this is often not the case more many families and genera. Nonetheless, the number of traits included can be adjusted to what is available and the binary nature of the trait analysis allows for coarser thresholds to be used.

2.6 Conclusion

Overall, an assessment protocol has been developed to assess the feasibility of AC for Proteaceae by combining species modelling, life-history traits, and ground truthing using land-use maps. This process was able to identify candidates for assisted colonisation as well as identify species that are at risk and may require alternative intervention strategies. Only 45-57 of the 191 species (depending on the time period) analysed were classified as being at low risk of adverse climate change impacts. This study found that setting implementation goals for 2040 and 2070 would be an adequate practical timeline for implementing AC strategies, and that timely climate change mitigation action is critical to reduce extinction risk of Proteaceae species.

3 Chapter 3: Growth and Reproductive Performance of *P. compacta* in Marginal and Core Populations

3.1 Abstract

Understanding population dynamics is important for the practical application of Assisted Colonisation (AC). One of the main implicit assumptions of successful AC is that viable populations can be established in sites of marginal suitability, likely to be found near the edges of species' distributions where conditions are projected to become more suitable with progressive climate change. *Protea compacta,* a species historically planted and harvested for the cut flower industry, provided a valuable opportunity to test this assumption, since it has been planted and artificially established in at least two sites currently determined by species distribution models (SDMs) to be marginally suitable in comparison to the apparent core of its geographic range. Measurements of vegetative growth, phenotypic characteristics, disease and reproductive performance in two core and two marginal sites unexpectedly showed higher growth rates and flowerhead production at an individual-level in marginal sites, but also higher rates of Witches' Broom occurrence and severity of infection. This pattern appears to result from higher population densities in core sites (likely due to high rates of seedling survival post-fire), leading to significantly lower individual branching, growth and flowerhead production. This explanation is supported by the findings of a finer scale study at one of the marginal sites, where high population densities were found locally in wetter microhabitats. These results suggest that the relaxation of intraspecific competition in establishing populations in marginal bioclimatic conditions may compensate for lower survivorship at lower population densities, supporting population establishment and in this case, potentially favouring the practical implementation of AC. This unexpected result, while tentative due to limited sample sizes and site replication, implies that a more coherent understanding of species range dynamics and their relation to SDM projections is needed to increase the likelihood of successful implementation of assisted colonisation that is informed by SDM projections.

3.2 Introduction

Anthropogenic climate change is very likely to increase extinction risk for wild species that are already significantly under multiple threats, with endemic and near-endemic species in

biodiversity hotspots being particularly at risk (IPBES, 2019; Enquist *et al*., 2019). Significant dispersal limitations – which is widely identified as a limitation to autonomous adaptation (IPCC, 2014), is a critical trait amongst several traits that are thought to determine species' vulnerability (Pacifici *et al*., 2015), led to proposals for active conservation interventions such as assisted colonisation (Hough-Goldburg *et al*., 2008). However, in plants, this method remains largely untested partly due to significant concerns around possible negative ecological impacts (see Richardson *et al*., 2009). Despite this, many authors continue to suggest the use of AC, without much attention paid to the pragmatic implementation of the technique, and in the absence of attempts to gauge the effort required, and thus the cost, as components of feasibility.

A fundamental assumption of AC is that the establishment of populations in novel sites will facilitate an enhanced rate of range shift. For AC implementation, translocating species into sites that are identified as currently marginal but are projected to become more suitable in the future seems the most pragmatic approach, but the ecological feasibility of such an approach remains unclear.

Species range shifts have been well documented during the Pleistocene and Holocene; however, this work has focused on Northern Hemisphere ecosystems that have been exposed to rapid deglaciation and thus the apparent selection for long distance dispersal traits (Carlson *et al*., 2008). The rate of anthropogenic climate change is now rapidly changing the climate in ways that will shift the current bioclimatic thresholds that govern the range limits of species (Monzón *et al*., 2011) in Southern Hemisphere biodiversity hotspots like the Cape Floristic Region (CFR). Biodiversity hotspots have accumulated large numbers of endemic and near-endemic species with limited range sizes and short distance dispersal traits due to extended periods of climatic stability (Linder, 2003). These biota appear not to have shifted range to a large extent (as reflected by muted community compositional change) over even the large warming trend that accompanies the termination of the Pleistocene, and Holocene climate trends (Chase *et al*., 2011). This raises questions about how amenable such species are to enhanced range shift strategies needed for the implementation of AC.

The current lack of coherent understanding of range dynamics for dispersal-limited species poses a significant barrier to the practical implementation of strategies such as AC with confidence (Gaston, 2009; Kerr, 2020). Niche theory can provide a meaningful framework for exploring aspects of implementing AC.

Niche theory defines the environmental space in which a species occurs as the realised niche and the fundamental niche as the environmental space that is potentially environmentally suitable (Vandemeer, 1972; Chase, 2011). Species Distribution Models (SDMs) may show biases in the projected fundamental niche of species since commonly the baseline data used in models are observed occurrences (Wolmarans *et al.,* 2010). This becomes particularly problematic when projecting species that have limited dispersal capabilities (like many in the Cape), since they likely do not fill their fundamental niche which may lead to inaccuracies in predictive models.

Currently, species distribution models (SDMs) are used to project species range shifts into the future to gauge the vulnerability of at-risk species, however, SDMs rely on certain parameters and therefore do have their limitations when directly applied to real-world scenarios. Thuiller et al. (2008) critiqued SDMs by explaining that models may fail to accurately depict the migration of plants, especially at the leading and trailing edges of species distributions. Since AC heavily involves these transitional areas, developing an in-depth understanding of range dynamics becomes another critical element to the practical implementation of AC. Therefore, it is important to understand how SDM outputs can translate into real-life practical application.

SDMs model the realised niche of species since observed occurrences are used as the baseline for projections. The assumption that observed occurrences reflect the realised niche may be violated when projecting species that have limited dispersal capabilities, since they likely do not fill the geographic range represented by their realised niche (Schurr *et al.*, 2008), and this would compromise to some extent the credibility of the models. However, currently, SDMs are the most widely used, cost effective modelling technique available. A pragmatic approach that presents itself is the use of SDM-derived habitat suitability scores to assess the potential for AC implementation to guide the translocation of populations into sites that are identified as currently marginal but are projected to become more suitable under climate change; however, the feasibility of implementing this approach has not been well tested. Therefore, it is important that understanding is gained into how SDM projections can be applied in the real world.

As a result, my third Chapter is an exploratory investigation into how habitat suitability would influence the establishment, vegetative growth, physical characteristics, and reproduction of a Protea species in sites projected by SDMs to have high environmental

suitability (so-called "core" sites) and sites projected to have relatively low environmental suitability (so-called marginal sites). Understanding the range dynamics of a species is expected to help inform the role of SDM outputs in the practical implementation of assisted colonisation.

Protea compacta has been planted extensively in the Western Cape due to its desirability in the cut flower industry (Turpie, 2003), and populations were established artificially some decades ago in at least two sites that are defined as marginal, and in which they did not occur naturally. These populations have not been managed for several fire cycles and can thus be considered self-sustaining. This provides an opportunity to examine range dynamics of a species across its range – focusing on naturally established populations in its core and artificially established marginal areas. For this, I selected two sites in the core of *P. compacta*'s range (Kogelberg Nature Reserve and Fernkloof Nature Reserve), and two marginal sites which are confirmed to support artificially planted populations (Grootbos Nature Reserve and Agulhas National Park). Measurement of the growth and reproduction of *P. compacta* in these settings will test if populations in marginal sites have significantly adversely lower performance in relation to core site populations, and thus call into question the practical implementation of AC.

SDMs provide projections of climatic changes at a broad scale, but individual plants are known to experience climate at much finer scales since, microhabitats are able to buffer or amplify the effects of climate change (Woods *et al*., 2015; Pincebourde *et al*., 2016). High climatic heterogeneity found within a landscape, where differences in slopes, vegetative cover and surface substrates all contribute to habitat suitability (Sears *et al*., 2011; Ashcroft *et al*., 2012) might provide an additional axis for refining an AC implementation and the theoretical potential in using these microclimatic differences to buffer broader climate unsuitability for marginal sites. For this reason, the performance of *P. compacta* individuals were explored in different microhabitats at one of the marginal sites.

I aimed to test the assumptions that would underpin an AC approach that relies on habitat suitability as a predictive tool for identifying suitable translocation site, by comparing plant performance in so-called "core" and "marginal" sites. I further explored at an even finer spatial scale, in a single marginal site, the potential buffering role of microclimatic differences that could be used to further assist in the establishment of a population in such a site.

Key questions, Aims and Hypotheses

Aims: (i) To compare the performance of *P. compacta* in sites of high climatic suitability (i.e., well within their contemporary range) with those planted in marginally unsuitable areas (i.e., at the margin of their contemporary range) and (ii) to assess whether the performance differences in a range of microhabitats in a marginal site offers potential to overcome lower overall site suitability.

Central questions:

- How much does the growth and reproductive performance of *P. compacta* individuals differ between populations growing in core and marginal bioclimatic conditions?
- Are there differences in growth, reproduction and disease susceptibility found in *P. compacta* individuals in differing microhabitats in marginal sites?

Hypotheses:

- Individuals in *P. compacta* populations growing under optimal conditions will have higher growth and flowerhead production, and lower disease susceptibility.
- The growth and flowerhead production of individuals in a range of microhabitats in a marginal site will reflect the bioclimatic suitability at these finer scales.

3.3   Methodology

3.2.1 Study species

Protea compacta, commonly known as the Bot River Sugarbush, is listed on the IUCN Red List as 'Near Threatened' (IUCN, 2020). *P. compacta* is found between 20m – 700m above sea-level with most occurring at 180 m (median). They are mostly found in sandstone (81%), in deep sandy soils, with a gentle incline (Protea Atlas, 2008). They are hermaphroditic, and birds (80%), and occasionally bees and beetles are their main pollinators (Protea Atlas, 2008). *P. compacta* produces approximately 700 seeds per annum (Foden & Rebelo, *unpublished*). Their seeds are serotinous and use wind plume dispersal, re-seeding after fires. Therefore, their generation time is ~20 years, fire dependent (Protea Atlas). *P. compacta* reaches 50% flowering by 2 – 3 years (time taken for 50% of the population to reach flowering) and reaches 100% flowering (time taken for 100% of the population to reach flowering) at 7 years (Foden & Rebelo, *unpublished*). Flowering has been recorded to take place from April/May

to October, with peak flowering in August (94% flowering). Historically, *P. compacta*'s flowering period was recorded from April to September, with peak flowering in May/June (Protea Atlas, 2008).

P. compacta's growth season is between November and March, with peak growth occurring in December (93%). Most individuals on average are between 1m – 2m in height are known to occur in stands. Alien invasives are predominantly *Fabaceae* (34%; mostly *Acacia*'s), found sparsely in *P. compacta* populations. This species is also known to struggle with Witches broom disease (caused by a Phytoplasma). The species' current distribution spans from Kleinmond to Struisbaai (Figure 3.1).
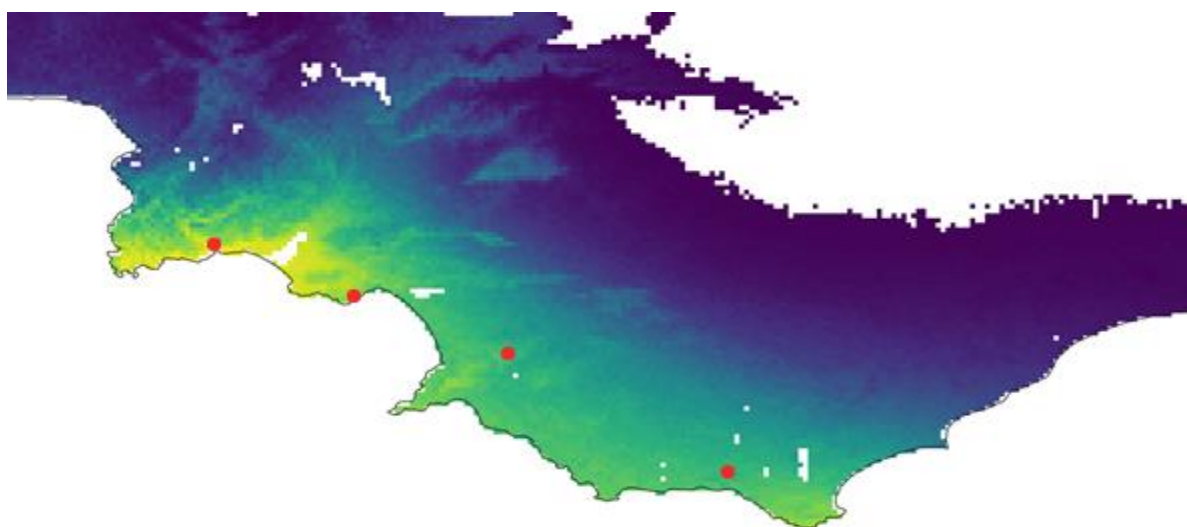
Figure 3.1 An SDM output map of *P. compacta*'s environmental suitability on the South-western coast of South Africa. The colour gradient indicates climatic suitability with dark blue representing low suitability while yellow indicates highest suitability. Study sites Kogelberg, Fernkloof, Grootbos, and Agulhas are indicated on the map (from left to right).

3.3.1 Growth and Reproductive Performance of *P. compacta* in Marginal and Core Populations

3.3.1.1 Study Area

The first part of the study investigated four sites across *P. compacta*'s range. Two core *P. compacta* populations and two marginal populations were chosen based on their high and low Maxent habitat suitability scores (Table 3.1) Kogelberg Nature Reserve (34°19'41.0"S, 18°59'19.7"E) and Fernkloof Nature Reserve (34°24'55.2"S, 19°13'33.4"E) were chosen as core sites and Grootbos Nature Reserve (34°31'24.0"S, 19°29'36.3"E) and Agulhas National Park (34°44'00.2"S, 19°51'56.0"E) were chosen as marginal sites (indicated in red dots in

Figure 3.1). All sites have confirmed *P. compacta* populations. Grootbos and Agulhas populations are confirmed as having derived from intentionally planted populations, with individuals present today at these sites either first- or second-generation populations that have self-established after previous fires. Grootbos last burned in 2006 (15 years ago), Agulhas in 2009 (12 years ago), Fernkloof in 2008 (13 years ago) and Kogelberg in 2011 (10 years ago), as confirmed by Reserve managers or local experts.

Table 3.1 Habitat suitability scores were extracted from Maxent generated *P. compacta* SDMs for current, 2040 and 2070. The 2040 and 2070 suitability scores were created using an average of five general circulation model predictions. Suitability scores for Kogelberg, Fernkloof, Grootbos and Agulhas are expressed as a percentage out of 100 for current, 2040 and 2070. Cut-offs for presence is set to above 50, therefore scores under 50 are indicative of a site being 'unsuitable'.

Site	Suitability Score (%)		
	Current	2040	2070
Kogelberg	82	84	81
Fernkloof	74	69	64
Grootbos	55	50	45
Agulhas	56	57	54

3.3.1.2   Experimental design

Site-based measurements

At each site, 15 individuals were randomly selected within a radius of 25-metres and various physical measurements were taken, resulting in a total of 60 measured individuals being measured at each site. To ensure randomised selection of individuals, a random walk procedure was followed within each selected habitat.

Documented site-level characteristics included slope (angle in º), aspect (N, S, E, W) and soil type (categorised using the guidelines developed by the Protea Atlas Project – https://www.proteaatlas.org.za/Protea_Atlas_Guide.pdf), rockiness (measured between 0-4, with 0 being no rocks and 4 being extremely rocky), evidence of harvesting (yes or no), and habitat disturbance (0-4, with 0 being undisturbed and four being highly disturbed). Wetland indicator species were used to assess drainage and saturation of a site (presence or absence). The time since the last fire (in years) for each site was recorded as a proxy for population age, and presence of alien invasive species was also noted.

Growth measurements

Growth per year can be easily distinguished in Proteas since each internode signifies an annual growth increment, and in *P. compacta*, shoot vegetative growth is largely restricted to mid-summer months of December and January. All growth measurements were made after February 2020 on the four most recently produced internodes, including the terminal (current season) shoot, reflecting the growing seasons of 2016/2017; 2017/2018, 2018/2019, and 2019/2020. The lengths and diameters (taken 50 mm above each node) of each internode were measured, and from these measurements, the growth volume of new shoots back-calculated for each year. This was done by calculating the mean accumulated diameter for each year for each site and subtracting this value from the measured diameter of each older internode (Figure 3.2).

Initial $2020D_i$ ⊘ $= 2020d_i$ $2020L_i$

Initial $2019D_i$ ⊘ $= 2019d_i - \sum_{i=1}^{n} ((2019d_i - 2020d_i)/n)$ $2019L_i$

Initial $2018D_i$ ⊘ $= 2018d_i - \sum_{i=1}^{n} ((2018d_i - 2020d_i)/n)$ $2018L_i$

Initial $2017D_i$ ⊘ $= 2017d_i - \sum_{i=1}^{n} ((2017d_i - 2020d_i)/n)$ $2017L_i$

Figure 3.2 Schematic description of all variables measured and derived in order to back-calculate the volume of new seasonal individual shoot growth for each of 4 previous years on a single shoot. The length (L) and measured diameter (d, labelled by the year in which the shoot was produced) of each of the four most recently produced internodes was determined on a single growing axis of 15 individual plants per site. While L in each year is assumed to be fixed once the growing season is complete, the *initial* diameter D of shoots produced in previous seasons was back-calculated by correcting for annual stem diameter incremental increases in subsequent years. This was done by calculating a site-specific mean annual increment increase as indicated in the figure (with n = 15) and subtracting this site-specific value from each internode's measured diameter $(YEAR)d_i$. Each individual shoot volume in the year in which it was produced could then be calculated as the volume of a cylinder with dimensions length L_i and diameter initial $(YEAR)D_i$.

Once diameter was adjusted to back-calculate the initial diameter measurements, length and diameter were used to calculate a single growth metric referred to as volumetric growth. The formula for the volume of a cylinder was used to approximate individuals' volumetric growth (cm^3) per year ($V = \pi r^2 h$).

Reproductive measurements

Retrospective flowerhead counts for the past four years were made and used as a proxy for reproductive rates. This translated into recording the number of flowerheads produced from the flowering seasons of 2017 to 2020 (flowering is generally centred on the month of August). For large individuals, counting individual flowerheads was not feasible, and in these cases the flowerheads in a representative proportion of the individual were counted and multiplied to estimate the total number of flowerheads. Flowerheads were not counted if the bud was aborted or if not open.

Other trait measurements

Nearest neighbour distances (in metres) were determined as the distance from the measured *P. compacta* to the nearest neighbouring conspecific individual. This measurement was used as a proxy to quantify intraspecific density. Complexity of branching was measured by ranking branching on a scale of 1 – 5, with 1 representing a monopodial individual, and 5 representing a high level of sympodial branching, referred to as high branching complexity. Disease prevalence was quantified by recording presence of Witches' Broom on a measured individual (yes or no), and the prevalence of Witches' Broom on each measured individuals' growing axis as a percentage of all axes measured.

Environmental data

The climatic determinants of annual vegetative growth and flowerhead production rates were investigated using Climate Research Unit (CRU) climatic data (Harris *et al*., 2020). The CRU TS database provides monthly data on a 0.5° x 0.5° grid covering land surfaces, with data provided from 1901 to 2019. Variables include temperature (℃), diurnal temperature range (℃), and precipitation (per month in mm). Data were categorised into seasons (December/January/February, March/April/May, June/July/August, and

September/October/November) for analysis. The 'current' suitability scores shown in *Table 3.1* were also included as a potential explanatory variable.

3.3.1.3 Statistical Analyses

R (version 4.0.3; R Core Team, 2013) was used for all statistical analyses and graphical outputs. Generalised linear models (GLM) built using the *glmer* function of the *lme4* R package (Bates *et al*., 2015), were used to test if there were significant difference in the vegetative growth (cm^3) and reproductive rates of *P. compacta* individuals between sites across the species' range. Growth followed a Gamma distribution, and the number of flowerheads had a Quasi-Poisson distribution.

A generalised linear mixed model (GLMM) was then performed using the *glmmTMB* function of the *glmmTMB* R package (Brooks *et al*., 2017) to investigate which environmental factors are the most important predictors of vegetative growth (cm^3) and number of flowerheads produced of *P. compacta*. Fixed environmental factors included mean precipitation in the driest quarter (mm), precipitation in the wettest quarter (mm), mean temperature in the warmest quarter (°C), mean temperature in the coldest quarter (°C), Maxent current habitat suitability score (%) and June, July, August mean diurnal range (°C). Warmest and driest quarter refers to December, January and February and the coldest and wettest quarter refers to June, July, and August. A principal component analysis (PCA) was performed using the *PCA* function of the *FactomineR* (Husson *et al.*, 2008) package in R, to eliminate collinear variables. Random effects included age (since last fire), year and individual nested in site. For model selection, a saturated model was built, and the *dredge* function of the *MuMin* R package (Barton, 2020) was used to find the model with an Akaike Information Criterion (AIC) at least two values lower than the other models (Burnham *et al*., 2002) – this model was used in the analysis. Growth most closely followed a Gamma distribution and number of flowerheads, a Poisson distribution. Model performance was analysed using the *simulateResiduals* function of the *DHARMa* R package (Hartig, 2020). An ANOVA was used to test for significant differences in maximum height (m) across sites using the *anova* function of the *stats* R package (R Core Team, 2013). Nearest neighbour (m), branching (scale 1-5) and witches' broom (yes or no, and % infection of individuals) all had non-parametric distributions and were tested for difference across sites with a Kruskal-Wallis test using the *kruskal.test* of the *stats* R package (R Core Team, 2013). The R package *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2020) were used for graphical outputs.

3.3.2   Investigating *P. compacta* microhabitat differences in the marginal site Agulhas National Park

3.3.2.1   Study Area

The second part of this study investigated fine-scale spatial variation in the growth, flowering, and disease measures in *P. compacta* populations in Agulhas National Park in order to explore the role microsites may play in establishment and survival under marginal climatic conditions. The Agulhas National Park supports approximately 2000 indigenous species in ~209km^2. This Park is situated at the most southern tip of Africa and has been identified by the United Nations Developing Programme (UNDP) as having the highest priority rating for conservation in South Africa (Kraaij *et al.* 2009). Approximately fifty years ago, before SANParks acquired the land, the northern area of the park was in private ownership and were farmed predominantly for producing flowers for the Fynbos cut flower industry. A population of *P. compacta* was established artificially and persists today with no interventions in the past five decades. Having persisted and regenerated through fire events, this population offers an opportunity to gain insights into assisted translocation practices that could be undertaken or avoided.

Three sub-sites were chosen at the Agulhas site, situated along the Soetanysberg mountain in Agulhas National Park. Stark differences were found between *P. compacta* density found in

Table 3.2 Three Agulhas sub-sites were chosen at different altitudes. The table below shows the altitudinal differences between the low, middle, and high elevation sub-sites in metres above sea level.

Sub-site	Altitude (metres above sea level)
Low	15 - 30
Middle	115 - 135
High	220 - 235

what may have been natural seeps and those that were found out of apparent seeps. Therefore, in each sub-site, dense patches, and sparser patches were selected to represent a range of population densities. The Low elevation sub-site (34°43'54.6"S, 19°44'50.5"E), is at the foot of the mountain in a low-lying area 15 m – 30 m above sea level (Table 3.2). The Middle elevation sub-site is between 115 m – 135 m above sea level. Data from the Middle elevation sub-site was used in the larger scale core and marginal site comparison. This sub-

site was selected *a priori* on the assumption that it most closely represents the average environmental conditions at the larger scale. Eight individuals from the Dense plot and seven from the Sparse plot at the Middle sub-site were selected to make up the 15 individuals for the core and marginal site comparisons. The High elevation sub-site (34°44'59.9"S, 19°51'08.2"E) is situated near the summit of the Soetanysberg mountain between 220m – 235m above sea level. All three sub-sites are within 10km of each other.

3.3.2.2   Experimental Design

Sub-sites and plots

Two plots were measured per sub-site, with one plot representing high *P. compacta* density (Dense plot) and another plot with low *P. compacta* density (Sparse plot). In each plot, 10 individuals were measured within a 25-metre radius. Flowerhead production, vegetative growth and other traits were measured as described above in section **3.3.1.2**. Each sub-site comprised 20 measured individuals with a total of 60 individuals measured across all three sub-sites. Sub-site descriptions and prominent features were noted as already described in section **3.3.1.2.**
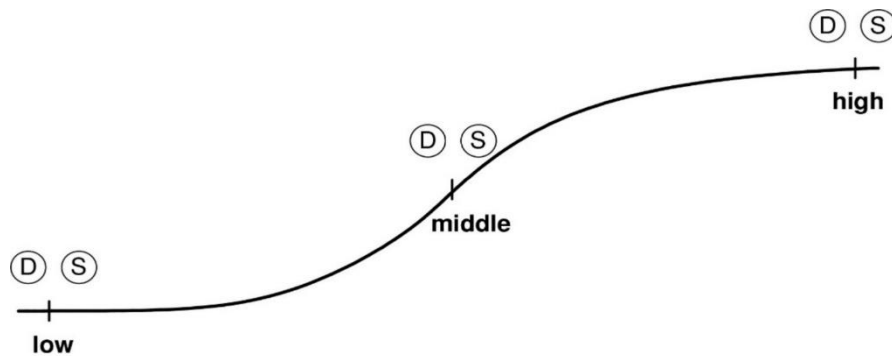
Figure 3.3 Visual representation of the Agulhas experimental design. Sub-sites at varying elevations were used (Low, Middle and High). Each sub-site comprised two plots, one dense (D) and one sparse (S) plot.

Growth, flowering, and other traits

Growth was measured using the same process as described in the range investigation, however, for mean diameter adjustment calculations, the samples were separated into plots (10 individuals). Flowering and other traits measured followed the same procedure as described previously in section **3.3.1.2.**

Testing microclimatic differences between sub-sites and plots

In each plot, two microloggers (DS1922L, Maxim Integrated, CA, USA), one measuring air temperature 10 cm above-ground and one measuring soil temperature 5 cm - were placed in the Dense and Sparse plots at each sub-site (12 microloggers in total). The microloggers had been pre-calibrated, and measured temperature at a 0.5 ℃ resolution. Readings were recorded every hour from February 2020 to February 2021. Temperature data were used to test for microclimatic differences between sub-sites and plots, as well as soil and air temperature differences. Volumetric soil moisture (m^3/m^3) was measured using a Decagon GS3 sensor with a handheld Decagon Procheck device, in Dense and Sparse plots of each of the plots and sub-sites in winter (July 2020) and in summer (February 2021). Readings were replicated three times, manually recorded, and the time of day of the reading was noted.

3.3.2.3   Statistical Analyses

P. compacta performance across sub-sites and plots was investigated to test for microhabitat driven effects. A GLM was built using the *glmer* function of the using the *lme4* R package (Bates *et al*., 2015) with sub-site (Low, Middle, High), plot (Dense or Sparse) and Year as factors. Soil and air temperatures were analysed using a repeated measures ANOVA. The *anova* function of the *stats* R package (R Core Team, 2013) was used to test for microclimatic differences between sub-sites and plots. Before conducting the analysis, hourly temperature data were converted into mean daily values and categorised into seasons (Summer, Winter, Autumn, and Spring). Soil moisture data was non-parametric therefore it was analysed using a Wilcoxon signed rank test to test for seasonal, sub-site and plot effects. The *Wilcoxon.*test function of the *stats* R package (R Core Team, 2013) was used to perform the Wilcoxon rank test. A two-way ANOVA was used to test for significant differences in maximum plant height (in metres) between sites and plots. A Kruskal-Wallis test was used to test for differences in the non-parametric data nearest neighbour distance (m), branching complexity (scale 1 - 5) and Witches' Broom (yes or no, and % infection of individuals). The R package *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2020) were used for graphical outputs.

3.4 Results

3.4.1 Growth and Reproductive Performance of *P. compacta* in Marginal and Core Populations

3.4.1.1 Vegetative Growth
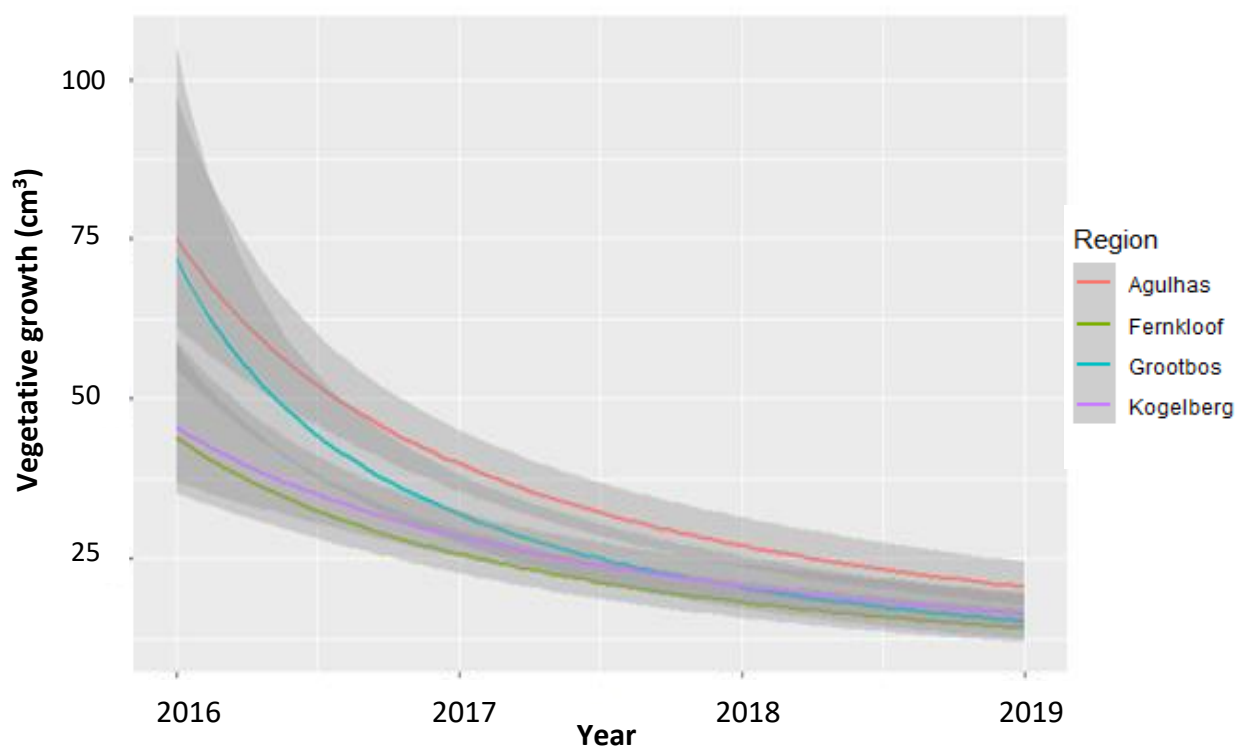
Figure 3.4 Vegetative growth (cm^3) of *P. compacta* individuals in marginal sites Agulhas and Grootbos, and core sites Fernkloof and Kogelberg between December 2016 to December 2019. *P. compacta* in Agulhas was found to have significantly higher vegetative growth than *P. compacta* in Grootbos, Fernkloof and Kogelberg and a significant decrease in vegetative growth was found between 2016 and 2019.

A generalised linear model (GLM) found that Site was a significant predictor of vegetative growth of *P. compacta* individuals (Table 3.3). Individuals at the Agulhas site were found to have significantly higher vegetative growth than individuals found in Kogelberg, Fernkloof and Grootbos (Figure 3.4). The factor Year was also found to be a significant predictor of growth, with vegetative growth significantly decreasing from 2016 to 2019. In 2016,

vegetative growth was found to have a mean of 54.31 cm^3 (var = 1210.11, sd = 34.79), whereas in 2019, vegetative growth had a mean of 13.79 cm^3 (var = 53.87, sd = 7.34).

Table 3.3 Summary of generalised linear model showing significant effects of Site and Year on vegetative growth (cm^3) of *P. compacta* in marginal (Grootbos) and core (Fernkloof and Kogelberg) sites. Agulhas was found to have significantly higher vegetative growth than Grootbos, Fernkloof and Kogelberg. During 2016 to 2019, vegetative growth was significantly less in the latter years. Parameter estimates, standard errors (SE), *t*-values and *p*-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	Predictor variables	Estimate	SE	t-value	p-value	
Vegetative growth	(Intercept)	928.700	60.980	15.230	**< 0.001**	***
	Site Fernkloof	-0.450	0.090	-4.710	**< 0.001**	***
	Site Grootbos	-0.220	0.090	-2.280	**0.020**	*
	Site Kogelberg	-0.340	0.090	-3.570	**< 0.001**	***
	Year	-0.460	0.030	-15.170	**< 0.001**	***

A generalised linear mixed model (GLMM) found that the coldest quarter was a significant predictor for vegetative growth (Table 3.4), with *P. compacta* individuals in sites with colder winters found to have lower vegetative growth (Figure 3.6 and Figure 3.9).

Table 3.4 Summary of generalised linear mixed model showing that the coldest quarter (mean temperature of June, July, and August in °C) was a significant predictor of vegetative growth (cm^3) in *P. compacta* across its range. Lower winter temperatures had a significant negative effect on vegetative growth. Parameter estimates, standard errors (SE), *z*-values and *p*-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	Predictor variables	Estimate	SE	z-value	p-value	
Vegetative growth	(Intercept)	3.2591	0.3025	10.774	**< 0.001**	***
	Coldest quarter	-0.19	0.1003	-1.982	**0.048**	*

Performance of vegetative growth GLMM model

The vegetative growth model fit the data well with residuals normally distributed (*p* = 0.928) and no significant deviations were found in the Kolmogorov-Smirnov test (K.S. test) or outlier test (Figure 3.5*a*). However, the model did not perform well in its ability to generalise
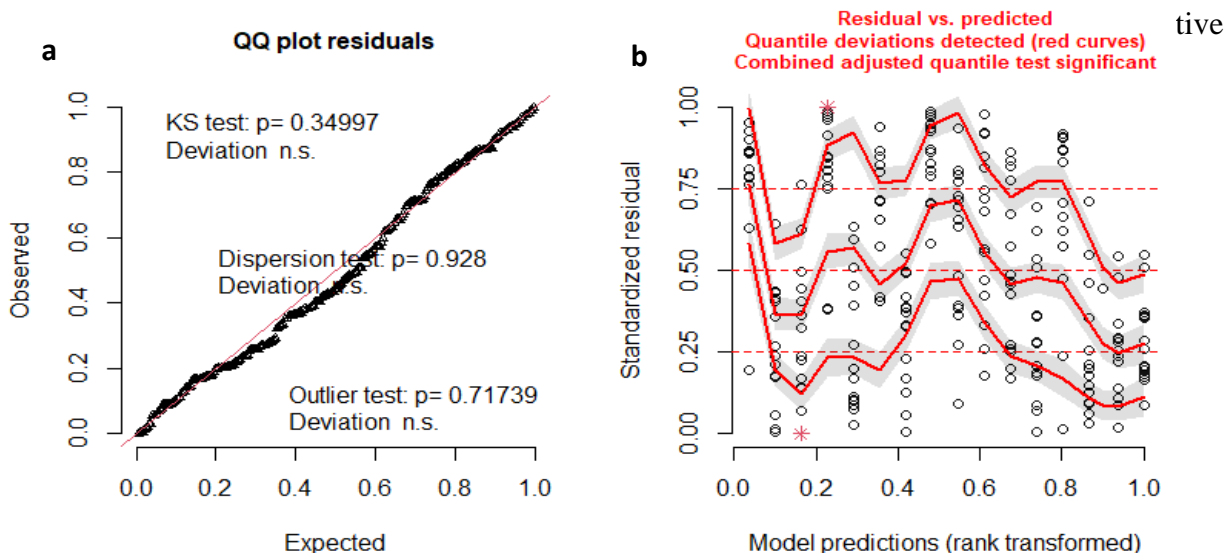
Figure 3.5 Performance of GLMM model for vegetative growth and environmental predictors. (a) Residuals fitted to a qq-plot showing model residuals are normally distributed with no significant deviations. (b) Residual versus predicted show significant deviation, which means the model fits well for this dataset, however, lacks predictive power.

December Growth and Environmental factors

Since 93% of growth occurs in December, the December environmental data were used to explore potential influences. The GLMM found that diurnal temperature range was the only significant predictor of vegetative growth (Table 3.5). The model suggests that when diurnal range was lower in December, the observed vegetative growth was higher. This prediction is in line with the Maxent-derived most influential predictor of bioclimatic suitability.

Table 3.5 Summary of generalised linear mixed model which found that diurnal range was a significant predictor of vegetative growth in December, with smaller diurnal ranges predicted to increase vegetative growth. Parameter estimates, standard errors (SE), z-values and p-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	Predictor variables	Estimate	SE	z-value	p-value	
Vegetative growth	(Intercept)	3.17	0.034	9.43	**< 0.001**	***
	Diurnal range	-0.179	0.05	-3.467	**< 0.001**	***
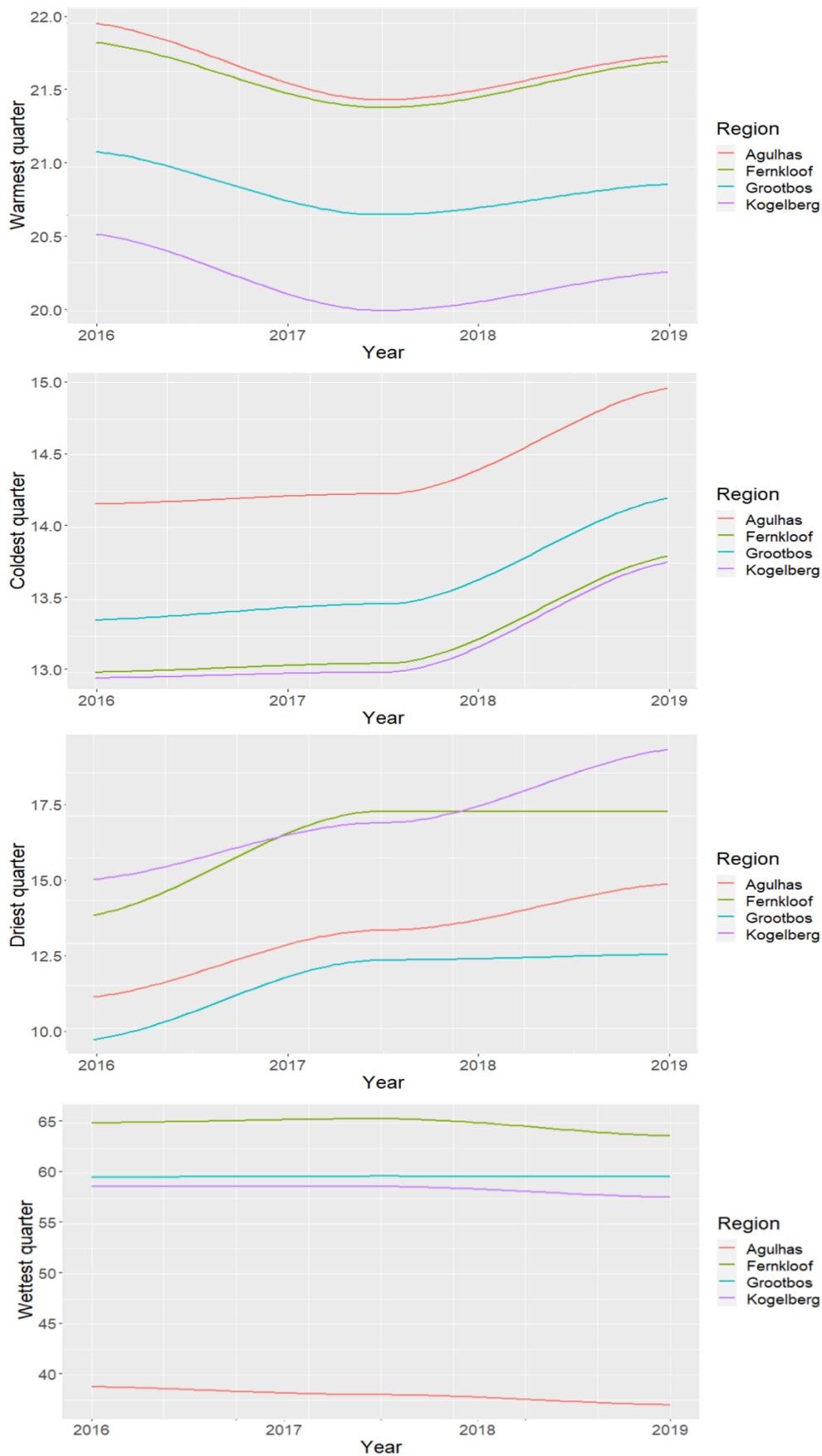
Figure 3.6 Mean monthly temperature (°C) in (a) the warmest quarter (December, January, February) and (b) the coldest quarter (June, July, August) from 2017 to 2019. Mean cumulative monthly precipitation (mm) in (c) the driest quarter (December, January, February) and (d) in the wettest quarter (June, July, August).

3.4.1.2   Reproduction
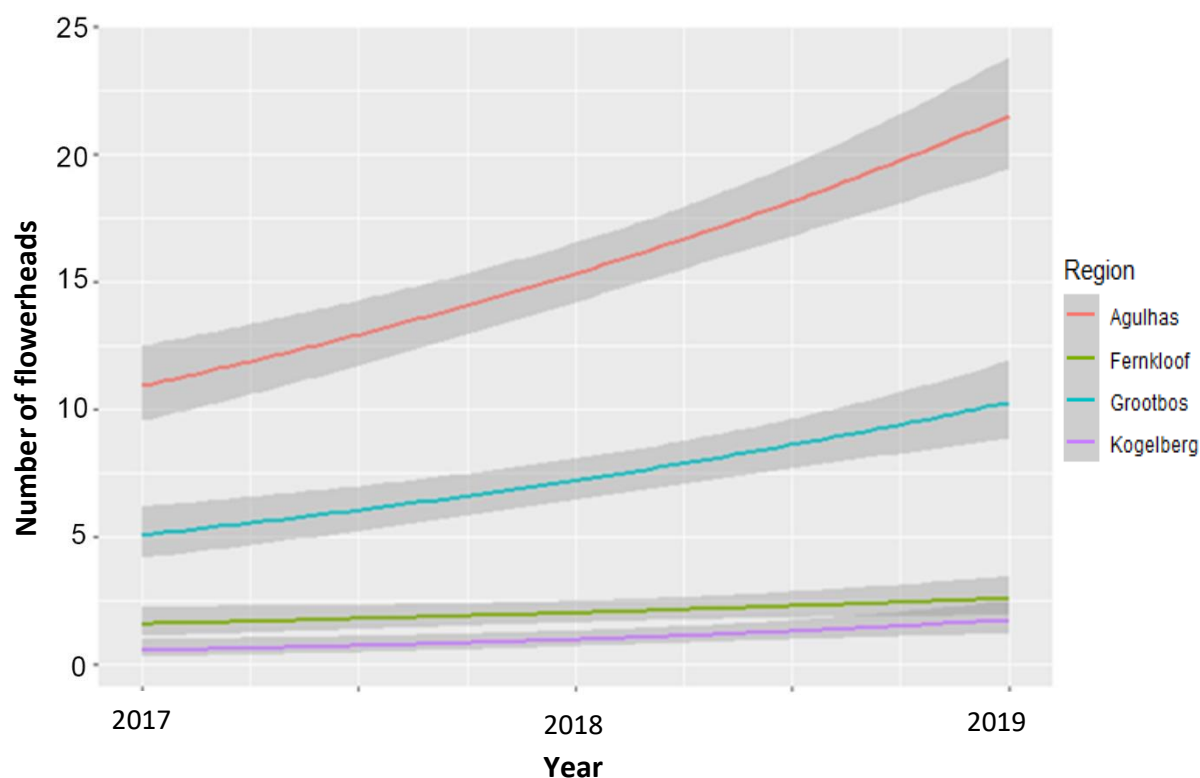
Figure 3.7 The number of flowerheads produced by *P. compacta* individuals in Agulhas, Fernkloof, Grootbos and Kogelberg produced between 2017 to 2019. Agulhas was found to produce significantly more flowerheads compared to other regions. Overall, the number of flowerheads produced increased significantly over time.

Site and Year were found to be significant predictors of the number of flowerheads produced by individual plants (Table 3.6). Individuals in Agulhas were found to produce significantly more flowerheads than individuals found in Grootbos, Fernkloof and Kogelberg (Figure 3.7).

Table 3.6 Summary of generalised linear model showing the differences in the number of flowerheads that were produced between sites in 2017, 2018 and 2019. Agulhas produced a significantly higher number of flowerheads compared to Grootbos, Fernkloof and Kogelberg. Parameter estimates, standard errors (SE), *t*-values and *p*-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	*Predictor variables*	*Estimate*	*SE*	*t-value*	*p-value*	
Number of Flowerheads	(Intercept)	-692.91	144.79	-4.79	**< 0.001**	***
	Site Fernkloof	-2.04	0.22	-9.412	**< 0.001**	***
	Site Grootbos	-0.75	0.13	-5.77	**0.020**	*
	Site Kogelberg	-2.68	0.29	-9.23	**< 0.001**	***
	Year	0.34	0.07	0.81	**< 0.001**	***

A generalised linear mixed model (GLMM) found that the previous driest quarter and the current suitability scores from Maxent were the most significant predictors of flowerhead production (Table 3.7). Wettest quarter was found to be marginally outside the theoretical definition of significant ($p = 0.06$). The model suggests that sites with a lower environmental suitability score produced significantly more flowerheads than sites in higher suitability areas. Additionally, sites receiving more summer precipitation produced more flowerheads (Figure3.6 and Figure 3.10).

Table 3.7 Summary of generalised linear mixed model found that current maxent suitability score and the driest quarter were significant predictors of flowerhead production. Increased summer rainfall was found to significantly increase the number of flowerheads produced. Parameter estimates, standard errors (SE), *z*-values and *p*-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	Predictor variables	Estimate	SE	z value	p value	
Number of Flowerheads	(Intercept)	1.151	0.11	10.86	**< 0.001**	***
	Wettest quarter	-0.39	0.21	-1.86	0.06	.
	Current suitability	-1.17	0.38	-3.11	**0.0018**	**
	Elevation	0.05	0.31	0.15	0.878	
	Driest quarter	0.52	0.078	6.77	**< 0.001**	***

Performance of reproductive rates GLMM model

The GLMM model for reproduction was found to perform well. Residuals were normally distributed with dispersion of $p = 0.922$ (Figure 3.8*a*). The K.S. test and outlier test also showed no significant deviations. No significant deviation was found between observed residuals and predicted residuals, which means this model had an adequate predictive ability (Figure 3.8*b*).
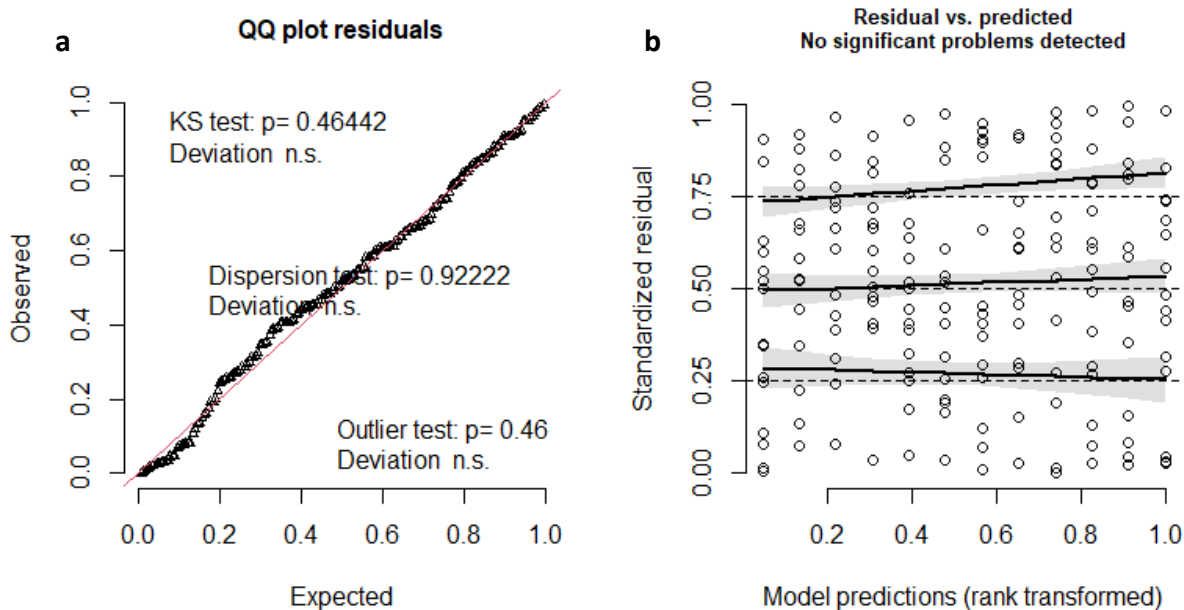
Figure 3.8 Performance of GLMM model for number of *P. compacta* flowerheads produced and environmental predictors. (1a) Residuals fitted to a qq-plot showing model residuals are normally distributed with no significant deviations. (1b) Residual versus predicted show no significant deviations, therefore model performance well for dataset and in prediction.
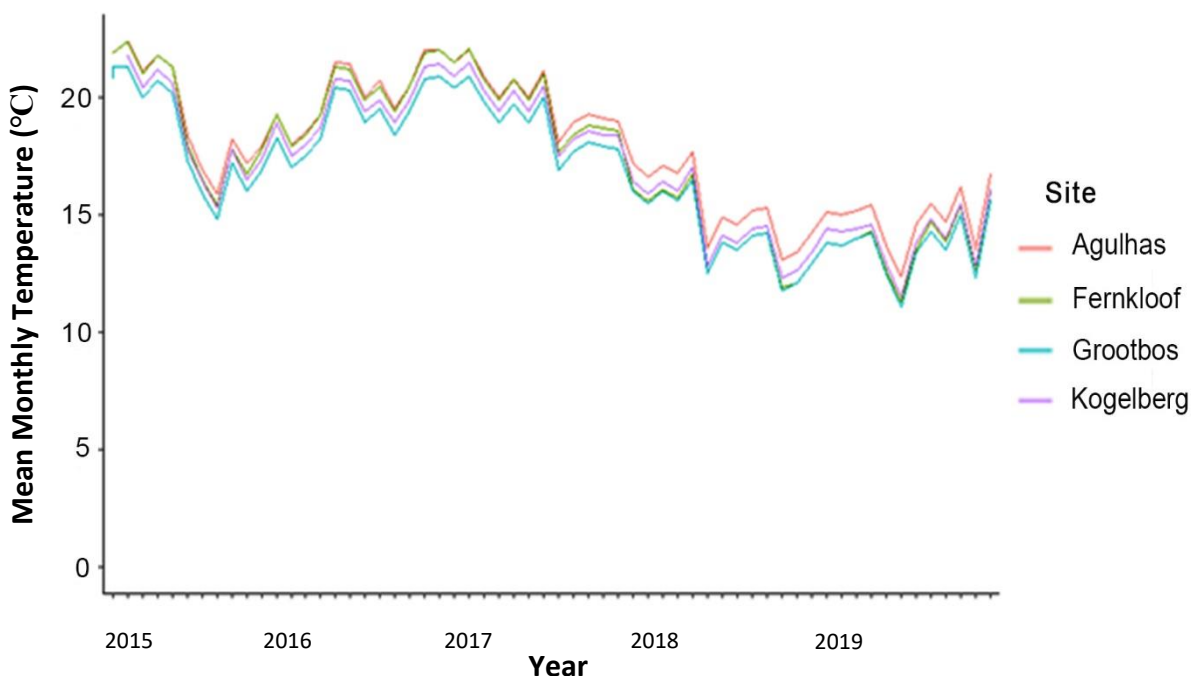
Figure 3.9 CRU data showing mean monthly temperature (°C) from January 2015 to December 2019 for Agulhas, Fernkloof, Grootbos and Kogelberg. Temperature in all Sites decreases between 2015 and 2019.
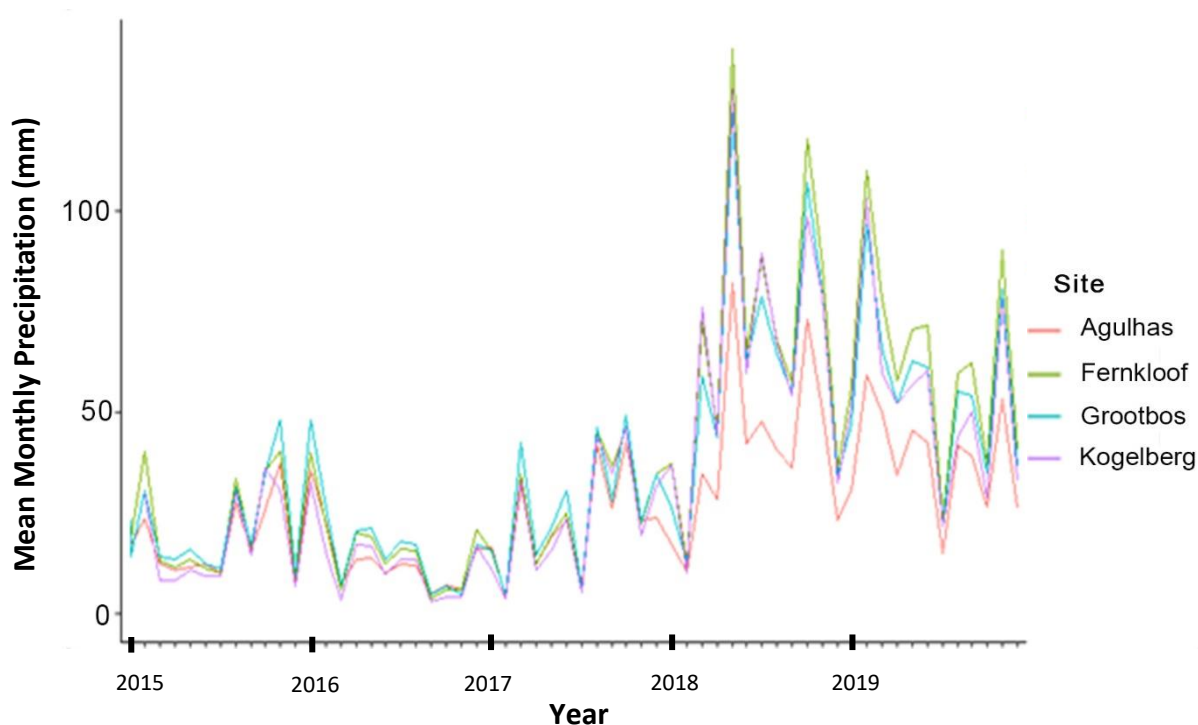
Figure 3.10 CRU data showing monthly precipitation (mm per month) from January 2015 to December 2019 for Agulhas, Fernkloof, Grootbos and Kogelberg. An overall increase in monthly precipitation is seen between 2015 and 2019.

3.4.1.3 Other plant traits

Maximum plant height

Individuals in Agulhas were significantly shorter compared to individuals found in Fernkloof and Grootbos ($F = 6.32$, df = 3, $p < 0.001$; Figure 3.11). Individuals in Kogelberg however were not found to be significantly different in height from individuals from those at any other sites.
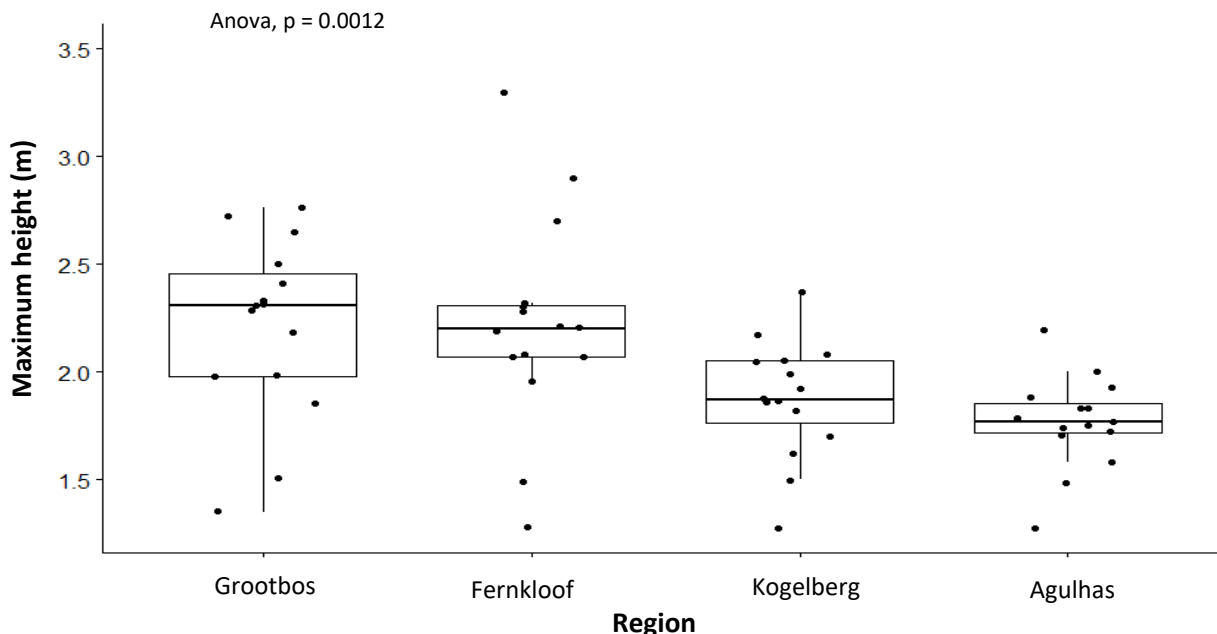
Figure 3.11 Maximum height (in metres) of *P. compacta* individuals in marginal sites, Agulhas and Grootbos, and core sites Fernkloof and Kogelberg. Individuals in Agulhas were significantly shorter in height compared to Grootbos and Fernkloof. Kogelberg was not found to be significantly different to any sites.

Nearest neighbour distances (population density proxy)

Grootbos was found to have the lowest intraspecific density, with a median distance of 3 m between *P. compacta* individuals (IQR = 2.96; Figure 3.12). Kogelberg and Fernkloof had the highest densities with 0.5 m and 0.6 m between *P. compacta* species, respectively (IQR = 0.4 and 0.65).
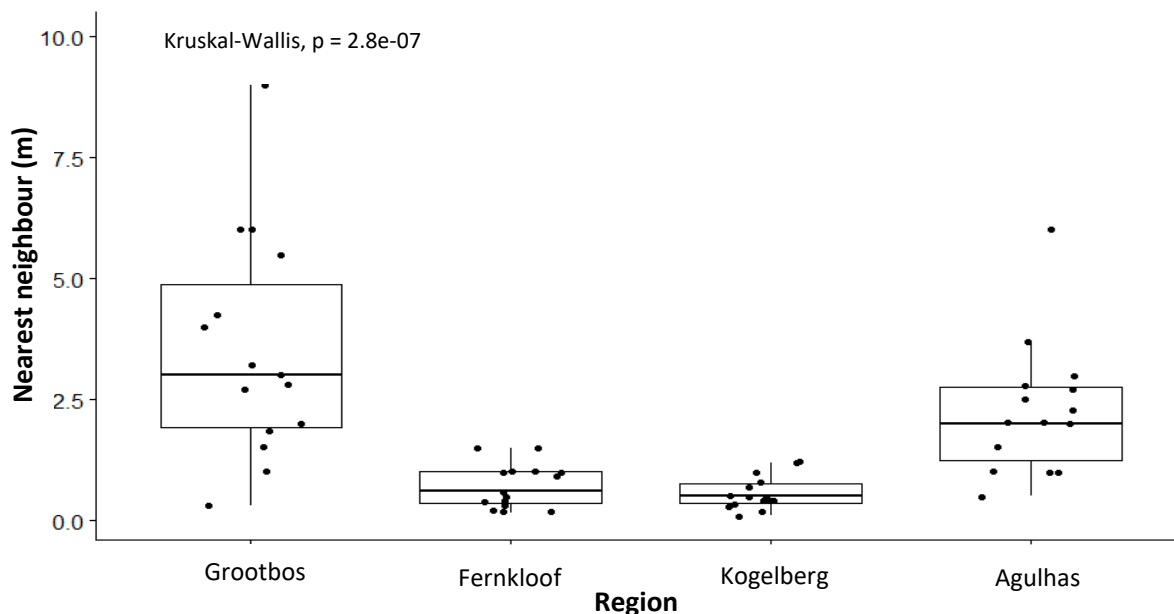
Figure 3.12 Nearest (intraspecific) neighbour of *P. compacta* individuals (in meters) in marginal sites Grootbos and Agulhas and core sites Kogelberg and Fernkloof. Nearest neighbour is used as a proxy for density. Fernkloof and Kogelberg had significantly higher density compared to Grootbos and Agulhas.

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Complexity of branching (monopodial - sympodial)

Agulhas was found to have significantly more sympodial individuals with most plants scored as five ($H = 41.2$, df = 3, $p < 0.001$; Figure 3.13a). No significant difference in branching was found between Kogelberg and Fernkloof. When compared as marginal and core sites, marginal sites, Grootbos and Agulhas had significantly higher complexity of branching compared to core sites, Fernkloof and Kogelberg ($H = 32.8$, df = 3, $p < 0.001$; Figure 3.13b).
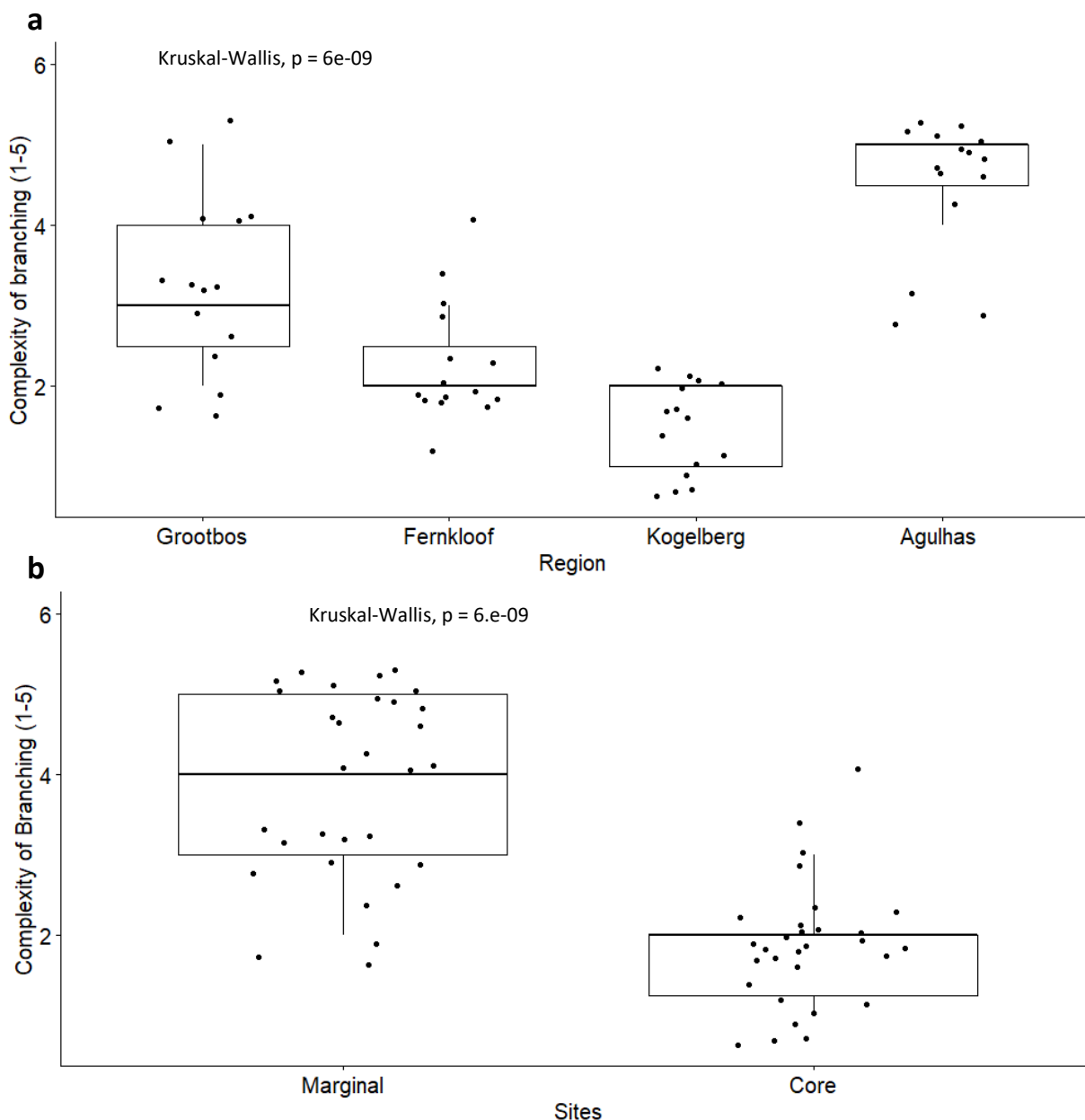
Figure 3.13 Complexity of branching of *P. compacta* individuals, scored from 1-5, with 1 as single-stemmed (monopodial) and 5 as high complexity of branching (sympodial). (a) Agulhas had significantly more highly branched individuals compared to other sites. (b) Marginal sites (Agulhas and Grootbos) show significantly higher complexity of branching compared to core sites (Fernkloof and Kogelberg).

Witches' Broom (disease prevalence)

Rates and severity of Witches' Broom varied significantly between sites ($H = 36.4$, df = 3, $p < 0.001$). Only one individual in Kogelberg had Witches' Broom, which spread over ~ 20% of the plant. The median number of Witches' Broom cases in Kogelberg was therefore zero (Figure 3.14*a*). Agulhas showed the most severe disease prevalence with a median of 50% spread on infected individuals (Figure 3.14*a*). Marginal sites had significantly more individuals with Witches' Broom and the severity of infection of individuals was also significantly higher ($H = 28.3$, df = 1, $p < 0.001$; Figure 3.14*b*).
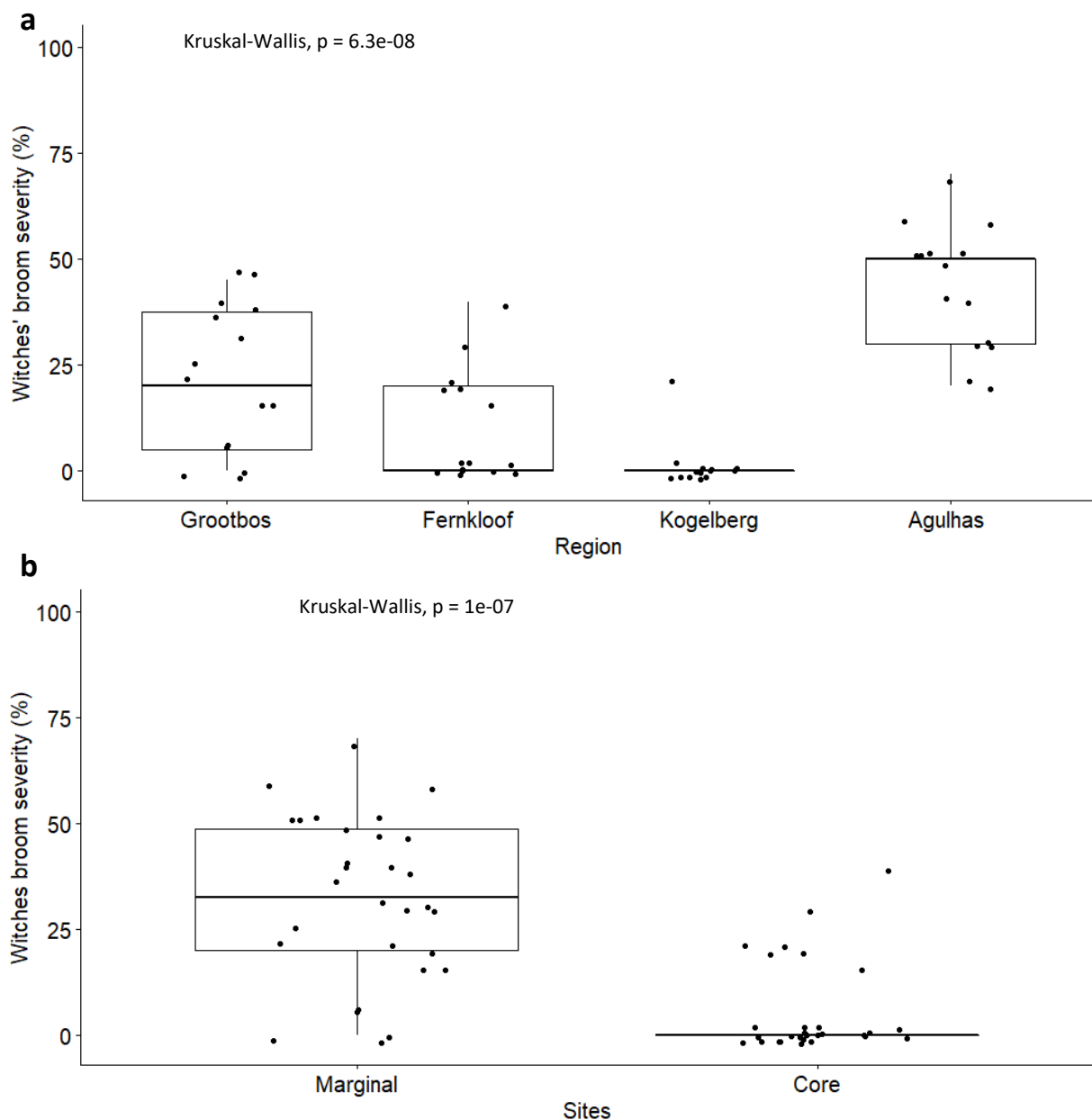
Figure 3.14 Witches' Broom disease was measured to ascertain disease prevalence in populations as percent (%) of infection per individual. (a) Severity of witches' broom was significantly worse in Agulhas with all individuals measured showing witches broom, whereas Kogelberg only had 1 individual with Witches' Broom. (b) Marginal sites showed significantly higher infection rates compared to core sites.

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3.4.2 Investigating *P. compacta* microhabitat differences in the marginal site Agulhas National Park

3.4.2.1 Microclimatic differences between sub-sites and plots

3.3.1.1 Soil Moisture
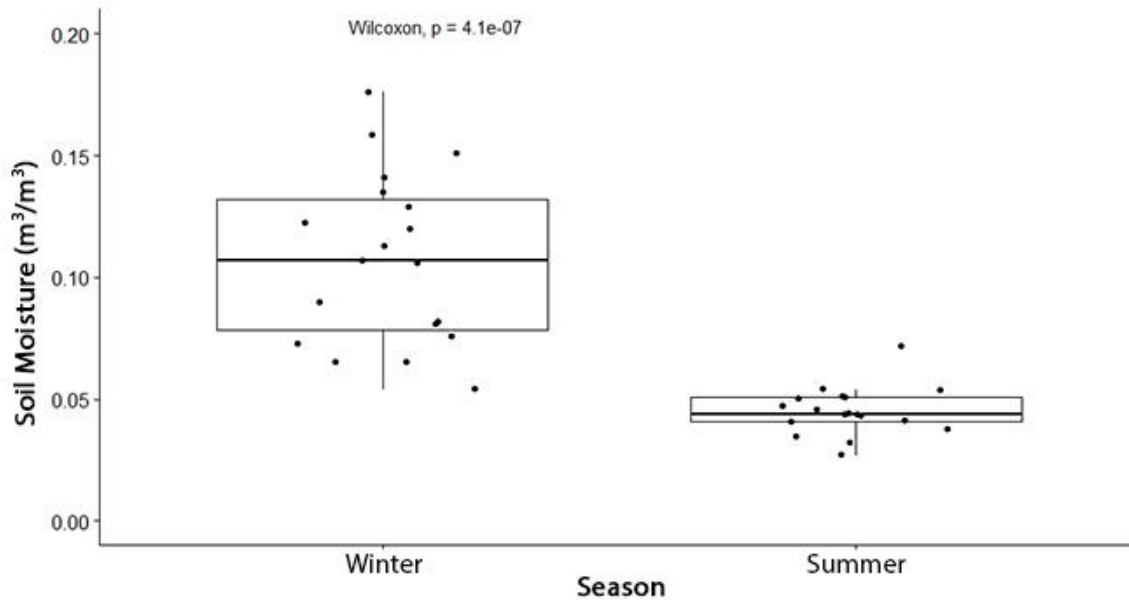
Figure 3.15 Volumetric soil moisture readings (m^3/m^3) for all Agulhas sub-sites (Low, Middle and High), taken in summer (February 2021) and winter (July 2020) months. Soil moisture was significantly higher in winter than in summer.

A Wilcoxon test showed that soil moisture was significantly higher in winter than summer months (effect size $r = 0.835$, $p < 0.001$; Figure 3.15). The median soil moisture reading in summer was 0.044 m^3/m^3 (IQR = 0.01), and the median in winter was 0.107 m^3/m^3 (IQR = 0.054). In summer (February), there was no significant difference in soil moisture between sub-sites (High, Middle, and Low elevation) or between Dense and Sparse plots. However, in winter, Dense plots were found to have significantly higher soil moisture compared to Sparse plots (effect size $r = 0.543$, $p < 0.05$; Figure 3.16), with Dense plots having a median reading of 0.122 m^3/m^3 (IQR = 0.029) and Sparse having a median reading of 0.076 m^3/m^3 (IQR = 0.016).
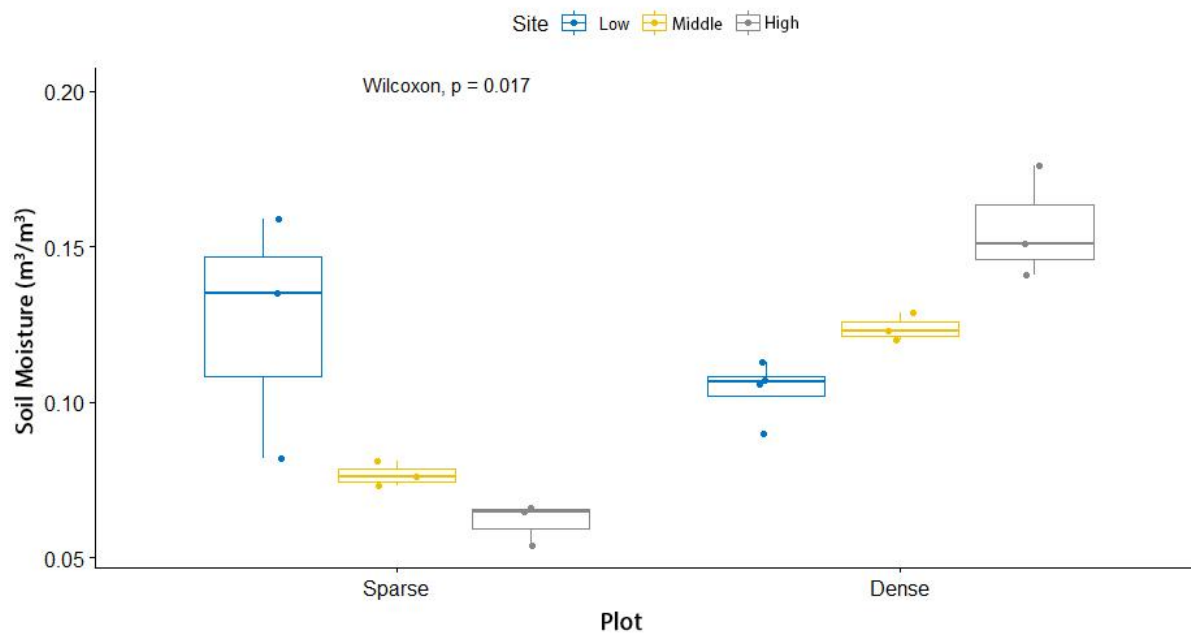
Figure 3.16 Volumetric soil moisture readings (m^3/m^3) taken in winter (July 2020) in dense and sparse plots at Low, Middle and High elevation sub-sites, Dense plots had significantly higher soil moisture than Sparse plots in winter. Differences between Low, Middle, and High elevation sub-sites in Agulhas are also shown.

3.3.1.2. Micrologger temperature data

Seasonality

The mean temperature for the year (February 2020 to February 2021), was recorded as 17.61 °C, with the lowest mean daily temperature recorded at 5.25 °C and the maximum recorded at 31.51 °C (Figure 3.17). Clear seasonality was found in air temperature, with seasons being significantly different in mean daily temperature ($F = 2596$, df $= 3$, $p < 0.001$). Soil temperatures were also significantly different winter and summer seasons ($F = 2596$, df $= 3$, $p < 0.001$).
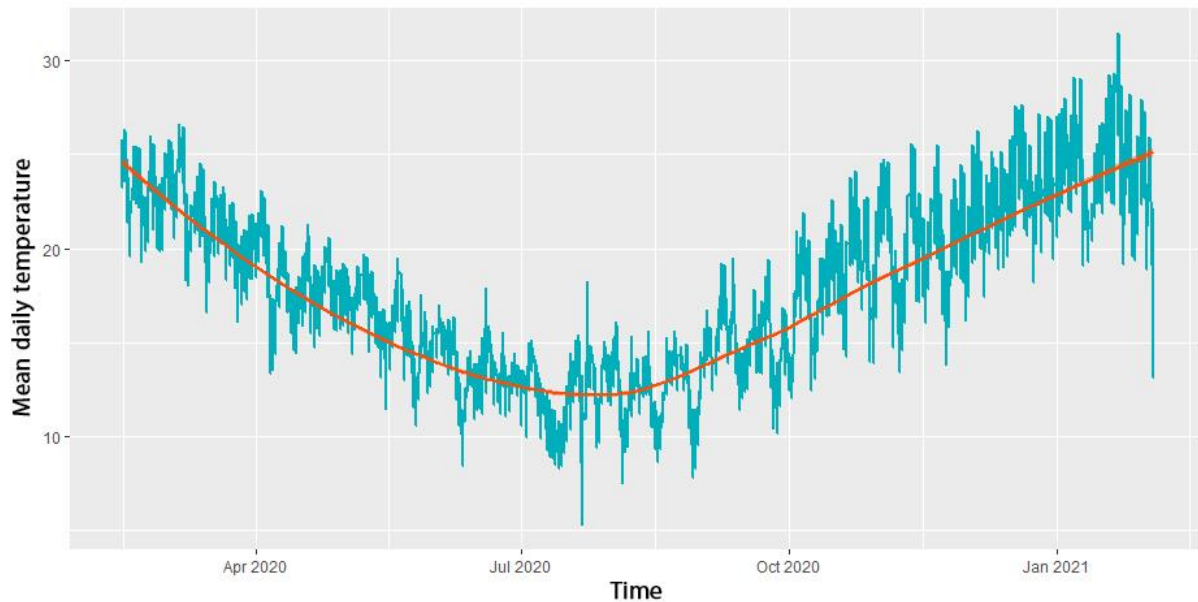
Figure 3.17 Combined air and soil mean daily temperature (°C) recorded from February 2020 to February 2021. Hourly temperature readings were averaged into daily mean temperatures and plotted. Red line illustrates the mean change over the year.

Soil and Air Temperature

Overall, soil temperature was significantly higher than air temperature ($F = 28.87$, df = 1, $p < 0.001$). The High elevation sub-site was significantly cooler than the Middle and Low elevation sub-sites ($F = 8.837$, df = 2, $p < 0.001$), but no significant difference in temperature was found between the Middle and Low elevation sub-sites. As expected, soil temperature in summer had the highest recorded temperature (31.51 °C), whereas air temperature in winter had the lowest temperature (5.25 °C) recorded (Table 3.7 and Table 3.8). Summer had a mean temperature of 23.01 °C and Winter had a mean temperature of 12.49 °C. Autumn had a mean of 18.21 °C and Spring had a mean temperature of 17.49 °C.

Table 3.8 Five-number summary of the air temperatures for each season of the year. Minimum, first quartile, median, third quartile and maximum temperatures are shown. The summary was calculated using the mean daily temperatures (℃).

Season	Air Temperature Five-number Summary				
	Minimum	Q1	Median	Q3	Maximum
Summer	13.09	20.83	22.37	23.82	29.26
Autumn	10.52	15.9	17.63	19.7	26.62
Winter	5.254	10.998	12.78	14.057	18.261
Spring	10.14	14.6	17.07	19.37	24.74

Table 3.9 Five-number summary of the soil temperatures for each season of the year. Minimum, first quartile, median, third quartile and maximum temperatures are shown. The summary was calculated using the mean daily temperatures (℃).

Season	Soil Temperature Five-number Summary				
	Minimum	Q1	Median	Q3	Maximum
Summer	18.18	22.45	23.8	25.23	31.51
Autumn	11.14	16.5	18.25	20.9	26.52
Winter	8.358	11.406	12.545	13.594	16.996
Spring	11.97	15.21	18.17	20.68	25.6

The Middle elevation sub-site was the only sub-site where air temperature was found to approach significance between dense and sparse plots ($F = 3.84$, df = 1, $p = 0.051$). Soil temperature was found to be the lowest at the High elevation sub-site ($F = 11.89$, df = 2, $p < 0.001$), with the Middle and Low elevation sub-sites showing no significant difference in soil temperature between them. The Middle elevation sub-site had a significantly higher soil temperature in the Sparse plot compared to the Dense plot ($F = 9.5$, df = 1, $p < 0.01$), whereas the Middle and High elevation sub-sites showed no soil temperature difference between the Dense and Sparse plots.

Summer and Winter
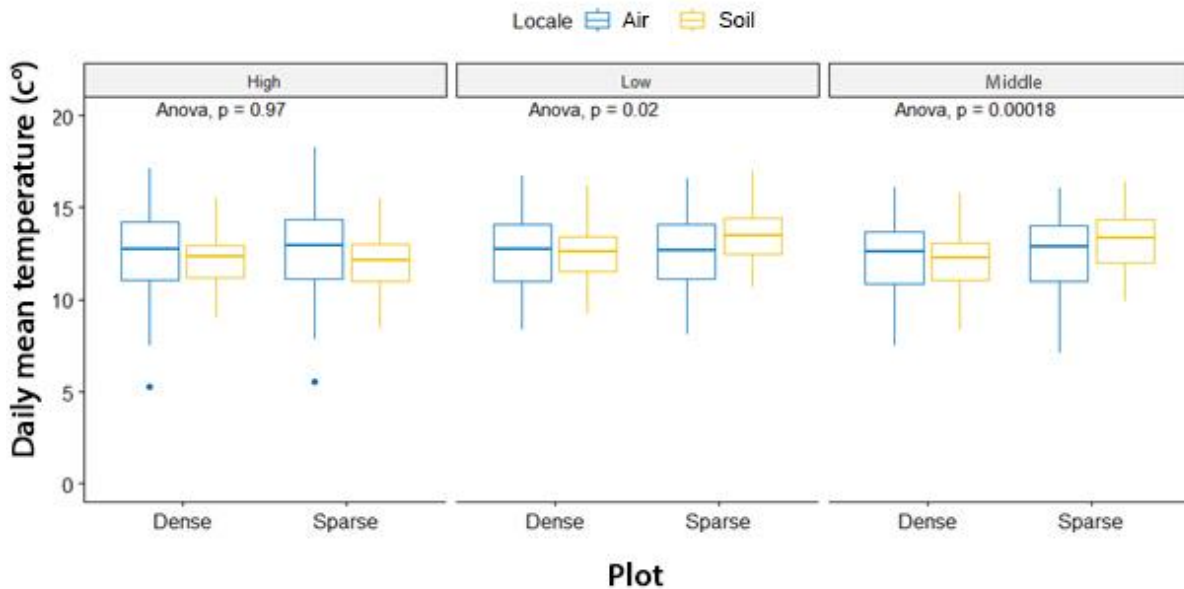
Figure 3.18 Winter (June, July, and August 2020) air and soil mean daily temperatures in dense and sparse plots at the High, Middle, and Low elevation sub-sites. Soil temperature in the Sparse plot at the Middle sub-site was significantly higher than the Middle Dense plot. Significance level between Dense and Sparse air and soil temperature for each sub-site is reported on the graph.

In winter, no significant difference in air temperature was found between sub-sites, however, soil temperature was significantly lower at the High elevation sub-site compared to the other two sub-sites ($F = 11.7$, df $= 2$, $p < 0.001$; Figure 3.18). At the High elevation sub-site, soil temperature was found to be lower than air temperature ($F = 6.68$, df $= 1$, $p < 0.05$), however, no differences in soil and air temperature were found between the Dense and Sparse plots. The Middle elevation sub-site showed the inverse, with no overall difference found between soil and air temperatures, but soil temperature in the Sparse plot was significantly higher than the soil temperature in the Dense plot ($F = 23.62$, df $= 1$, $p < 0.001$). The same pattern was found at the Low elevation sub-site, with no observed difference between air and soil temperature but soil temperature in the Sparse plot was significantly higher than the Dense plot soil temperature ($F = 16.44$, df $= 1$, $p < 0.001$).
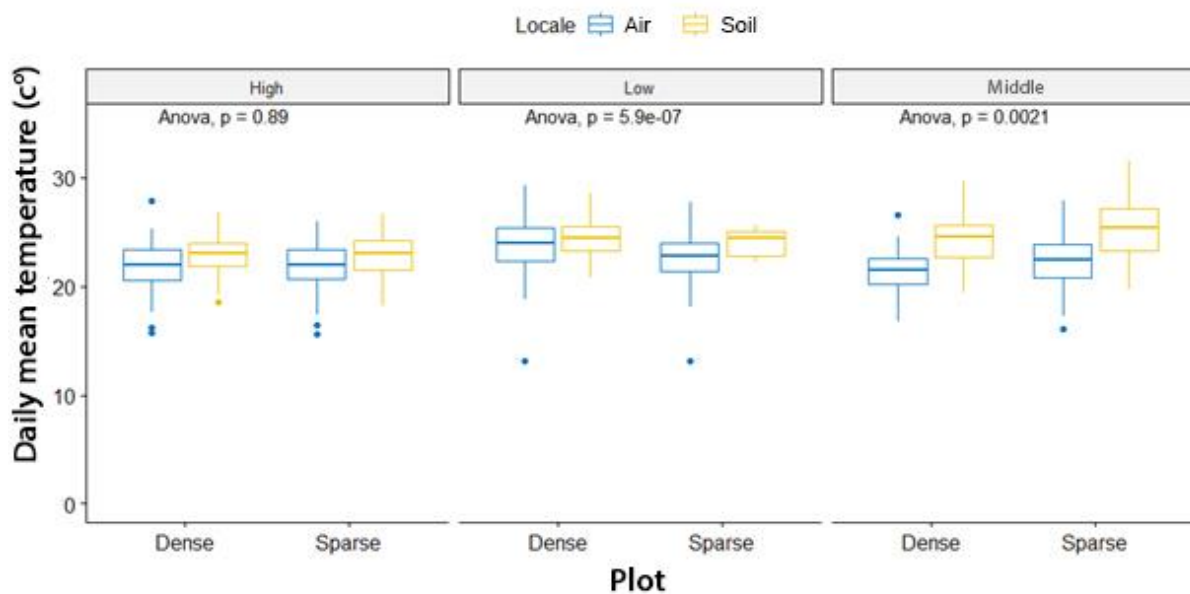
Figure 3.19 Summer (February 2020, December 2020, January 2021, and February2021) air and soil mean daily temperatures in Dense and Sparse plots at the High, Middle, and Low sub-sites. Soil temperature was significantly higher in all sub-sites. The Sparse plot in the Middle sub-site was significantly warmer than the Dense plot. In the Low sub-site, the Dense plot air temperature was found to be significantly warmer than the Sparse plot.

In summer, the Low elevation sub-site had a significantly higher air temperature compared to the Middle and High elevation sub-sites ($F = 20.24$, df $= 2$, $p < 0.001$), and the High elevation sub-site had a significantly lower soil temperature compared to the other sub-sites ($F = 35.21$, df $= 2$, $p < 0.001$). Soil temperature was significantly higher than air temperature in the Low, Middle and High sub-sites ($F = 132.8$, df $= 1$, $p < 0.001$; Figure 3.19). At the High elevation sub-site, like in winter, no difference in soil and air temperature was found between Dense and Sparse plots. At the Middle elevation sub-site, air and soil temperatures were significantly higher in the Sparse plot compared to the Dense plot ($F = 9.63$, df $= 1$, $p < 0.01$). At the Low elevation sub-site, air temperature was found to be significantly higher in the Dense plot ($F = 12.58$, df $= 1$, $p < 0.001$), but no significant difference was found between the Dense and Sparse plot soil temperature. Note that the Sparse plot soil temperature is only based on February 2020 summer readings and not December 2020, January 2021, and February 2021, due to a micrologger malfunction.

3.4.2.2   Growth and Reproductive performance

3.4.2.2.1 Vegetative growth
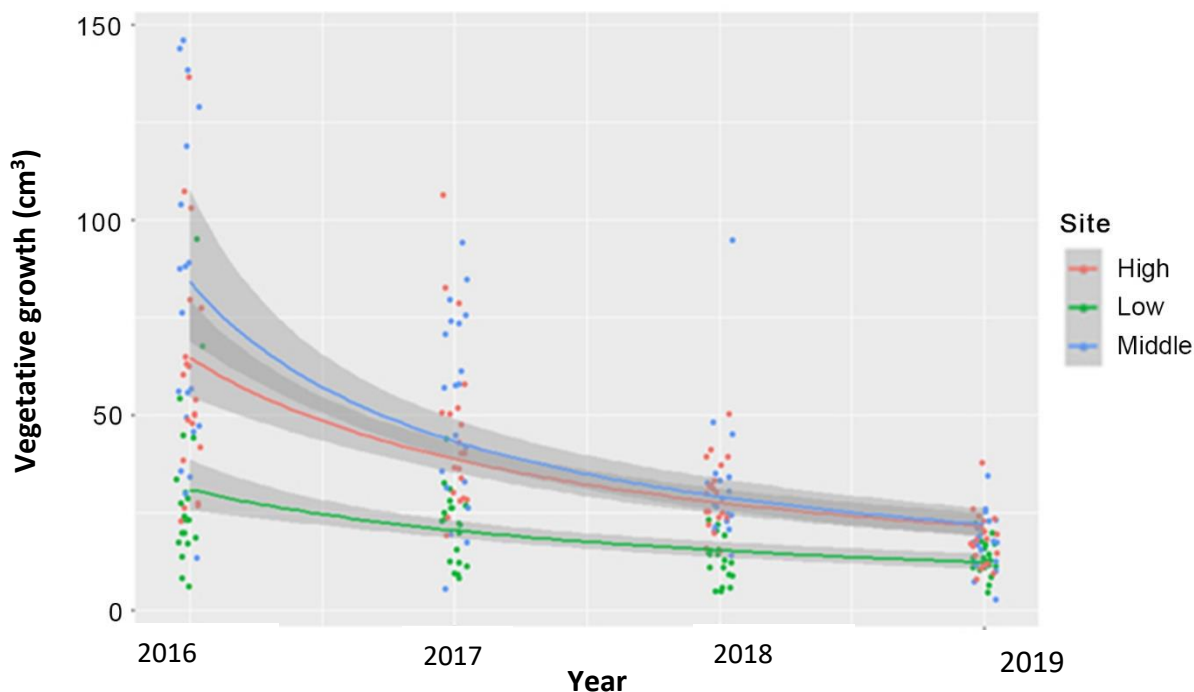
Figure 3.20 The vegetative growth (cm^3) of *P. compacta* individuals found in the Low, Middle, and High elevation sub-sites in Agulhas from 2016 to 2019. Vegetative growth was found to be significantly lower at the Low elevation sub-site. A significant decrease in vegetative growth was found between 2016 and 2019. with higher growth in 2016 (and higher variance in growth indicated in grey shading) and less growth in 2019 (and lower variance in growth indicated in grey shading).

A generalised linear model (GLM) using a Gamma distribution found that Sub-site and Plot were significant predictors of vegetative growth in the Agulhas sub-sites (Table 3.8). *P. compacta* individuals that were found at the Low elevation sub-site had significantly lower vegetative growth in comparison to the High sub-site (Figure 3.20). Vegetative growth at the Middle elevation sub-site was not significantly different from that of the High elevation sub-site. Year was also a significant predictor of vegetative growth, with growth significantly decreasing from 2016 to 2019. In 2016, the mean growth across sites was 55.85 cm^3 (var = 1345.54, sd = 36.86) and in 2019, mean growth was 16.04 cm^3 (var = 43.18, sd = 6.57). Plot was also found to be important, with vegetative growth being significantly lower in Dense plots compared to Sparse plots (Figure 3.21 and Figure 3.22).

Table 3.10 Summary of generalised linear model for vegetative growth (cm^3) in the marginal site Agulhas. Sub-site and Year were found to be significant predictors of *P. compacta* vegetative growth, with the Low elevation sub-site having the lowest vegetative growth, Sparse plots had significantly higher vegetative growth and Year was a significant predictor, with growth decreasing over time. Parameter estimates, standard errors (SE), *t*-values and *p*-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	Predictor variables	Estimate	SE	t-value	p-value	
Vegetative growth	(Intercept)	700.51	51.76	15.44	**< 0.001**	***
	Site Low	-0.61	0.07	-8.691	**< 0.001**	***
	Site Middle	0.12	0.07	1.64	**0.102**	
	Year	-0.39	0.026	-15.38	**< 0.001**	***
	Plot Sparse	0.2	0.057	4.81	**< 0.001**	***
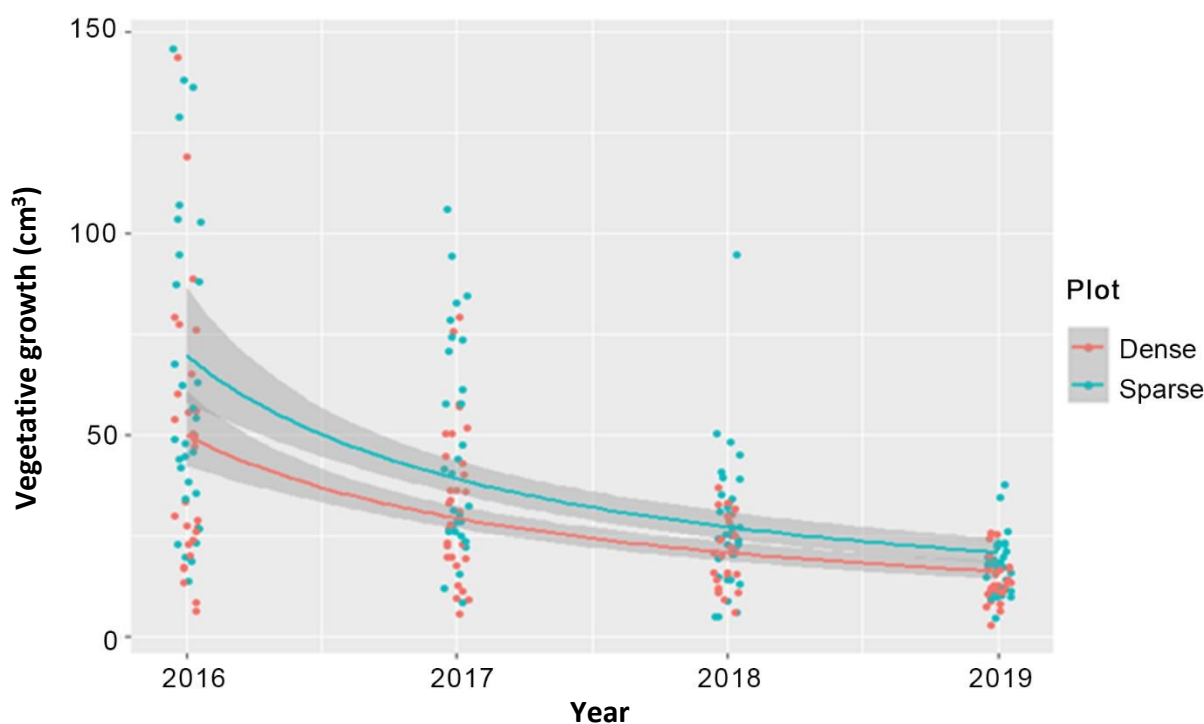
Figure 3.21 Vegetative growth (cm^3) of *P. compacta* individuals in Dense and Sparse plots in the marginal site Agulhas. Individuals found in Sparse plots had significantly higher vegetative growth than those in Dense plots. A significant decrease in vegetative growth was also seen over time.
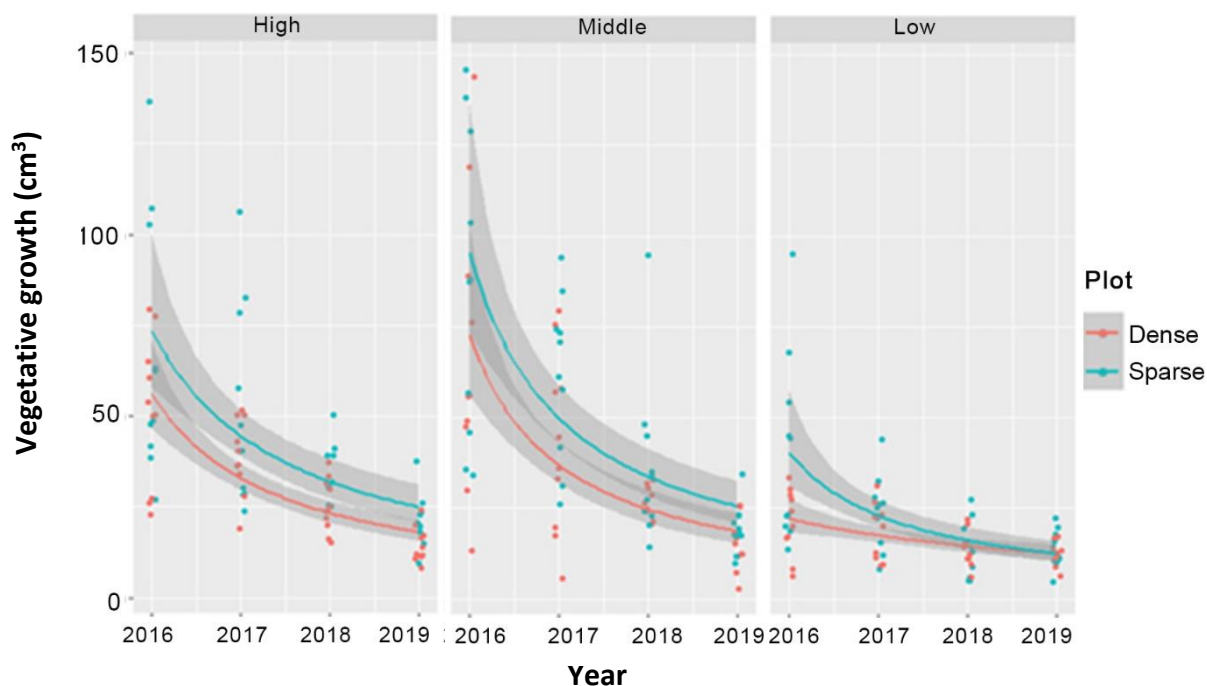
Figure 3.22 Vegetative growth (cm³) of *P. compacta* individuals in Dense and Sparse plots in Agulhas, separated into at Low, Middle and High elevation sub-sites.

3.4.2.2.2 Reproduction

A generalised linear model (GLM) found that Sub-site and Plot were significant predictors of the number of flowerheads found each year on individuals in Agulhas (Table 3.11). *P. compacta* individuals at the Low and Middle sub-sites produced significantly more flowerheads compared to the High elevation sub-site (Figure 3.23). Sparse plots were found to have significantly more flowerheads compared to Dense plots (Figure 3.24 and Figure 3.25).
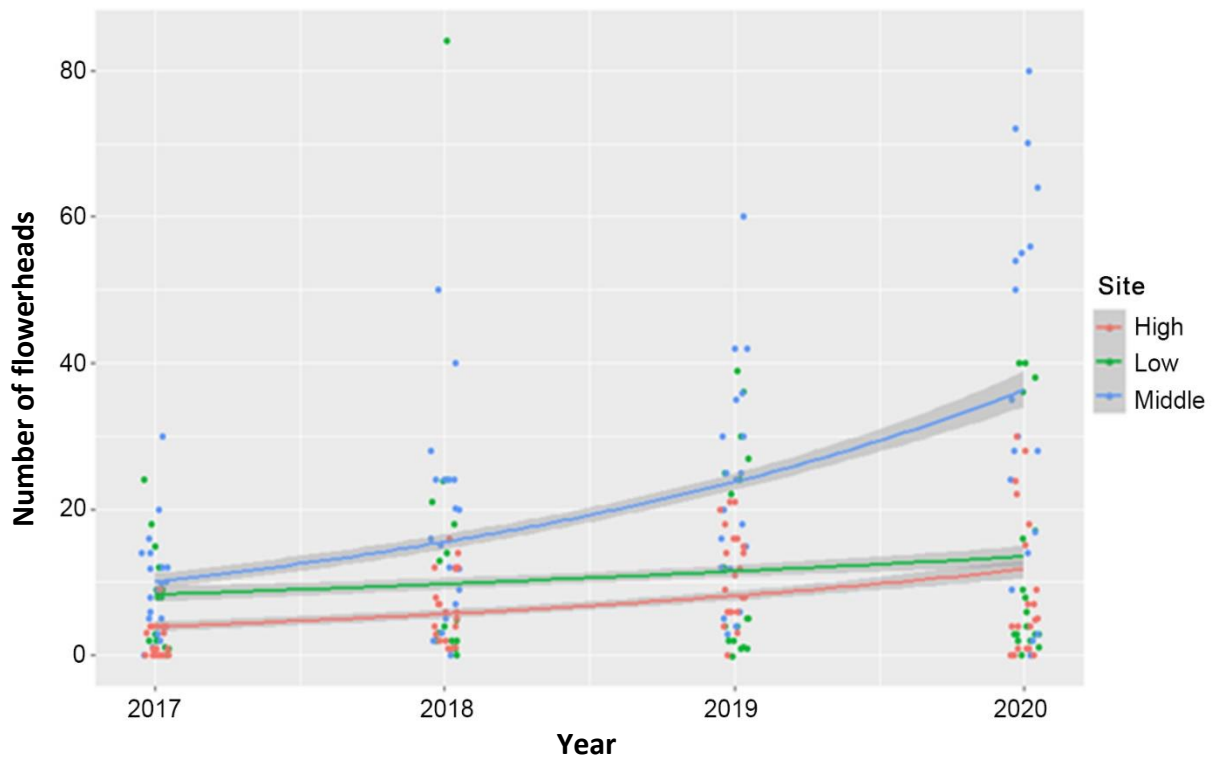
Figure 3.23 The number of flowerheads produced by *P.* compacta individuals in Agulhas at Low, Middle, and High elevation sub-sites. The Middle and Low sub-sites produced significantly more flowerheads than the High elevation sub-site. The number of flowerheads produced was also found to significantly increase over time.

Table 3.11 Summary of generalised linear model for the effect of Sub-site, Plot and Year on the number of flowerheads produced by *P. compacta* individuals in the marginal site Agulhas. The High elevation sub-site produced significantly less flowerheads than the Middle and Low elevation sub-sites. Further, Sparse plots produced significantly more flowerheads and Year was a significant predictor, with more flowerheads produced over time. Parameter estimates, standard errors (SE), *t*-values and *p*-values are given. Significant predictor variables indicated in bold with significance given as < 0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variable	Predictor variables	Estimate	SE	t-value	p-value	
Number of Flowerheads	(Intercept)	-625.63	132.45	-4.72	**<0.001**	***
	Sub-site Low	0.59	0.21	2.79	**0.006**	**
	Sub-site Middle	1.09	0.196	5.61	**<0.001**	***
	Plot Sparse	0.49	0.15	3.35	**<0.001**	***
	Year	0.31	0.07	4.74	**<0.001**	***
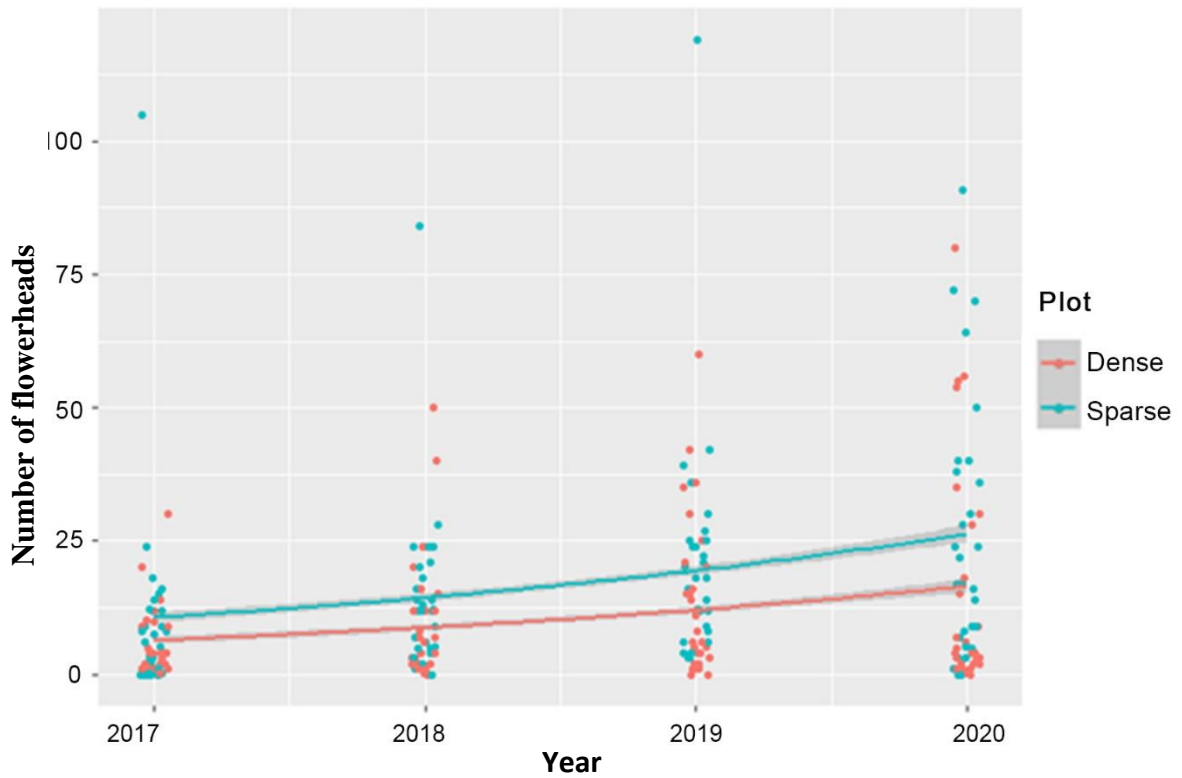
Figure 3.24 The number of flowerheads *P. compacta* individuals in Dense and Sparse plots produced across all three sub-sites in Agulhas. Sparse plots produced significantly more flowerheads than Dense plots.
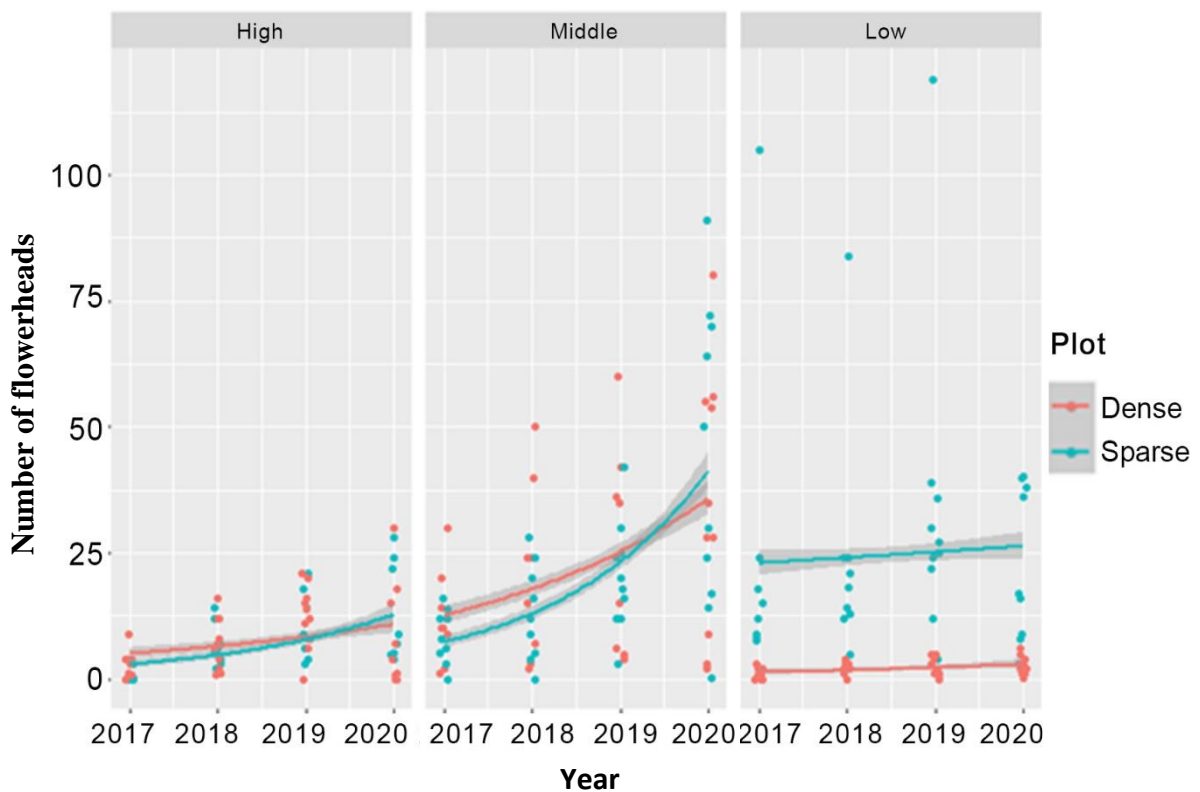
Figure 3.25 Number of flowerheads in Dense and Sparse plots separated into Low, Middle, and High elevation sub-sites. The Sparse plot at the Low elevation sub-site had significantly more flowerheads than the Dense plot.

3.4.2.2.3 Other plant traits

Maximum plant height

The Middle elevation sub-site had a significantly higher maximum height (m) of individuals compared to the Low and High sub-sites, with a mean height of 1.725 m (IQR = 0.335, H = 14.2, df = 2, $p < 0.001$; Figure 3.26a). No significant difference in height was found between the Low and High sub-sites ($\overline{X}$ = 1.38 m and 1.46 m, respectively). Individuals' maximum height of individuals in Dense plots were significantly taller ($\overline{X}$ = 1.58m), compared to Sparse plot individuals ($\overline{X}$ = 1.34, F = 6.3, df = 1. $p < 0.05$; Figure 2.26b).
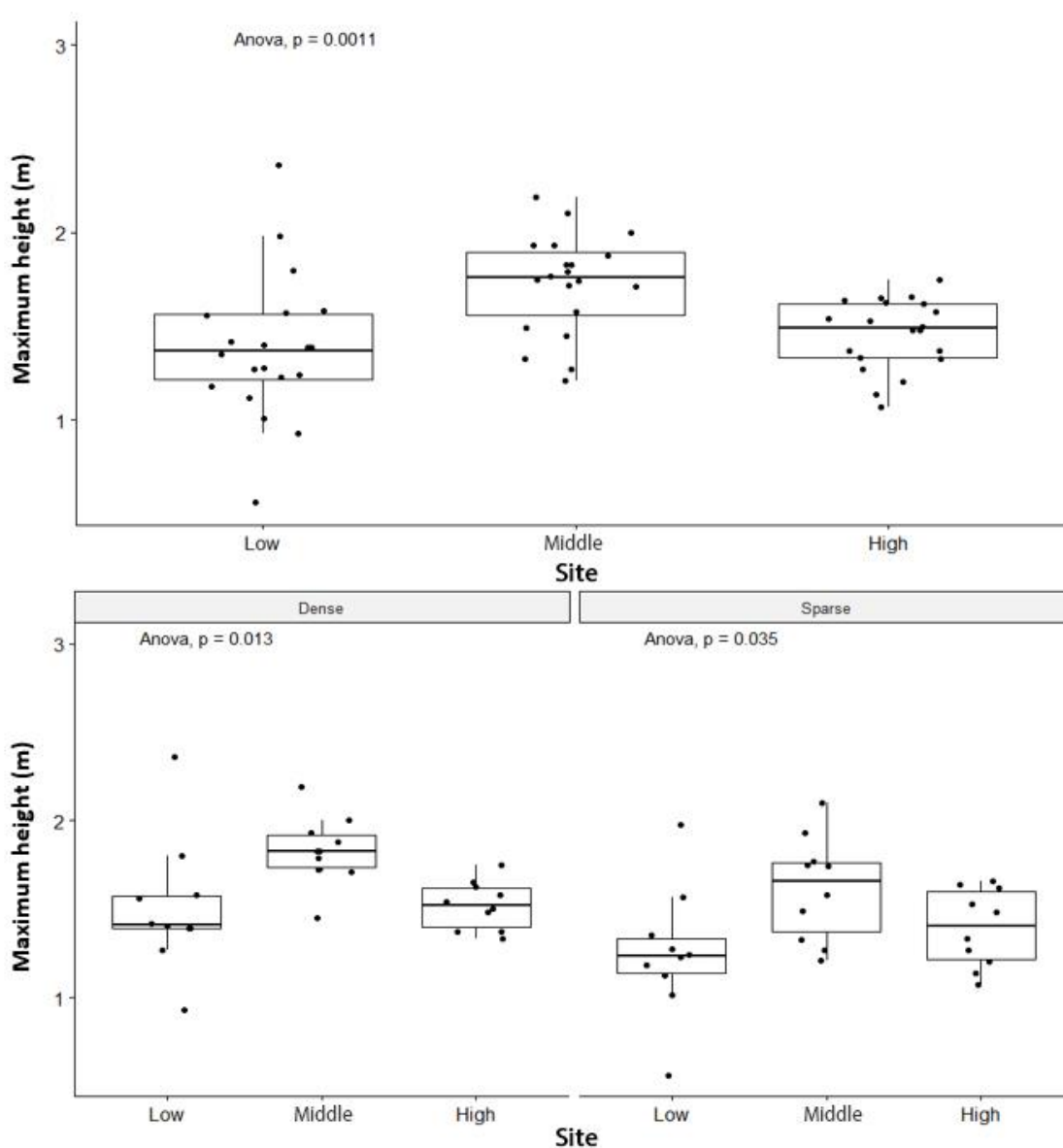
Figure 3.26 Maximum plant height (m) of *P. compacta* individuals (a) in High, Middle, and Low elevation sub-sites (b) maximum height differences in Dense and Sparse plots across all sub-sites in Agulhas.

Nearest neighbour distances (Population density proxy)

Nearest neighbour (intraspecific) distance was used as a proxy for measuring density of *P. compacta* individuals. These measurements were taken to confirm plots as 'Dense' and 'Sparse'. Overall, Dense plots were found to be significantly denser ($H = 21$, df = 1, $p < 0.001$), with a median of 1m between the individual and nearest neighbour (IQR = 1.5), whereas Sparse plots had a median of 3m (IQR = 2.17; Figure 3.27). The Dense plot at the Low elevation sub-site had a significantly higher density than the Sparse plot ($H = 14.4$, df = 1, $p < 0.001$) as well as the High elevation sub-site had a significant difference between Dense and Sparse plots ($H = 5.2$, df = 1, $p < 0.05$). The Dense and Sparse plots in the Middle elevation sub-site had an overall significance of $p = 0.052$ – though this is not theoretically significant, it has been taken as biologically significant.
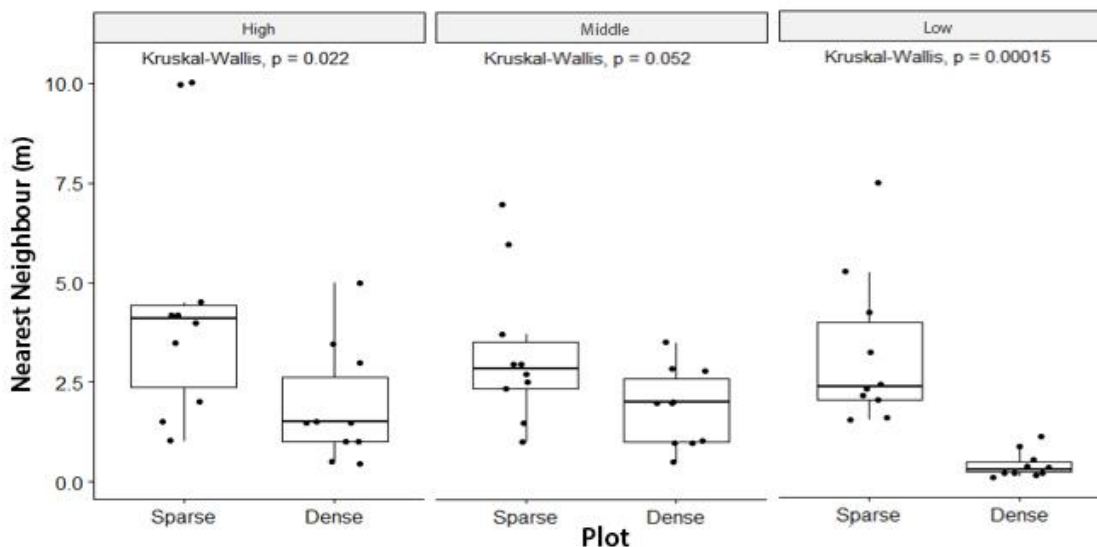
Figure 3.27 Nearest neighbour (in metres) was used as a proxy for density. Comparison between Dense and Sparse plots across High, Middle, and Low elevation sub-sites show that there is a significant difference in density between Dense and Sparse plots but also high variation.

Complexity of branching (monopodial - sympodial)

The Middle elevation sub-site had the highest occurrence of complex sympodial branching, meaning individuals at this sub-site had a multi-stemmed growth form ($H = 16.3$, df = 2, $p < 0.001$; Figure 3.28*a*). However, no significant difference was found between branching complexity in High and Low sub-sites. At the Low elevation sub-site, a significant difference was found between Dense and Sparse plots where the Sparse plot had complex branching and the Dense plot had monopodial growth and reduced branching ($H = 12.4$, df = 1, $p < 0.001$;

Figure 3.28*b*). Within the High and Middle elevation sub-sites, no significant difference in branching was found, however, the High sub-site had a close to significant difference ($p = 0.084$), with individuals found in the Dense plot, having slightly more complex branching.
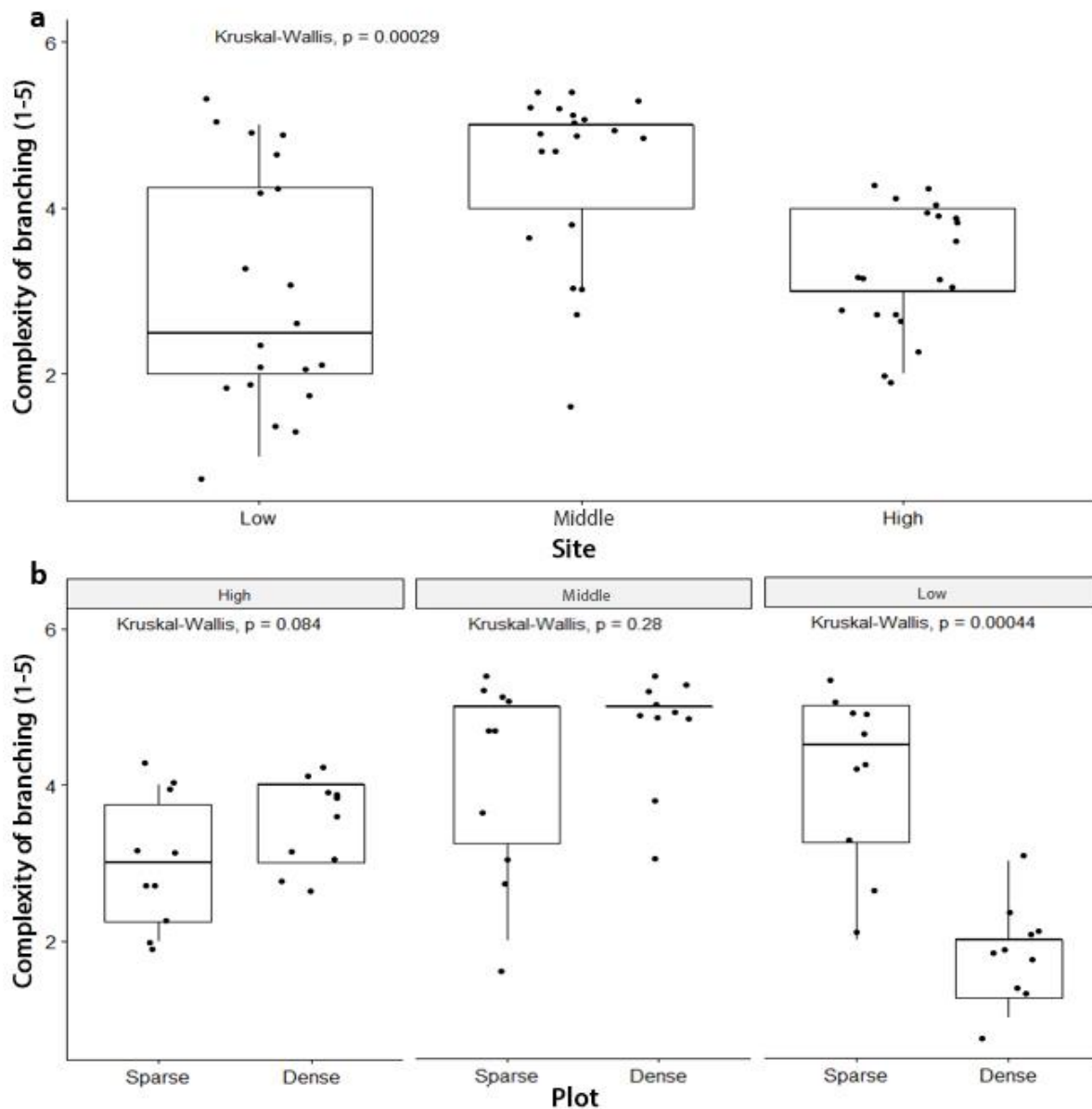
Figure 3.28 Branching complexity of *P. compacta* individuals in (a) High, Middle, and Low elevation sub-sites showed a significant difference in branching, with the Middle sub-site having a high number of individuals with complex branching. (b) Dense and Sparse plots in High, Middle, and Low sub-sites. The Low elevation sub-site showed significantly less branching in the Dense plot than the Sparse plot.

Witches' Broom (disease prevalence)

There was a significantly higher prevalence of Witches' Broom found in the Middle and Lower sub-sites ($H = 21.1$, df $= 2$, $p < 0.001$), with significantly less found at the High sub-site (Figure 3.29). There was no overall difference found between Dense and Sparse plots, however, there was less found at the High sub-site, with the Dense plot having more Witches' Broom than the Sparse. However, the Sparse plot had zero noted occurrences of Witches' Broom. The percent infection of individuals was documented, with the High sub-site having the least spread on individuals with Witches' Broom ($H = 21.1$, df $= 2$, $p < 0.001$) and no significant difference in severity or occurrence was found between Dense and Sparse plots.
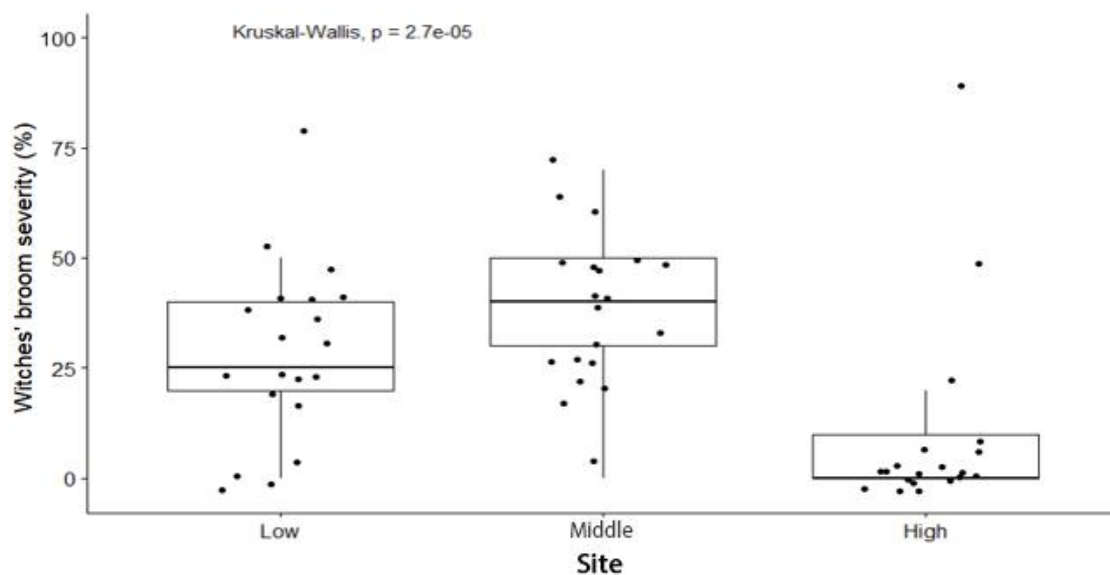
Figure 3.29 Witches' Broom (a *Phytoplasma* infection) was used to ascertain disease prevalence in the sub-site populations as percent of infection per individual (%). Severity of Witches' Broom was significantly worse in the Middle elevation sub-site with all individuals measured showing Witches' Broom, compared to Low and High sub-sites. The High elevation sub-site had the lowest rates of Witches' Broom compared to the other two sub-sites.

3.5   Discussion

The potential of assisted colonisation (AC) to reduce extinction risk has been interrogated from various angles in the literature, however, this work has mainly focused on the risks, ethics, and acceptability of this strategy (Richardson *et al*., 2009). This has led to a lack of empirical and mechanistic testing, meaning that the practical implementation of AC remains largely untested for plant species. Plant species range shifts are known to have been driven by

a changing climate in geological time (Oldfather & Ackerly, 2019), with large-scale vegetation change recorded globally during the terminal Pleistocene (Pickett *et al.*, 2004). The inference from these observations is that some parts of species ranges become unsuitable, while other parts that are unsuitable (marginal sites) become more suitable over time, resulting in geographic range shifts, particularly for well dispersed species. Prolonged climatic stability in areas like the CFR has led to high rates of endemism (Enquist *et al.*, 2019). Lower rates of historical climatic change, combined with topographic diversity and edaphic heterogeneity, are thought to be explanations for the evolution of anti-telechory, vicariance and disruptive evolution (Cowling & Pressey, 2001; Cramer *et al.*, 2014).

Theoretical understanding of range dynamics and what factors limit species' distributions may provide a meaningful framework for AC implementation, however the current lack of coherent understanding (Gaston, 2009; Kerr, 2020), presents a significant barrier to implementing AC with confidence.

Gaston (2009) notes that understanding the determinants of species distributional limits remains poorly integrated, partly due to the lag between theory and empirical studies. The dilemma facing AC suggests that this remains the case. To inform the implementation of AC, understanding species' range dynamics, including the processes governing growth and reproduction in bio-climatically optimal habitat ('core' sites) and bio-climatically sub-optimal habitat ('marginal' sites) is central. For AC implementation, translocating populations into marginal sites that are projected to become more suitable in the future seems to be the most reliable way to mimic autonomous range shift dynamics.

The Central-Peripheral Hypothesis (CPH), a classical theory, has generally been used to explain species range dynamics. It dictates that a species' abundance and suitability is highest at the core of their range and uniformly decreases towards the periphery of their ranges. Therefore, using the classical understanding of population dynamics, one can expect lower population densities, lower genetic variation, lower fitness and higher mortality in marginal habitats near the edge of species' distributions (Brown, 1984; Sagarin & Gaines, 2002). Subsequent studies have found that this hypothesis is more often not the case, with empirical support remaining weak – in fact, species ranges have been found to show more complex dynamic (Gaston, 2009; Pirnon *et al.*, 2017; Dallas *et al.*, 2017).

The design of AC implementation relies heavily on targeting currently marginal areas, therefore it's success would be strongly dictated by population dynamics in marginal sites,

with classical theory predictions suggesting that implementation will be challenging due to the reasons listed above. In this study, the results found for *P. compacta* did not fully align with classical theory.

Core populations of *P. compacta* were found to have higher density than those in marginal sites, aligning with predictions by classical theory, however individual vegetative growth and flowerhead production was found to be significantly lower which does not align with predictions. This could be attributed to the effects of dense stands and smaller intraspecific nearest neighbour distances on their growth form. These dense populations were found to favour monopodial growth form, with minimal branching observed. Reduced branching would mean a reduced number of terminal ends available to produce flowers. This finding is contrary to assumptions that core site individuals would tend to be larger and produce more flowerheads (Abeli *et al*., 2014).

Core sites which are associated with high habitat suitability, likely results in high seedling survivorship (Schupp, 1995; Bond & Midgley, 1995), and as demonstrated by Slingsby *et al.* (2017), drought post fire is a critical driver of seedling mortality. Therefore, the high density of *P. compacta* populations found in Kogelberg and Fernkloof are likely due to high habitat suitability promoting high survivorship of seedlings. With more seedlings able to establish in favourable conditions and density increasing, over time intraspecific competition would intensify (Richardson & Smiseth, 2017). Intraspecific competition has been found to be four to five-fold more intense for a given individual than interspecific competition (Adler *et al*., 2018). Combined with the natural tendency for *P. compacta* to grow in 'stands', this may be main the drivers responsible for the monopodial branching and lower flowerhead production. In fact, Watkinson (1980), found in a field manipulation experiment of a single species stand, that at a certain age and density, individuals displayed lower growth and reproductive outputs. Thus, the most likely explanation for *P. compacta* populations in core sites having lower flowerhead production and shoot growth is a monopodial branching pattern due higher intraspecific competition (Berntson & Wayne, 2000; Freschet *et al*., 2018), resulting from higher seedling survivorship after fire event-synchronised germination of seed populations that are concentrated spatially due to anti-telechory.

The converse was found in marginal sites, where lower seedling survivorship likely due to lower habitat suitability, results in lower intraspecific densities, and a form of competitive release that may allow for sympodial branching, and for their high growth and reproductive

output. Harder *et al.*, (2007), notes that from an evolutionary perspective, the role of vegetative growth is fundamentally to serve reproduction, therefore an individual's architecture should reflect this. However, this is compromised when there are conflicting vegetative and reproductive demands which may lead to vegetative characteristics that do not optimise photosynthetic capacity and resource distribution (Harder *et al.*, 2007). Therefore, this trade-off can lead to growth forms being less branched in dense populations and sparse individuals having more complex growth forms (Dudley & Schmitt, 1996).

Marginal sites are assumed to be exposed to adverse conditions, which can cause selection of individuals that are more locally adapted which can increase the phenotypic plasticity of marginal groups (Sexton *et al.*, 2009). *P. compacta* individuals in marginal sites display high phenotypic plasticity in growth form and complexity of branching which may be partly if not predominantly responsible for individuals yielding more flowerheads due to more available terminal ends. Also, *P. compacta* found at the High elevation sub-site in Agulhas had noticeably larger, broader leaves compared to individuals found in the low site (personal observation).

This raises interesting questions about the role local provenance may play in successful assisted colonisation implementation. Local provenance (i.e., seed sourcing) is an important step for ecological restoration work (Hancock & Hughes, 2014), and it most likely holds similar importance in the implementation of AC, however more exploration of this is needed. Seed sourcing from a species' marginal sites could offer higher adaptive capacity than core site genetic material (Vergeer & Kunin, 2013). However, this may not always be the case, and marginal populations can either become a source of speciation or become locally extinct (Levin, 1970; Abeli *et al.*, 2014).

Flowering across *P. compacta*'s range was found to be significantly different between core and marginal sites. Flowering was low in 2016 which aligns with findings that in higher temperatures, vegetative growth is favoured (Bezuidenhout, 2010). Following 2016, temperature decreased, and precipitation increased. This led to flowerhead production in Agulhas and Grootbos significantly increasing. However, no significant increase in flowerhead production in Kogelberg and Fernkloof was found. This further validates that reproduction in these studied core *P. compacta* sites are more strongly determined by density. However, with only two localities, more sites would need to be investigated to validate these findings.

Across *P. compacta*'s range, vegetative growth was found to be higher when temperature was higher. This finding aligns with my model prediction and previous studies' looking at a *P. compacta* hybrid, 'Pink Ice' (Bezuidenhout, 2010; Louw *et al*. 2015). Temperatures in 2015 and 2016 were significantly higher than preceding years. In 2016, all populations had higher growth responses, however, marginal sites Agulhas and Grootbos were found to have significantly higher growth than core sites Kogelberg and Fernkloof. In 2019, there was no significant difference in growth found between sites. This shows that *P. compacta* populations in core and marginal sites performed similarly in 'average' years but variance in growth response was found in adverse conditions. Kawecki (2008), notes that though marginal habitats can satisfy niche requirements most of the time, however, marginal sites have small safety margins which makes them more vulnerable to extinction. Bezuidenhout (2010), also found more within-group growth variation in higher temperature treatments (ambient +3.1°C) which is consistent with our findings in 2016.

Marginal *P. compacta* populations also exhibited higher occurrence of Witches' Broom, however the reason for this cannot be deduced in this study. It is suggested that as global temperatures increase the spread of pathogens will also spread (Garrett *et al*., 2006; Ahanger *et al*., 2013), which may indicate that some species may be more susceptible to disease in areas with lower environmental suitability.

Marginal sites do carry some risk for potential AC candidates, however, the results found in this study suggest microsite choices in marginal sites may have the ability to offset site unsuitability and increase likelihood of AC success. Contrary to classical theory, marginal parts of a species range may have an overall lower occupancy, however it is not uncommon to observe fragmentation of population structure (Gaston 2003; Gaston 2009; Yakimowski & Eckert, 2007). In Agulhas, differences in growth, reproduction and soil moisture were found between Low, Middle, and High elevation sub-sites and importantly within these sub-sites. Sparse plots were found to perform better than dense plots within elevation sub-sites, with growth and flowering higher in sparse plots.

Interestingly, dense plots in Agulhas (a marginal site) were found to have comparable trends to core site individuals, resulting in similar adverse impacts on branching and flowering. Low flowerhead production and monopodial branching was found in dense plots in Agulhas.

Growth rates were also low, resembling core sites. Soil moisture measurements in winter showed dense plots had significantly higher soil moisture content compared to sparse plots, indicating that dense plots may follow seep lines. Looking at *P. compacta* seedling strategy, Richards *et al*. (1995), found that they exploit early water availability by prioritising root length growth at the expense of water efficiency. This strategy changes at some point and adult *P. compacta* are extremely water efficient. The increase in resource availability allowed for the high survivorship. This indicates that microsites within Agulhas (marginal site), were similar to conditions found in the core site.

This is an important finding as it implies that careful and purposeful microsite choice could offset overall site unsuitability. However, this is problematic as it also means that predicting potential AC recipient sites is not as simple as using SDM suitability scores as a guideline. Therefore, this reaffirms the point that range dynamics are complex and therefore undertaking site selection is more challenging than classical CPH range theory suggests. Pironon *et al.* (2017) proposed a reframing of the CPH model, where instead of a uniform decrease of abundance and demographic performance from the distributions centre to periphery, they propose that it is more of an oscillating decrease from centre to periphery, with suitability and abundance varying over a smaller turnover but following the same overall pattern of decrease. The microhabitat findings in this study, though limited in sample size, appear to align with the Pironon *et al.* (2017) CPH reframing.

Soil temperature is often overlooked in studies even though its influence on biochemical reactions, germination and root growth is widely accepted (Thompson & Grime, 1983). Jacobs *et al*., (2011) found in a study spanning 27-years that soil temperature had increased by 1 °C in a Netherlands grassland. In this study, soil temperature was found to be warmer than air temperature and had a higher variance. Song *et al*. (2013), notes that asymmetric warming of air and soil could lead to complex effects on species adaptive strategies as they deal with different temperature interfaces above and below ground. The asymmetry found in this study could be exacerbated by sandy soil type, since soil type is known to play a role in heat flux and retention with dry sandy soils warming and cooling more rapidly compared to other soil types (Cellier & Robin, 1996). Vegetation density has also been found to play a role in soil and air temperatures (Song *et al*., 2013). Song *et al*. (2013), found that soil temperature tended to be lower with higher vegetation density. This is seen in the middle site, where the sparse plot is significantly warmer than the dense plot. However, the opposite is

found at the low site, where soil temperature was warmer in the dense plot. This may be due to gaps in the data from an ibutton malfunction or it suggests that there may be a quadratic function found where if *P. compacta* is too dense, it no longer buffers soil temperatures but increases it. However, further exploration into this is needed.

A potential pitfall of this study is the limited number of sites and replicates within sites. This means that results found in this Chapter may not be readily generalisable. However, this study does highlight the importance of understanding population and range dynamics when considering the implementation of AC. Furthermore, in the marginal and core site investigation, Kogelberg was the youngest site and in 2016 was six years old (full flowering maturity said to be seven years), so even though age was included as a random factor in analysis, the lack of flowers in that year could be age related. However, the same cannot be said for the other sites, for example, the Fernkloof population which is older than the Agulhas population however produced less flowerheads.

Differences in phenology were noted by the Protea Atlas project, with flowering historically peaking in May/June and currently peak flowering is found in August. Phenology may differ between core and marginal sites; however, this was not documented in this study. And personal observation of leaf size differences at the top site also indicates *P. compacta* has high plasticity/adaptive capacity. This highlights again the importance of the addition of traits into AC selection since favourable traits may allow for higher AC success. Furthermore, Bond *et al*. (1995), note that while population densities are often attributed to exogenous factors, endogenous factors may play a dominant role in fluctuations of the observed population densities of reseeders, in particular. The mechanism they identify also operates via self-regulating factors due to stand density feedback effects.

3.6   Conclusion

This chapter was able to demonstrate that *P. compacta* populations in marginal sites are still able to perform well in relation to core *P. compacta* populations. The high suitability of core sites suggests that the high survivorship of seedlings results in dense population stands which produce less flowerheads and have a lower individual seed set. Individuals in sparse marginal sites in Agulhas may not have high seedling survivorship, however, those that survive were

found to perform well. They were also found to have more sympodial structures and produced more flowerheads.

Marginal sites were found to have higher occurrence of disease, namely Witches' Broom, however core sites were found to have little to no Witches' Broom present. Denser plots in Agulhas were however found to have similar pitfalls to *P. compacta* populations found in the core range. Individuals found in dense plots were found to have less branching, and thus lower flowerhead production, and were found to have significantly higher soil moisture in winter, suggesting they follow natural seeps. This supports the observation of higher survivorship dense plots, most likely due to post-germination water availability. There is also risk with marginal sites experiencing adverse post-fire conditions that could impede seedling establishment, however, the variation found in performance, temperature and soil moisture in Agulhas suggests that microclimatic positioning within a marginal site could potentially offset unsuitability and mitigate risk however, it is likely that there are more factors that aid or abed plant performance in marginal sites and warrants further investigation. It is important to note that the results found in this study cannot be generalised since it looks at one species, however it does provide valuable insight into considerations for successful AC implementation. Careful ecological consideration is needed when choosing recipient sites for species, as complex range and population dynamics pose a major challenge to implementing AC with confidence. Therefore, more mechanistic, and empirical testing is needed to guide AC decision-making.

4 Synthesis: Assisted Colonisation as a Strategy to Reduce Extinction Risk for Western Cape Proteaceae

4.1 Background

Anthropogenic impacts such as land fragmentation, habitat degradation and climate change are leading drivers of floral and faunal biodiversity loss (Parmesan, 2006; Bellard *et al*., 2012). Despite the widespread recognition of their adverse impacts, climate change trends and anthropogenic impacts have continued to intensify in the past few decades (IPBES, 2019), and international efforts to reduce greenhouse gas emissions remain inadequate to limit global warming to below 3°C during the course of this century (Christiansen *et al*., 2018). Several efforts to project the impacts on biodiversity conclude that such levels of warming are likely to cause substantial rates of species extinctions (IPCC, 2014; Urban *et al.*, 2016; Warren *et al*., 2018), particularly in areas of high endemic diversity (Enquist *et al*., 2019). This is because endemic species may lack the capacity to tolerate rapid shifts in climatic conditions and may be unable to adequately track climate change through range shifts (IPCC, 2014).

Shifts in species distributions which are consistent with and attributable to climate change have already been documented (Parmesan, 2006; Parmesan & Yohe, 2003; Rumpf *et al*., 2018). Based on these observations of species responses and modelling of species ranges using SDM approaches (Thuiller *et al*., 2008), conservation strategies are being developed that will increase the likelihood of reducing species extinctions (Hannah *et al*., 2002) However, such strategies also recognise the need for active interventions that go beyond the passive efforts to expand protected areas to permit species range shifts (Hannah *et al*. 2020). This is due to the fact that some proportion of indigenous and endemic biota appear to lack the capacity to adapt *in situ*, or to shift their geographical range because of dispersal and establishment limitations (Foden *et al*., 2013). Therefore, widely accepted and implemented conservation practices aimed at supporting the adaptive capacity of species (e.g., Hannah *et al*., 2002) may require adjustments to account for the fact that there are already signs of the velocity of climate change exceeding species' ability to adapt *in situ* or autonomously migrate (Prober *et al*., 2019; Foden *et al*., 2013).

There appears to be some fraction of wild species that are projected to be at high risk of extinction due to climate change and anthropogenic impacts, with little prospect for

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persistence in the wild (Hannah *et al.,* 2002, von Maltitz *et al*., 2006). For such species, *ex situ* interventions would permit the conservation of their genetic material at the least. However, between this group of *ex situ* candidates, and species able to adapt naturally via range shifts and natural selection, there is a group whose persistence in the wild is largely limited due to dispersal limitations. The potential of an alternative active interventionist strategy for such species, termed assisted colonisation (AC, and also often referred to as assisted translocation or assisted migration), has long been discussed in the literature with regard to climate change adaptation. The strategy is aimed at moving species from their current range into their future predicted areas in order to reduce climate change extinction risk (Hough-Guldberg *et al*., 2008; Hewitt *et al*., 2011).

Africa is thought to be particularly vulnerable to anthropogenic temperature increases, with the observed rate of temperature change nearly double the global average (Archer *et al*., 2018), and current trends projected to continue even with reasonable mitigation efforts (Osborn & Jones, 2014; Davis *et al*., 2017). Areas of high diversity with restricted range endemics are likely to support a high proportion of species that could be candidates for AC, as discussed in Chapter 1 of this thesis. The Cape Floristic Region (CFR) is a hyper-diverse area at the Southern tip of Africa with almost 9000 species in a ~ 90 000km^2, with many having limited dispersal capabilities and restricted ranges, including the iconic Proteaceae family (Goldblatt & Manning, 2002; Allsopp *et al*., 2014). Previous assessments of climate change vulnerability using Proteaceae (Midgley *et al*., 2006), have indicated that a significant proportion of endemic species are at risk of range shifts, and possibly entire range displacements, under anthropogenic climate scenarios projected by the end of the century (van Wilgen *et al*., 2015). The ability of many species to track the climate is constrained by anti-telechory (short-range seed dispersal), which appears to have evolved under the intermediate fire return interval of this vegetation type (Whelan, 1986). Dispersal is thus not only spatially constrained, but also limited to only a few events per century. As a consequence, species community compositional changes appear to show a climatic lag (Slingsby *et al*., 2017), as roughly decadal fires can lead to punctuated shifts in community compositions when juveniles fail to establish in novel environments.

The Proteaceae is the largest Fynbos family and has been extensively documented, with large amounts of distributional and trait data available (Foden & Rebelo, *unpublished*). As a dominant life form in the Fynbos Biome, many of its species support and underpin keystone

ecological processes (Collins & Rebelo, 1987; Cowling & Holmes, 1992). This combined with its prominence in the international cut flower industry (Turpie *et al.*, 2003), make Proteaceae an attractive study family for the potential for implementing AC, which could play an important role in reducing their extinction risk. However, to date, a detailed assessment of the potential and risk of this interventionist strategy has not been conducted in the context of the CFR.

SDM approaches have allowed for proactive, rather than reactive conservation planning (Pereira *et al.*, 2010), providing snapshots into what species assemblages may look like if species are able to colonise under various climatic scenarios. It has been especially useful in informing the expansion of protected areas (Hannah *et al.*, 2020) and by analysing such data over multiple time steps, this approach can help in identifying geographic "chains" of sites, creating a network of sites that support range adjustment over time (Williams *et al.*, 2005; Phillips *et al.*, 2018). In chapter 2 of this thesis, I applied this approach using a dataset of SDMs of 191 Proteaceae species (obtained from SPARC) to identify potential AC candidates. However, tests of the successful implementation of AC for plants remain scarce (Hällfors *et al.*, 2017; Prober *et al.*, 2019), and a number of significant objections and concerns about the cost and viability of this strategy have been raised.

Monzón *et al.* (2011), expressed the view that the rate and scale of climate change exposes a lack of knowledge about ecosystems, communities, and species range dynamics; if so, active intervention via range dynamics remains highly experimental. Even if strong candidates for AC can be identified, there are numerous questions that emerge around the practical implementation of the strategy. These relate to considerations of hybridisation risk, but pragmatically, as identified in the hypotheses of Chapter 3 of this thesis, a number of questions can be raised about the ecological viability of translocated populations.

To deepen our understanding and progress with implementation of AC, investigating the physiological and population level factors underpinning range dynamics becomes critical. Given that recipient sites are likely to be marginal or, at best, sub-optimal, in terms of climatic suitability, the following key questions can be raised: Can viable populations of an AC candidate be established in sub-optimal sites? Is their growth and reproductive output compromised under sub-optimal conditions? Are they more susceptible to pests and diseases under such conditions?

While answers to such questions are critical for a clear assessment of the potential value of AC, not only for Fynbos Proteaceae but more broadly for the strategy as a whole, a credible test of the approach in well-controlled experimental situation would require a large investment of time and resources. The selection of *P. compacta* as a study species in this thesis allows a partial assessment of some key questions in sites in which the species had been artificially planted for wildflower production. This is because the species was planted in at least two sites representing sub-optimal growing conditions, or as referred to in this thesis as 'marginal'. After abandonment of these farmed populations, they have since naturalised in these sites and appear to have self-maintained ecologically through a number of life cycles. Furthermore, the exploration of individual growth and flowerhead production at a finer spatial scale, representing a range of sub-habitats within one of these sub-optimal sites, tests further the generality of the findings, and provides insights into site-specific introduction strategies for AC purposes.

4.2   Main Findings

4.2.1   Identifying Suitable Candidate Species in the Proteaceae for Future Assisted Colonisation Adaptation Responses

Traditional conservation strategies are geared towards building the adaptive capacity of species in the wild, but for species that have limited dispersal capabilities and restricted ranges, there are already signs that the velocity of climate change is exceeding their ability to adapt *in situ* or to track their preferred bioclimatic conditions via range migration. Such species are commonly projected to face extinction in the absence of targeted intervention. Assisted colonisation (AC) has long been suggested as a response aimed at aiding species to shift their distributions and enhance the chances of persistence within their future projected suitable range. Assisted colonisation may be most relevant in biodiversity hotspots, characterised by range restricted species with limited dispersal capacity, and thus could play an important role in reducing extinction risk of endemic species in the Cape Floristic Region (CFR). The CFR is a hyper-diverse region with high numbers of endemic species, many of which have been identified as vulnerable to projected anthropogenic climate change, however, a detailed assessment of the potential of AC in the context of the CFR has not yet been done. A hierarchical analysis using a combination of SDM-based spatial metrics and species life-history traits was conducted to test if AC would be a suitable intervention

strategy for 191 Proteaceae species. The analysis highlighted 31 suitable AC candidates, 14 of which would require sustained intervention up to 2070 at least, 7 that would require short-term intervention (over the next three decades), and 11 for whom successful intervention beyond 2040 is dependent on aggressive climate change mitigation efforts. Furthermore, AC was found to be an unnecessary intervention strategy for 141 Proteaceae species. These species were evaluated and classified as likely persisters, potential persisters and non-persisters depending on their relative range loss and gain. Between 79 -126 species regarded as non-persisters were identified as requiring alternative intervention, depending on the time-period in question, while 45-57 species were identified as likely persisters and require no targeted intervention for climate change adaptation beyond the maintenance of the current protected area network.

Candidates' range shifts identified over a single 6-decade period (current-2070) vs. two successive 3-decade periods (current-2040 and 2040-2070) revealed significantly more species classified as highly vulnerable in the current-2070 period. This demonstrates that a consideration of finer time scales widens the scope for identifying AC candidates and highlights the importance of timely action to reduce extinction risk of several species. AC appears, based on these theoretical criteria, to be a viable conservation strategy for some Proteaceae.

4.2.2   Growth and Reproductive Performance of *P. compacta* in Marginal and Core Populations

This chapter tested one of the main implicit assumptions of successful AC, namely that viable populations can be successfully established in sites of marginal suitability (likely to be found near the edges of species' distributions) where conditions are projected to become more suitable with progressive climate change. The choice of *Protea* compacta, a species historically planted and harvested for the cut flower industry, provided a valuable opportunity to explore this assumption, since it has been planted and artificially established in at least two sites currently determined to have sub-optimal bioclimatic suitability in comparison to the identified core of its geographic range. They also suggest that microhabitat variation could be used to buffer introduced populations in marginal sites against adverse climatic events.

Surprisingly, measurements of vegetative growth and reproductive performance in two core and two marginal sites showed higher growth rates and flowerhead production at individual-level in marginal sites. This pattern appears to be a result of individuals being released from strong intraspecific competition, which allowed more widely spaced individuals (less dense) to produce more branched growth forms with greater numbers of terminal shoots available for flowerhead production, and likely greater potential rates of shoot growth. On the other hand, higher disease susceptibility was noted in the two sub-optimal sites, indicating that these populations might be susceptible to diminished performance if this susceptibility were to become more prevalent.

The observed high densities of individuals with monopodial growth forms in core sites is likely due to high rates of seedling survival post-fire. This pattern was repeated at finer spatial scale in the more detailed study of one of the marginal sites, where locally high population densities and similar monopodial growth forms were found in wetter microhabitats. These findings suggest that the relaxation of strong effects from intraspecific competition in establishing populations in marginal bioclimatic conditions may compensate for lower population densities, supporting population establishment and in this case, favouring the practical implementation of AC in species like Proteaceae with strong density-dependent feedback.

The generalisation of these findings beyond *P. compacta* or even beyond the Proteaceae remains unclear; nonetheless this study identified some critical questions for those advocating AC approaches and even those who assume autonomous range shifts of plant species provide a safeguard against climate change. Such questions include how population dynamics in marginal areas enhance or reduce species' range shifts, what mechanisms underpin the limitations of species ranges, and what mechanisms permit plant species to occupy areas of range that are not ideal, but nonetheless support viable populations.

4.3   Implications for Implementation

4.3.1   Identifying Suitable Candidate Species in the Proteaceae for Future Assisted Colonisation Adaptation Responses

The results of this study suggest that AC could be a viable option for some Proteaceae species. The list of species identified as of concern need further investigation and would

likely benefit from *ex situ* conservation. It also suggests that timeous action would increase the survival rate of species. When assessing species on a longer timescale (current to 2070), there are far fewer species identified as suitable for this conservation strategy and far more identified as of concern. However, if candidate species reach target areas by 2040, the overall survival rate of species is much higher than if intervention is delayed, an outcome that may be extremely valuable in a scenario of climate change "overshoot".

The methodology used in this thesis could be applied for a multitude of species and genera. The addition of a trait-based analysis allowed for species that were classified as probable candidates to become strong candidates since their high establishment and colonisation traits made them more likely to be successful. This also resulted in some initially strong candidates being excluded due to extremely unfavourable traits. Therefore, trait consideration is an important addition to the protocol developed by Hällfors *et al.* (2017) to maximise the chances of a higher success rate of AC and increase the efficiency of the species selection. This study had access to extensive trait data, but generally this is not available for many species. Nonetheless, the simple binary system on which the trait analysis is based allows for a wide range of trait information to be included, including the option of adjusting the number of traits according to what is available. The division of candidates into Sustained intervention, Short-term intervention and Mitigation dependent is a novel categorisation, and illustrates how different degrees of intervention can be determined. This enables better future planning of intervention and makes calculating associated costs easier for conservationists and funders.

Prober *et al*. (2019), has introduced the notion of conservation objectives evolving from restoration-focused to ecological renovation-focused. Restoration implies restoring something to a historical state, however, this becomes increasingly difficult to attain as climate change progresses and species ranges shift (Thomas, 2011). In order to reduce biodiversity loss, this kind of paradigm shift may support wider application of AC approaches.

4.3.2 Growth and Reproductive Performance of *P. compacta* in Marginal and Core Populations

Some novel insights were gained into how AC may be implemented. This part of the study raised some less-explored aspects around range dynamics in the context of AC application.

This study was able to show that marginal sites of *P. compacta* could effectively sustain introduced *P. compacta* populations, and though several implications emerged. Marginal site populations were found to be more susceptible to disease, which makes this a necessary consideration for translocated AC candidates. An unexpected result was found at marginal sites, with individuals showing higher flowerhead production compared to core sites. This suggests that, contrary to initial expectations, reduction in apparent bioclimatic suitability may not always result in lower individual plant performance. The variation in performance found across distinct microhabitats in the marginal site, Agulhas also revealed that the use of microclimatic conditions within marginal sites could buffer AC candidates against unfavourable climatic conditions. Finally, plasticity and adaptive capacity in stem growth and branching likely contributed to *P. compacta*'s success in marginal, adverse conditions - this further confirms the need to include species traits in AC candidate selection.

These findings extend beyond their immediate utility for AC implementation practices and can also inform more traditional ecological restoration practices. As one example, the persistence of rare species could potentially benefit from targeted establishment in microhabitats that could buffer them against unsuitable conditions.

4.4   Future Research

Assisted Colonisation (AC) has long been discussed in the literature, however, there is a lack of empirical information about its practical implementation. The many knowledge gaps about its feasibility are a barrier to the potential testing and implementation of this strategy. This study aimed to provide a preliminary assessment of AC in the CFR context, but can also provide a foundation on which other research can be built.

Future research could include performing this candidate identification approach on other taxonomic groupings that have restricted ranges and limited dispersal capabilities, or even other biodiversity hotspots. Since this is a pioneer study testing how AC could be implemented in the context of the CFR, several areas of the methodology could be expanded and improved.

For example, the exploration of land-use and recipient site suitability could have been quantified using certain landscape metrics (e.g., patch size and patch connectivity) and incorporated as spatially-based metrics. This method not only identifies suitable AC

candidates, but it also enables a vulnerability assessment to be performed. Species that are flagged as potential persisters could be further studied to confirm whether they need targeted intervention. These species could also be used as an early warning system with trends indicating progression of environmental change.

Investigating marginal and core sites provided a novel basis for how AC could be implemented in the future, but more research is needed to validate these findings beyond the single species studied for this purpose. The use of *P. compacta* did successfully highlight several aspects of range dynamics that should be rigorously tested, and more species would need to be investigated for these responses in order to provide a more generalised conclusion of how to implement AC more broadly.

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Appendix A

List of the 191 Proteaceae species used in this this study.

	Species names		Species names
1	*Aulax pallasia*	52	*Leucadendron teretifolium*
2	*Aulax umbellata*	53	*Leucadendron thymifolium*
3	*Brabejum stellatifolium*	54	*Leucadendron tinctum*
4	*Diastella buekii*	55	*Leucadendron verticillatum*
5	*Diastella divaricata*	56	*Leucospermum arenarium*
6	*Diastella fraterna*	57	*Leucospermum bolusii*
7	*Diastella parilis*	58	*Leucospermum catherinae*
8	*Diastella proteoides*	59	*Leucospermum conocarpodendron*
9	*Diastella thymelaeoides*	60	*Leucospermum cordifolium*
10	*Leucadendron album*	61	*Leucospermum erubescens*
11	*Leucadendron argenteum*	62	*Leucospermum gracile*
12	*Leucadendron brunioides*	63	*Leucospermum heterophyllum*
13	*Leucadendron burchellii*	64	*Leucospermum hypophyllocarpodendron*
14	*Leucadendron chamelaea*	65	*Leucospermum lineare*
15	*Leucadendron cinereum*	66	*Leucospermum muirii*
16	*Leucadendron concavum*	67	*Leucospermum mundii*
17	*Leucadendron conicum*	68	*Leucospermum parile*
18	*Leucadendron coniferum*	69	*Leucospermum patersonii*
19	*Leucadendron cordatum*	70	*Leucospermum pedunculatum*
20	*Leucadendron coriaceum*	71	*Leucospermum pluridens*
21	*Leucadendron corymbosum*	72	*Leucospermum praecox (fixed)*
22	*Leucadendron daphnoides*	73	*Leucospermum praemorsum*
23	*Leucadendron diemontianum*	74	*Leucospermum prostratum*
24	*Leucadendron dregei*	75	*Leucospermum reflexum*
25	*Leucadendron dubium*	76	*Leucospermum rodolentum*
26	*Leucadendron elimense*	77	*Leucospermum secundifolium*
27	*Leucadendron eucalyptifolium*	78	*Leucospermum spathulatum*
28	*Leucadendron floridum*	79	*Leucospermum tomentosum*
29	*Leucadendron foedum*	80	*Leucospermum tottum*
30	*Leucadendron galpinii*	81	*Leucospermum truncatulum*
31	*Leucadendron glaberrimum*	82	*Leucospermum vestitum*
32	*Leucadendron globosum*	83	*Leucospermum winteri*
33	*Leucadendron gydoense*	84	*Mimetes arboreus*
34	*Leucadendron lanigerum*	85	*Mimetes argenteus*
35	*Leucadendron laxum*	86	*Mimetes capitulatus*
36	*Leucadendron levisanus*	87	*Mimetes fimbriifolius*
37	*Leucadendron linifolium*	88	*Mimetes hirtus*
38	*Leucadendron loranthifolium*	89	*Mimetes hottentoticus*
39	*Leucadendron modestum*	90	*Mimetes palustris*
40	*Leucadendron nervosum*	91	*Mimetes pauciflorus*
41	*Leucadendron nitidum*	92	*Mimetes saxatilis*
42	*Leucadendron platyspermum*	93	*Mimetes splendidus*
43	*Leucadendron procerum*	94	*Orothamnus zeyheri*
44	*Leucadendron pubescens*	95	*Paranomus abrotanifolius*
45	*Leucadendron rubrum*	96	*Paranomus bolusii*
46	*Leucadendron salignum*	97	*Paranomus centaureoides*
47	*Leucadendron sericeum*	98	*Paranomus dispersus*
48	*Leucadendron sessile*	99	*Paranomus longicaulis*
49	*Leucadendron spissifolium*	100	*Paranomus roodebergensis*
50	*Leucadendron stellare*	101	*Paranomus sceptrum-gustavianus*
51	*Leucadendron strobilinum*	102	*Paranomus spathulatus*

	Species names			Species names
103	*Paranomus spicatus*		148	*Serruria candicans*
104	*Paranomus tomentosus*		149	*Serruria cyanoides*
105	*Protea acaulos*		150	*Serruria decipiens*
106	*Protea acuminata*		151	*Serruria decumbens*
107	*Protea angustata*		152	*Serruria effusa*
108	*Protea aspera*		153	*Serruria elongata*
109	*Protea aurea*		154	*Serruria fasciflora*
110	*Protea burchellii*		155	*Serruria flagellifolia*
111	*Protea caespitosa*		156	*Serruria flava*
112	*Protea compacta*		157	*Serruria florida*
113	*Protea convexa*		158	*Serruria fucifolia*
114	*Protea coronata*		159	*Serruria furcellata*
115	*Protea cryophila*		160	*Serruria glomerata*
116	*Protea cynaroides*		161	*Serruria heterophylla*
117	*Protea decurrens*		162	*Serruria hirsuta*
118	*Protea denticulata*		163	*Serruria inconspicua*
119	*Protea effusa*		164	*Serruria incrassata*
120	*Protea glabra*		165	*Serruria kraussii*
121	*Protea grandiceps*		166	*Serruria leipoldtii*
122	*Protea lacticolor*		167	*Serruria linearis*
123	*Protea laurifolia*		168	*Serruria meisneriana*
124	*Protea lepidocarpodendron*		169	*Serruria millefolia*
125	*Protea longifolia*		170	*Serruria nervosa*
126	*Protea lorea*		171	*Serruria pinnata*
127	*Protea montana*		172	*Serruria reflexa*
128	*Protea nitida*		173	*Serruria rosea*
129	*Protea obtusifolia*		174	*Serruria roxburghii*
130	*Protea odorata*		175	*Serruria rubricaulis*
131	*Protea pityphylla*		176	*Serruria trilopha*
132	*Protea punctata*		177	*Serruria triternata*
133	*Protea recondita*		178	*Serruria villosa*
134	*Protea repens*		179	*Sorocephalus capitatus*
135	*Protea restionifolia*		180	*Spatalla barbigera*
136	*Protea rupicola*		181	*Spatalla caudata*
137	*Protea scabra*		182	*Spatalla colorata*
138	*Protea scolymocephala*		183	*Spatalla curvifolia*
139	*Protea scorzonerifolia*		184	*Spatalla longifolia*
140	*Protea stokoei*		185	*Spatalla mollis*
141	*Protea subulifolia*		186	*Spatalla prolifera*
142	*Protea susannae*		187	*Spatalla propinqua*
143	*Protea venusta*		188	*Spatalla racemosa*
144	*Serruria adscendens*		189	*Spatalla setacea*
145	*Serruria aemula*		190	*Spatalla squamata*
146	*Serruria bolusii*		191	*Spatalla tulbaghensis*
147	*Serruria brownii*			

Appendix B

Species list of strong and probable AC candidates which occur in at least one of the analysed time periods (current-2040, 2040-2070, current- 2070).

	Classification	Species name		Classification	Species name
1	Strong	*Diastella proteoides*	26	Probable	*Leucospermum prostratum*
2	Strong	*Leucadendron concavum*	27	Probable	*Leucospermum truncatulum*
3	Strong	*Leucadendron coriaceum*	28	Probable	*Mimetes splendidus*
4	Strong	*Leucadendron corymbosum*	29	Probable	*Paranomus bolusii*
5	Strong	*Leucadendron lanigerum*	30	Probable	*Protea coronata*
6	Strong	*Leucadendron laxum*	31	Probable	*Protea glabra*
7	Strong	*Leucadendron modestum*	32	Probable	*Protea repens*
8	Strong	*Leucospermum arenarium*	33	Probable	*Protea restionifolia*
9	Strong	*Leucospermum mundii*	34	Probable	*Protea scabra*
10	Strong	*Leucospermum parile*	35	Probable	*Serruria aemula*
11	Strong	*Leucospermum praemorsum*	36	Probable	*Serruria candicans*
12	Strong	*Leucospermum spathulatum*	37	Probable	*Serruria effusa*
13	Strong	*Paranomus roodebergensis*	38	Probable	*Serruria elongata*
14	Strong	*Paranomus spathulatus*	39	Probable	*Serruria flagellifolia*
15	Strong	*Protea burchellii*	40	Probable	*Serruria reflexa*
16	Strong	*Protea lorea*	41	Probable	*Spatalla colorata*
17	Strong	*Serruria flava*	42	Probable	*Spatalla racemosa*
18	Strong	*Serruria leipoldtii*	43	Strong	*Diastella fraterna*
19	Strong	*Serruria linearis*	44	Strong	*Leucospermum pluridens*
20	Probable	*Leucadendron chamelaea*	45	Strong	*Spatalla curvifolia*
21	Probable	*Leucadendron cordatum*	46	Strong	*Spatalla squamata*
22	Probable	*Leucadendron elimense*	47	Probable	*Paranomus longicaulis*
23	Probable	*Leucadendron teretifolium*	48	Probable	*Serruria decipiens*
24	Probable	*Leucospermum cordifolium*	49	Probable	*Serruria millefolia*
25	Probable	*Leucospermum gracile*	50	Probable	*Spatalla barbigera*

Appendix C

Species list of possible and unsuitable species and their corresponding persistence in current to 2040 and 2040 to 2070.

	Time-step	Species names	Classification	Persistence Ability
1	Current-2040	*Aulax pallasia*	Unsuitable	Non-Persisters
2	Current-2040	*Aulax umbellata*	Possible	Non-Persisters
4	Current-2040	*Diastella buekii*	Unsuitable	Potential Persisters
5	Current-2040	*Diastella divaricata*	Unsuitable	Non-Persisters
6	Current-2040	*Diastella fraterna*	Possible	Non-Persisters
7	Current-2040	*Diastella parilis*	Unsuitable	Potential Persisters
9	Current-2040	*Leucadendron album*	Unsuitable	Non-Persisters
10	Current-2040	*Leucadendron argenteum*	Unsuitable	Non-Persisters
12	Current-2040	*Leucadendron burchellii*	Unsuitable	Non-Persisters
13	Current-2040	*Leucadendron cinereum*	Possible	Potential Persisters
14	Current-2040	*Leucadendron conicum*	Unsuitable	Non-Persisters
17	Current-2040	*Leucadendron diemontianum*	Unsuitable	Non-Persisters
18	Current-2040	*Leucadendron dregei*	Unsuitable	Non-Persisters
19	Current-2040	*Leucadendron dubium*	Unsuitable	Non-Persisters
20	Current-2040	*Leucadendron eucalyptifolium*	Unsuitable	Non-Persisters
24	Current-2040	*Leucadendron glaberrimum*	Unsuitable	Non-Persisters
25	Current-2040	*Leucadendron globosum*	Unsuitable	Non-Persisters
26	Current-2040	*Leucadendron gydoense*	Unsuitable	Non-Persisters
30	Current-2040	*Leucadendron nervosum*	Unsuitable	Non-Persisters
31	Current-2040	*Leucadendron nitidum*	Unsuitable	Non-Persisters
32	Current-2040	*Leucadendron platyspermum*	Unsuitable	Non-Persisters
34	Current-2040	*Leucadendron pubescens*	Unsuitable	Potential Persisters
35	Current-2040	*Leucadendron rubrum*	Unsuitable	Potential Persisters
41	Current-2040	*Leucadendron strobilinum*	Unsuitable	Non-Persisters
43	Current-2040	*Leucadendron tinctum*	Possible	Non-Persisters
46	Current-2040	*Leucospermum catherinae*	Possible	Non-Persisters
51	Current-2040	*Leucospermum lineare*	Possible	Non-Persisters
53	Current-2040	*Leucospermum patersonii*	Unsuitable	Non-Persisters
55	Current-2040	*Leucospermum pluridens*	Possible	Non-Persisters
57	Current-2040	*Leucospermum reflexum*	Unsuitable	Non-Persisters
59	Current-2040	*Leucospermum secundifolium*	Unsuitable	Non-Persisters
60	Current-2040	*Leucospermum tomentosum*	Possible	Non-Persisters
61	Current-2040	*Leucospermum tottum*	Unsuitable	Non-Persisters
62	Current-2040	*Leucospermum vestitum*	Possible	Non-Persisters
63	Current-2040	*Leucospermum winteri*	Possible	Non-Persisters
64	Current-2040	*Mimetes arboreus*	Unsuitable	Non-Persisters
65	Current-2040	*Mimetes argenteus*	Unsuitable	Non-Persisters
66	Current-2040	*Mimetes capitulatus*	Unsuitable	Non-Persisters
67	Current-2040	*Mimetes fimbriifolius*	Unsuitable	Potential Persisters
69	Current-2040	*Mimetes hottentoticus*	Unsuitable	Non-Persisters
70	Current-2040	*Mimetes palustris*	Unsuitable	Non-Persisters
71	Current-2040	*Mimetes pauciflorus*	Unsuitable	Non-Persisters
73	Current-2040	*Orothamnus zeyheri*	Unsuitable	Non-Persisters
74	Current-2040	*Paranomus abrotanifolius*	Possible	Non-Persisters
75	Current-2040	*Paranomus centaureoides*	Unsuitable	Non-Persisters
76	Current-2040	*Paranomus dispersus*	Possible	Non-Persisters
77	Current-2040	*Paranomus longicaulis*	Possible	Non-Persisters
78	Current-2040	*Paranomus sceptrum-gustavianus*	Unsuitable	Non-Persisters

	Time-step	Species names	Classification	Persistence Ability
79	Current-2040	*Paranomus spicatus*	Unsuitable	Non-Persisters
80	Current-2040	*Paranomus tomentosus*	Unsuitable	Non-Persisters
82	Current-2040	*Protea acuminata*	Unsuitable	Non-Persisters
84	Current-2040	*Protea aspera*	Unsuitable	Potential Persisters
85	Current-2040	*Protea aurea*	Possible	Non-Persisters
86	Current-2040	*Protea caespitosa*	Unsuitable	Non-Persisters
88	Current-2040	*Protea convexa*	Unsuitable	Non-Persisters
89	Current-2040	*Protea cryophila*	Unsuitable	Non-Persisters
93	Current-2040	*Protea effusa*	Unsuitable	Non-Persisters
94	Current-2040	*Protea grandiceps*	Unsuitable	Non-Persisters
95	Current-2040	*Protea lacticolor*	Unsuitable	Non-Persisters
96	Current-2040	*Protea laurifolia*	Unsuitable	Potential Persisters
97	Current-2040	*Protea lepidocarpodendron*	Possible	Potential Persisters
99	Current-2040	*Protea montana*	Unsuitable	Non-Persisters
100	Current-2040	*Protea nitida*	Unsuitable	Potential Persisters
103	Current-2040	*Protea pityphylla*	Unsuitable	Non-Persisters
104	Current-2040	*Protea punctata*	Unsuitable	Non-Persisters
105	Current-2040	*Protea recondita*	Unsuitable	Non-Persisters
106	Current-2040	*Protea rupicola*	Unsuitable	Non-Persisters
108	Current-2040	*Protea scorzonerifolia*	Unsuitable	Non-Persisters
109	Current-2040	*Protea stokoei*	Unsuitable	Non-Persisters
112	Current-2040	*Protea venusta*	Unsuitable	Non-Persisters
114	Current-2040	*Serruria bolusii*	Unsuitable	Non-Persisters
116	Current-2040	*Serruria cyanoides*	Unsuitable	Non-Persisters
117	Current-2040	*Serruria decipiens*	Possible	Non-Persisters
119	Current-2040	*Serruria fasciflora*	Possible	Non-Persisters
120	Current-2040	*Serruria florida*	Unsuitable	Non-Persisters
128	Current-2040	*Serruria kraussii*	Unsuitable	Non-Persisters
129	Current-2040	*Serruria meisneriana*	Unsuitable	Non-Persisters
130	Current-2040	*Serruria millefolia*	Possible	Potential Persisters
131	Current-2040	*Serruria nervosa*	Unsuitable	Non-Persisters
133	Current-2040	*Serruria rosea*	Unsuitable	Non-Persisters
137	Current-2040	*Serruria triternata*	Unsuitable	Non-Persisters
139	Current-2040	*Sorocephalus capitatus*	Unsuitable	Non-Persisters
140	Current-2040	*Spatalla barbigera*	Possible	Non-Persisters
141	Current-2040	*Spatalla caudata*	Unsuitable	Non-Persisters
142	Current-2040	*Spatalla curvifolia*	Possible	Non-Persisters
143	Current-2040	*Spatalla longifolia*	Unsuitable	Potential Persisters
144	Current-2040	*Spatalla mollis*	Unsuitable	Non-Persisters
145	Current-2040	*Spatalla prolifera*	Unsuitable	Non-Persisters
146	Current-2040	*Spatalla propinqua*	Unsuitable	Potential Persisters
147	Current-2040	*Spatalla setacea*	Unsuitable	Non-Persisters
148	Current-2040	*Spatalla squamata*	Unsuitable	Non-Persisters
149	Current-2040	*Spatalla tulbaghensis*	Unsuitable	Non-Persisters
1	2040-2070	*Aulax pallasia*	Unsuitable	Non-Persisters
2	2040-2070	*Aulax umbellata*	Unsuitable	Non-Persisters
4	2040-2070	*Diastella buekii*	Unsuitable	Potential Persisters
5	2040-2070	*Diastella divaricata*	Unsuitable	Non-Persisters
6	2040-2070	*Diastella parilis*	Unsuitable	Potential Persisters
8	2040-2070	*Leucadendron album*	Unsuitable	Non-Persisters
9	2040-2070	*Leucadendron argenteum*	Unsuitable	Potential Persisters
11	2040-2070	*Leucadendron burchellii*	Unsuitable	Non-Persisters
12	2040-2070	*Leucadendron chamelaea*	Possible	Non-Persisters
14	2040-2070	*Leucadendron concavum*	Possible	Non-Persisters
15	2040-2070	*Leucadendron conicum*	Unsuitable	Non-Persisters

	Time-step	Species names	Classification	Persistence Ability
17	2040-2070	*Leucadendron cordatum*	Possible	Potential Persisters
19	2040-2070	*Leucadendron diemontianum*	Unsuitable	Non-Persisters
20	2040-2070	*Leucadendron dregei*	Unsuitable	Non-Persisters
21	2040-2070	*Leucadendron dubium*	Unsuitable	Non-Persisters
22	2040-2070	*Leucadendron elimense*	Possible	Non-Persisters
23	2040-2070	*Leucadendron eucalyptifolium*	Unsuitable	Non-Persisters
27	2040-2070	*Leucadendron glaberrimum*	Unsuitable	Non-Persisters
28	2040-2070	*Leucadendron globosum*	Unsuitable	Non-Persisters
29	2040-2070	*Leucadendron gydoense*	Unsuitable	Non-Persisters
30	2040-2070	*Leucadendron laxum*	Unsuitable	Non-Persisters
34	2040-2070	*Leucadendron nervosum*	Unsuitable	Non-Persisters
35	2040-2070	*Leucadendron nitidum*	Unsuitable	Non-Persisters
36	2040-2070	*Leucadendron platyspermum*	Unsuitable	Non-Persisters
38	2040-2070	*Leucadendron pubescens*	Unsuitable	Potential Persisters
41	2040-2070	*Leucadendron sericeum*	Unsuitable	Potential Persisters
45	2040-2070	*Leucadendron strobilinum*	Unsuitable	Non-Persisters
46	2040-2070	*Leucadendron teretifolium*	Possible	Potential Persisters
48	2040-2070	*Leucadendron tinctum*	Unsuitable	Non-Persisters
51	2040-2070	*Leucospermum catherinae*	Possible	Non-Persisters
53	2040-2070	*Leucospermum cordifolium*	Possible	Non-Persisters
59	2040-2070	*Leucospermum mundii*	Possible	Non-Persisters
60	2040-2070	*Leucospermum patersonii*	Unsuitable	Non-Persisters
61	2040-2070	*Leucospermum pedunculatum*	Unsuitable	Potential Persisters
63	2040-2070	*Leucospermum prostratum*	Possible	Potential Persisters
64	2040-2070	*Leucospermum reflexum*	Unsuitable	Non-Persisters
66	2040-2070	*Leucospermum secundifolium*	Unsuitable	Non-Persisters
67	2040-2070	*Leucospermum spathulatum*	Unsuitable	Non-Persisters
68	2040-2070	*Leucospermum tomentosum*	Possible	Potential Persisters
69	2040-2070	*Leucospermum tottum*	Unsuitable	Non-Persisters
70	2040-2070	*Leucospermum truncatulum*	Possible	Non-Persisters
71	2040-2070	*Leucospermum vestitum*	Unsuitable	Non-Persisters
72	2040-2070	*Leucospermum winteri*	Possible	Non-Persisters
73	2040-2070	*Mimetes arboreus*	Unsuitable	Non-Persisters
74	2040-2070	*Mimetes argenteus*	Unsuitable	Non-Persisters
75	2040-2070	*Mimetes capitulatus*	Unsuitable	Non-Persisters
76	2040-2070	*Mimetes fimbriifolius*	Unsuitable	Potential Persisters
78	2040-2070	*Mimetes hottentoticus*	Unsuitable	Non-Persisters
79	2040-2070	*Mimetes palustris*	Unsuitable	Non-Persisters
80	2040-2070	*Mimetes pauciflorus*	Unsuitable	Non-Persisters
82	2040-2070	*Orothamnus zeyheri*	Unsuitable	Non-Persisters
83	2040-2070	*Paranomus abrotanifolius*	Unsuitable	Non-Persisters
84	2040-2070	*Paranomus bolusii*	Possible	Non-Persisters
85	2040-2070	*Paranomus centaureoides*	Unsuitable	Non-Persisters
86	2040-2070	*Paranomus dispersus*	Unsuitable	Non-Persisters
87	2040-2070	*Paranomus sceptrum-gustavianus*	Unsuitable	Non-Persisters
88	2040-2070	*Paranomus spathulatus*	Possible	Non-Persisters
89	2040-2070	*Paranomus spicatus*	Unsuitable	Non-Persisters
90	2040-2070	*Paranomus tomentosus*	Unsuitable	Non-Persisters
91	2040-2070	*Protea acaulos*	Unsuitable	Potential Persisters
92	2040-2070	*Protea acuminata*	Unsuitable	Non-Persisters
94	2040-2070	*Protea aspera*	Unsuitable	Non-Persisters
95	2040-2070	*Protea aurea*	Possible	Non-Persisters
96	2040-2070	*Protea caespitosa*	Unsuitable	Non-Persisters
98	2040-2070	*Protea convexa*	Unsuitable	Non-Persisters
99	2040-2070	*Protea coronata*	Possible	Non-Persisters

	Time-step	Species names	Classification	Persistence Ability
100	2040-2070	*Protea cryophila*	Unsuitable	Non-Persisters
104	2040-2070	*Protea effusa*	Unsuitable	Non-Persisters
105	2040-2070	*Protea grandiceps*	Unsuitable	Non-Persisters
106	2040-2070	*Protea lacticolor*	Unsuitable	Non-Persisters
107	2040-2070	*Protea laurifolia*	Unsuitable	Potential Persisters
108	2040-2070	*Protea lepidocarpodendron*	Possible	Non-Persisters
110	2040-2070	*Protea montana*	Unsuitable	Non-Persisters
111	2040-2070	*Protea nitida*	Unsuitable	Potential Persisters
114	2040-2070	*Protea pityphylla*	Unsuitable	Non-Persisters
115	2040-2070	*Protea punctata*	Unsuitable	Non-Persisters
116	2040-2070	*Protea recondita*	Unsuitable	Non-Persisters
117	2040-2070	*Protea repens*	Possible	Potential Persisters
119	2040-2070	*Protea rupicola*	Unsuitable	Non-Persisters
121	2040-2070	*Protea scorzonerifolia*	Unsuitable	Non-Persisters
122	2040-2070	*Protea stokoei*	Unsuitable	Non-Persisters
123	2040-2070	*Protea subulifolia*	Unsuitable	Non-Persisters
125	2040-2070	*Protea venusta*	Unsuitable	Non-Persisters
126	2040-2070	*Serruria adscendens*	Possible	Non-Persisters
127	2040-2070	*Serruria aemula*	Possible	Potential Persisters
128	2040-2070	*Serruria bolusii*	Unsuitable	Non-Persisters
130	2040-2070	*Serruria candicans*	Unsuitable	Non-Persisters
131	2040-2070	*Serruria cyanoides*	Unsuitable	Potential Persisters
133	2040-2070	*Serruria effusa*	Possible	Non-Persisters
134	2040-2070	*Serruria fasciflora*	Possible	Non-Persisters
135	2040-2070	*Serruria flagellifolia*	Possible	Non-Persisters
136	2040-2070	*Serruria florida*	Unsuitable	Non-Persisters
137	2040-2070	*Serruria fucifolia*	Possible	Potential Persisters
144	2040-2070	*Serruria kraussii*	Unsuitable	Non-Persisters
145	2040-2070	*Serruria leipoldtii*	Possible	Non-Persisters
146	2040-2070	*Serruria meisneriana*	Unsuitable	Non-Persisters
147	2040-2070	*Serruria nervosa*	Unsuitable	Non-Persisters
149	2040-2070	*Serruria reflexa*	Possible	Potential Persisters
150	2040-2070	*Serruria rosea*	Unsuitable	Non-Persisters
152	2040-2070	*Serruria rubricaulis*	Unsuitable	Non-Persisters
154	2040-2070	*Serruria triternata*	Unsuitable	Non-Persisters
156	2040-2070	*Sorocephalus capitatus*	Unsuitable	Non-Persisters
157	2040-2070	*Spatalla caudata*	Unsuitable	Non-Persisters
158	2040-2070	*Spatalla colorata*	Unsuitable	Non-Persisters
159	2040-2070	*Spatalla longifolia*	Unsuitable	Potential Persisters
160	2040-2070	*Spatalla mollis*	Unsuitable	Non-Persisters
161	2040-2070	*Spatalla prolifera*	Unsuitable	Non-Persisters
162	2040-2070	*Spatalla propinqua*	Unsuitable	Potential Persisters
163	2040-2070	*Spatalla racemosa*	Possible	Potential Persisters
164	2040-2070	*Spatalla setacea*	Unsuitable	Non-Persisters
165	2040-2070	*Spatalla tulbaghensis*	Unsuitable	Non-Persisters