Understanding distributional responses of vegetation to changes in climate and fire regime in the Cape Floristic Region

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Summary

As evidence of climate change and its impact on biodiversity continues to grow, anticipating and understanding ecological responses to climate change is ever more critical. In fire-prone ecosystems, such as those found in the Cape Floristic Region (CFR), a major concern is that changes in climate will likely lead to dramatic shifts in fire activity (e.g. increased fire frequency) that will significantly affect the distribution, composition, and functioning of vegetation. Effectively mitigating and/or adapting to the potential loss of biodiversity and altered ecosystem function in this region hinges on an in-depth understanding of how vegetation in the CFR interacts with the environment and, more importantly, how vegetation will respond to changes in both climate and fire regime.

Our understanding of how climate change may impact vegetation is largely derived from distribution models. Vegetation distribution models have been used for decades to investigate species-environment relationships, predict future distribution patterns, and test ecological theories. These models are founded on the premise that vegetation distributions are determined by the spatial distribution of environmental variables that are significantly correlated with, or limit, plant distributions. However, while much emphasis is placed on the role of climate and topography as key determinants of vegetation distributions, other critical ecosystem components (e.g. fire regime) that have significant effects on the composition and distribution of vegetation are rarely incorporated in vegetation distribution models. Given the importance of fire as a driver of vegetation formations and assemblages in the CFR, the exclusion of fire variables from vegetation distribution models potentially constrains the generation of accurate and appropriate information, critical for the management and conservation of biodiversity in the region.

The exclusion of fire covariates from distribution studies is partly a result of a lack of fire data, coupled with the widely accepted, but limited, view that climate is the chief determinant of species distributions and also a key determinant of fire regime. To this end, a proxy for fire return interval data, derived from vegetation recovery rates estimated from satellite data, combined with climate and edaphic data, was used to model and analyse the distribution of fynbos vegetation in CFR. Firstly, the importance of fire as a determinant of fynbos species distributions, relative to climate, was evaluated. This was complimented by an assessment of the effect of life history traits on plant species sensitivity to changes in ecological regime. To achieve this first objective, the distributions of 52 closely related fynbos plant species pairs (104 species), classified across two growth forms

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(graminoids and shrubs) and their respective fire response strategies (seeders and resprouters) were modelled using Maxent, and subsequently analyzed. Secondly, the potential impacts of changes in climate and fire regime on future fynbos distributions were assessed by modelling the future distributions of 22 fynbos vegetation types under 44 Phase 5 Coupled Model Intercomparison Project (CMIP5) general circulation models (GCMs) using multinomial linear regression. Lastly, an overlay analysis of projected distributions of fynbos species and vegetation types was used to assess whether fynbos species respond in unison or as individuals to changes in climate and fire regime. The selected species in this final analysis consisted of 74 endemic species and 358 important species (species that are either high in abundance or frequency of occurrence, or predominant in a given vegetation unit), which facilitated a comparison of the potential impacts of changes in climate and fire regime between the two sets of species.

Findings from this research identified fire return interval as a major determinant of fynbos species distributions. Although, the predictive power of the fire variable was greatly reduced when considered in conjunction with the other climate and edaphic variables, it was still among the most important predictors, and including fire data has the potential to add to our understanding of plant species distributions in fire-prone ecosystems. This was particularly apparent in the case of seeder graminoids and shrubs, where both graminoids and shrubs were found to be negatively associated with longer fire return intervals, while seeder species were significantly more sensitive to fire than resprouters.

Projected changes in fire return interval and temperature will potentially have a significant impact on future vegetation distributions, with vegetation types with longer fire return intervals and warmer summer and winter temperatures being at most risk. It was also noted that projected changes in fire regime will likely have a greater impact on vegetation distributions than changes in rainfall regime. Comparing the distribution models of endemic and important species with models for the major vegetation types highlighted that species responses to changes in climate and fire regime largely conformed to the Clementsian concept of communities as organisms, with less than 30% of the species showing individualistic responses. As a result, the species composition of all vegetation types was altered when projected under future scenarios, with species from the present-day vegetation types either being lost or retained, while others were gained, in the projected vegetation types. The change in species composition largely stemmed from the replacement of some species in the present-day vegetation type by the same number of different species in the corresponding future vegetation type. The implications of this is that the underlying

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species composition of fynbos vegetation types will likely be altered under future climate and fire regime, thus disrupting the functioning of those vegetation types.

The role of natural disturbance regimes, such as fire, in determining species distributions is generally overshadowed by the long-standing view of climate being the chief driver of species distributions. This research provides evidence for the contribution of fire in shaping species' distributions in fire-prone ecosystems, and highlights the need for the development and inclusion of estimates of fire regime components in vegetation distribution studies and vulnerability assessments. This is especially important since fire regimes are sensitive to a range of global change drivers beyond just changing climate (e.g. land use and invasive species).

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CHAPTER 1

1. INTRODUCTION

1.1 Background

The Cape Floristic Region (CFR), is an area of extremely high plant diversity and endemism located in the south-western tip of South Africa (Cowling et al., 1992). The CFR contains approximately 9000 plant species, 69 % of which are endemic (Goldblatt & Manning, 2002). The dominant vegetation type in the CFR is fynbos, comprised largely of hard-leaved, evergreen Mediterranean type shrubs adapted to periodic fires. The fynbos is characterized by four major plant types: restioids, ericoids, proteoids, and geophytes (Cowling & Richardson, 1995). According to Odendaal et al., (2008) fynbos biodiversity generates close to R77 million rand a year, through eco-tourism and harvesting of products such as wildflowers, and plants that provide food and drugs (Van Wilgen et al., 1996), such as rooibos (*Aspalathus linearis*) and honey bush (*Cyclopia*) teas. Another major ecosystem service provided by the fynbos is water supply, acting as the natural cover in the mountain areas that provide the Western Cape Province with 3000 million m^3 of water supply per year (Le Maitre et al., 1997).

Based on its biological value and manifold threats, the CFR is defined as a biodiversity hotspot (Myers et al., 2000). Current threats to this region include a combination of various human activities such as agricultural expansion, urban encroachment and development, and the invasion of alien plant species (Rouget et al., 2014). It is estimated that approximately 30% of the CFR has been transformed through agriculture, urbanization and invasive alien plant species (Rouget et al., 2003). Bellard and coworkers (2014) describe the CFR as one of the three most vulnerable biodiversity hotspots to global change, highlighting fire regime and rising atmospheric CO_2 as further threats likely to affect regions such as the CFR.

As the evidence of climate change and its impact on biodiversity increases (Cavanaugh et al., 2014; Vergés et al., 2016; Slingsby et al., 2017), anticipating and understanding species distributional responses to climate change is ever more critical. Climate change poses a significant threat to plant diversity in the CFR. It is anticipated that the geographic ranges of plant species will expand, contract and fragment over time in response to changing climate (Parmesan & Yohe, 2003; Midgley et al., 2006). Shifts in vegetation distributions ultimately lead to the disruption of ecosystem functions such as water purification and carbon sequestration (Franklin et al., 2016),

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and present significant challenges for society, e.g. health risks, food insecurity and resource conflicts (Pecl et al., 2017). Mitigating and/or adapting to these impacts will require an enhanced scientific understanding of biological responses to climate change.

There is also growing evidence that anthropogenic climate change may induce alterations in fire regimes that could significantly influence vegetation distribution in the CFR, particularly in the fynbos (Bowman et al., 2009; van Wilgen et al., 2010; Wilson et al., 2010, 2015; Kraaij et al., 2013b). Although the fynbos is a fire-dependent ecosystem, that requires periodic fires to ensure the persistence of its high species diversity (Cowling et al., 1992), projected climate change trends within the CFR suggest alterations in the fire regime which may adversely affect its overall biodiversity (Midgley et al., 2005). The following trends in climate change are expected for the CFR: (i) decreased rainfall by an average of 41 mm by 2020 (Bomhard et al., 2005) particularly along the western coast and adjacent interior (Lumsden et al., 2009) (ii) increased rates of evapo-transpiration, and drying of fuel load, (iii) increased prevalence of hot and dry "berg" winds, and (iv) increased carbon uptake in vegetation (particularly by invasive alien species) which will amplify the rate of increase in the quantity of fuel load (IPCC, 2013). It is anticipated that a combination of these factors will cause changes in the fire regime that will significantly affect the functioning, structure and composition of vegetation within the CFR (Mouillot et al., 2002; Midgley et al., 2005). In light of this, improving our capacity to predict vegetation responses to changes in both climate and fire regime will be critical for the management and conservation of biodiversity in the CFR.

1.2 Problem statement

Anticipating vegetation responses to projected changes in both climate and fire regime is crucial for the future management of vegetation in fire-prone ecosystems, such as the CFR. The majority of vulnerability assessments rely on distribution models focused on the impacts of climate change on biodiversity (e.g. Midgley et al., 2003; Klausmeyer & Shaw, 2009; Ackerly et al., 2015), while the potential impacts of fire regime change generally remain overlooked. These models are founded on the premise that vegetation distributions are determined by the spatial distribution of environmental variables that are significantly correlated with, or limit, plant distributions (Franklin 1995). Vegetation distribution models have been used for decades to predict future distribution patterns (Bomhard et al., 2005; Lucas et al., 2017), investigate species-environment relationships (Moretti et al., 2006), and test ecological theories (Danz et al., 2013). Given that fire

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is a significant driver of vegetation formations and assemblages in the CFR (Bond & Keeley, 2005; Keeley et al., 2011), the exclusion of fire covariates from vegetation models may potentially limit our understanding of the role of fire in determining species distributions, and how changes in fire regimes may alter future distributions in the CFR.

The exclusion of fire covariates in distribution studies is partly a result of the widely accepted, but limited, view that climate is the chief determinant of species distributions (Bond et al., 2005), and also a lack of fire data (Flannigan et al., 2009). However, there is growing recognition that other factors such as disturbances (e.g. fire) and biotic interactions contribute to shaping species distributions (Abbott & Le Maitre, 2009; Yates et al., 2010). Furthermore, advancements in remote sensing offer an opportunity for non-climatic variables, such as fire, to be incorporated into distribution models (He et al., 2015). Nonetheless, only a few studies to date have investigated the role of fire as a predictor of vegetation distribution in fire-prone ecosystems such as the CFR (see Tucker et al., 2012; Crimmins et al., 2014).

The species level assessments by Tucker et al., (2012) and Crimmins et al., (2014) indicate that fire has limited influence on the current distribution of plant species in fire-prone ecosystems, possibly due to fire regimes largely being a product of climate (Bond & Keeley, 2005; Wilson et al., 2010). This suggests that fire-related variables may be an unnecessary addition to distribution models and that climatic variables are sufficient predictors of vegetation distributions in fire-prone ecosystems. However, there is a need for more rigorous testing on this matter, with the following issues being given due consideration. Firstly, fire response traits (e.g. resprouting) will likely result in differential species responses to changes in climate and fire (Treurnicht et al., 2016). Therefore, the influence of fire response traits on species distributions may need to be accounted for when investigating the role of fire as a predictor of plant species distributions. Secondly, in the interest of conservation and management planning at landscape scales such as the CFR, it may be useful to assess the relative importance of fire in shaping species distributions in the context of vegetation units rather than individual species. Lastly, it is important to not only understand how fire shapes current plant species distributions, but also how anticipated changes in fire regimes will impact future distributions.

1.3 Aim and objectives

The overarching goal of this dissertation is to enhance our scientific understanding of the drivers and underlying ecosystem processes that shape vegetation distributions in the CFR, particularly

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focussing on the importance of fire regimes and species responses to disturbances. To this end, the current and future distribution of fynbos vegetation in the CFR is modelled and examined. The distribution models utilized are integrated with fire return interval data derived from a combination of burned area maps dating from the 1950s (Wilson et al., 2010) and ten years (2000-2010) of remotely sensed Moderate Resolution Imaging Spectroradiometer (MODIS) 500m resolution 16-day gridded Normalized Difference Vegetation Index (NDVI) data (Wilson et al., 2015). While the fire return interval data used are proxies derived from vegetation recovery rates, there are few datasets of this kind and none exist for most flammable ecosystems. Therefore, this dataset provided a unique opportunity to address the following key objectives:

1. Investigate the importance of fire as a predictor of plant species distributions in the CFR relative to climate and soils, and if this varies among species with different life histories.

2. Evaluate the contribution of fire in determining the distribution of fire-prone fynbos vegetation types, and the potential impacts of changes in climate and fire regime on their future distributions.

3. Compare potential species level and community (i.e. vegetation type) level responses to projected changes in climate and fire regime in the CFR.

1.4 Research design

The dissertation is structured into six chapters (Table 1-1). This first chapter provides a brief description of the study area, highlighting the threat of climate change and altered fire regimes to the persistence of fynbos species in the CFR. An overview of limitations associated with distribution models, a tool commonly used in climate change impact assessments, is also provided. This chapter also conceptualises the research problem, presents the study aim and objectives, and lays out the research design. Chapter 2 provides a review of relevant literature pertaining to the functioning and maintenance of fynbos species, potential impacts of projected climate and fire regime changes in the CFR, as well as vegetation distribution modelling, highlighting critical research gaps to which this study makes its contribution. Chapters 3 to 5 are data chapters written as independent and potentially publishable units, therefore there is some content overlap between them (particularly the introduction and method sections). These three chapters follow the development and assessment of distribution models tailored towards improving our understanding of vegetation distributions in response to changes in climate and fire regime in the CFR. Chapter

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6 concludes the dissertation, highlighting key findings, contribution to body of knowledge and opportunities for further research.

Table 1-1. Dissertation structure and chapter content

Chapter no.	Chapter title	Main points
1	Introduction	Background Research problem Aim and objectives Research design
2	Theoretical framework	Fynbos ecology Future climate and fire regime projections Vegetation distribution modelling
3	Fire and life history affect the distribution of plant species in a biodiversity hotspot (under review)	Addresses objective 1. Species level analysis of the importance of fire as a driver of fynbos distributions. Evaluation of the effect of life history traits on plant species sensitivity to environmental changes.
4	Vegetation response to projected changes in climate and fire regime in a Mediterranean type ecosystem	Addresses objective 2. Vegetation type level analysis of the contribution of fire and climate as drivers of fynbos distributions. Modelling and evaluation of fynbos distributions under projected climate and fire regime.
5	Contrasting species- and vegetation-based assessments of the vulnerability of a Mediterranean type ecosystem to changing climate and fire	Addresses objective 3. Analysis of species versus vegetation type level responses to projected changes in climate and fire regime in the CFR.
6	Synthesis	Reiteration of research aims and key finding. Contributions to existing body of knowledge. Limitations and directions for future research. Conclusion

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CHAPTER 2

2. THEORETICAL FRAMEWORK

2.1 Fynbos ecology

The Cape Floristic Region is divided into five distinctive vegetation types: fynbos, karoo steppe, succulent shrubland, forest thicket, and evergreen forest (Goldblatt, 1997), with fynbos being the dominant vegetation type. The distribution of these vegetation types varies over an east-west gradient, as the occurrence of fynbos decreases moving eastwards and is replaced by a predominance of thicket and succulent Karoo (Cowling & Proches, 2005). Fynbos is an evergreen, fire-prone shrubland that covers 80% of the CFR and accounts for over 7000 floral species in the region (Cowling & Richardson, 1995; Cowling & Proches, 2005). Four major growth forms exist within fynbos: proteoid large leafed woody shrubs, ericoid fine leafed bushes, restioid reed-like bushes, and geophytes sustained by large underground storage organs (Cowling et al., 1996).

2.2 Climate

Plant growth and reproduction in fynbos is largely determined by the climatic, fire and edaphic regimes prevalent to the CFR. Fynbos vegetation is characterised by a Mediterranean climate (Köppen, 1931) in the western areas of the CFR, and a relatively temperate climate in the east (Cowling, 1992). As a result, rainfall in the west of the CFR is largely concentrated in the winter months, while summers are hot and dry. The eastern area of the CFR, is however less strongly seasonal, receiving more bimodal rainfall (Deacon et al., 1992; Schulze, 2007; Southey, 2009; van Wilgen et al., 2010). Species richness in the CFR has been found to be strongly associated rainfall seasonality and reliability, with western areas being richer in species than eastern areas due to the predictable winter rains (Cowling & Proches, 2005). Precipitation in the CFR is also described by a gradient of aridity towards the interior, where fynbos transitions into semi-arid karoo vegetation. Water availability is central to the distribution of growth forms that exist within fynbos, with asteraceous fynbos followed by restoid, graminoid, proteoid and Waboomveld fynbos occurring at the most arid extreme, while ericoid and wet restoid fynbos occur towards the moistest extremes (Rebelo et al., 2006). Mean summer temperatures in the CFR generally range from 30°C in the lower lying areas to 25°C in the mountain regions, while winter months are characterised by widespread frost on the mountain peaks that may last for several weeks (Cowling & Proches, 2005). Temperature is particularly important for the persistence for fynbos species as

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it affects physiological functioning (e.g. water and nutrient assimilation), as well as growth processes such as germination and bud break (Midgley et al., 2002; Brown & Botha, 2004).

2.2.1 Fire

Fire has been a common and natural global process for millions of years, and is considered to have a significant influence on the maintenance, distribution and function of fire prone ecosystems such as the fynbos in the CFR (Bond & Keeley, 2005). Fires in the fynbos mainly occur during the dry, hot summer period (Cowling et al., 1992), although winter fires are common in the humid coastal mountain ranges to the east of the CFR (Kraaij & van Wilgen, 2014). The majority of the fires in the fynbos have return intervals ranging between 10-30 years, with few stands surviving beyond 40 to 50 years without burning; these fires seldom burn stands younger than 7 years (Keeley et al., 2012). Fires in the CFR are a product of both human activities as well as natural ignitions (Forsyth & van Wilgen, 2008), with lightning acting as the dominant natural ignition (Cowling et al., 1992; Seydack et al., 2007). The frequent occurrence of fires in the CFR is considered a significant factor in the evolution of numerous plant reproductive strategies identified in fynbos e.g. fire cued germination and flowering, as well as the storage of seeds in the canopy and soil (Le Maitre & Midgley, 1992; Cocks & Stock, 1997; Brown et al., 2003; Keeley et al., 2012). Ash from fires has also been found to act as a mineralizing agent in coastal fynbos systems (Stock & Lewis, 1986b).

2.2.1.1 Life history traits

Given the relationship between fire and fynbos, life history traits of fynbos species are based on plant regeneration strategies or responses to fire, and are therefore also referred to as fire response traits (van Wilgen & Forsyth, 1992). Life history traits describe the adaptations employed by an individual during different stages in its life cycle (i.e.: growth, reproduction and survival) in response to environmental conditions. Fynbos plant species respond to fire disturbance either by regenerating through seedling recruitment or resprouting. Life history traits are generally divided into three categories: Non-sprouters or obligate seeders, facultative seeders and obligate resprouters (Bell et al., 1984; Keeley et al., 2012; Pratt et al., 2012; Marais et al., 2014).

Obligate seeders, also referred to as post-fire seeders or reseeders, die during fires and recruit their seedlings from dormant, fire stimulated seed banks stored either in the soil or in the canopy in serotinous cones. Germination usually occurs during the wet winters after a fire when the canopy is open (Keeley, 1998). Obligate seeders recruit in large numbers, are quick growing and drought resistant and can outcompete sprouter seedlings in filling the gaps created by the fire, and to renew

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their seed banks before the next fire (Le Maitre & Midgley, 1992). Obligate seeder species can live up to 15 years or more, and are prone to shorter life cycles when fires occur (van Wilgen & Forsyth, 1992). Obligate seeders are prominent in the fynbos, with a number of them being short-lived fire ephemerals e.g. monocarpic therophytes and annuals (Le Maitre & Midgley, 1992; van Wilgen & Forsyth, 1992) and longer living shrubs e.g. Proteaceae (Schurr et al., 2012). The persistence of obligate seeder species under varying fire frequencies is highly dependent on the length of the primary juvenile period and the accumulation of sufficient seed reserves (Gill, 1975; Altwegg et al., 2014; Pausas & Keeley, 2014a). Examples of long-lived obligate seeder species in the CFR include *Protea repens* and *Leaucadendron laureolum* (Goldblatt & Manning, 2000)

Facultative sprouters are species that both resprout and recruit seedlings from fire cued seed banks post fire (Syphard & Franklin, 2010). On the other hand, facultative seeder species regenerate during the post fire period by resprouting from lignotubers and recruit from seed in gaps of open canopy and under the partial shade of resprouters (Pratt et al., 2012; Marais et al., 2014). Facultative seeder species have been observed to mostly sprout after mild fires, and tend to be weak sprouters as compared to their high effectiveness in seedling recruitment (van Wilgen & Forsyth, 1992), where they rely on competitive strategies and resilience against stress to ensure seedling survival (Bellingham & Sparrow, 2000).

Obligate resprouter species resprout vigorously only after a fire from dormant buds and have no other apparent adaptations to fire (Trollope et al., 2004). An obligate resprouter does not have a fire resistant seed bank, neither does is it recruit seedlings after a fire (Pratt et al., 2012), but usually stores its seed in a fleshy exterior fruit facilitating dispersal by vertebrates (Keeley, 1997). These seeds are extremely sensitive to fires and generally short lived. Therefore, unlike obligate seeders and facultative seeders species, obligate resprouter species rely on long fire free periods to establish and transition into adults mature enough to survive a fire (Keeley, 1992).

2.2.2 Edaphic conditions

Fynbos vegetation is supported by a range of nutrient-poor sandy soils to richer clay soils arising from Aeolian marine sands and underlying layers of sandstone, granite and shale (Goldblatt & Manning, 2000). Variation in the distribution of fynbos plant species along edaphic gradients is well documented (Cowling, 1990; Richards et al., 1997; Cramer et al., 2014; Cowling & Potts, 2015). Proteoid fynbos, for example, generally occurs in deep fertile soils at the base of mountains, while ericoids prefer higher elevations with organic-rich fine grain soils and restioids dominate

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shallow dry soils on the warm north facing slopes (Cowling & Holmes, 1992a; Cowling et al., 1997). Studies by Lechmere-Oertel & Cowling (2001) and Esler et al., (2015) have also found soil type to be a strong limiting factor of fynbos species, highlighting the exclusion of fynbos species from relatively heavier, fertile soils in particular.

2.3 Climate and fire regime change in the CFR

Climate, chiefly temperature and precipitation, is a well understood driving force behind vegetation distribution (Köppen, 1931; Brovkin, 2002). This renders plant diversity in the CFR particularly at risk in light of current climate change projections, which anticipate warmer and drier conditions prevailing over the CFR in the future (Midgley et al., 2005; IPCC, 2013). With regards to species distribution, depending on the resilience of the native species, changes in climate may result in the displacement of native species by alien species which have a greater capacity to thrive under the changes (Scholze et al., 2006). In addition, communities may become more homogenous as generalist species increase at the expense of endemic specialist species that have evolved over long periods of stable climate conditions (Sommer et al., 2010). Consequently, various bioclimatic models have been employed over the years to predict future species distributions in the CFR under the projected climate scenarios (e.g. Tolley et al., 2009; Rödder & Lötters, 2010). Midgley and coworkers (2002), in particular, predict that the extent of fynbos may decrease by 51 to 65% under climate scenarios projected for 2050. Such projections are a significant cause for concern, as fynbos accounts for 70% of the plant species in the CFR (Cowling & Proches, 2005).

As with climate change, the fire regime over the CFR has been changing over time. The general consensus is that fires are becoming more frequent and fire return intervals shorter, with suggested causes ranging from alterations in fire weather (van Wilgen et al., 2010; Wilson et al., 2010), and increasing human populations (Forsyth & van Wilgen, 2008), to modification of fuel loads by fauna and alien plant species (van Wilgen et al., 2010; Pausas & Keeley, 2014b). Increased frequency and short fire return intervals in the CFR can affect the survival and post fire recovery of fynbos plant species, particularly the dominant overstorey shrubs (particularly non-sprouting Proteaceae), leaving gaps for the invasion of alien tree species (Forsyth & van Wilgen, 2008).

Given the importance of both climate and fire in shaping the distribution, composition and function of vegetation in the CFR, a thorough understanding of how each element contributes to the persistence of fynbos species, will be crucial for mitigating and/or adapting to biodiversity losses

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in the CFR. However, the complex feedback between climate, vegetation and fires presents a significant challenge in separating the roles that climate and fire play in shaping the distribution of fynbos species. For instance, changes in climate lead to alterations in the fuel load, which in turn cause changes in the fire regime (Mouillot et al., 2002). Similarly, climate change, which translates to changes in fire weather, may also modify the fire regime (Wilson et al., 2010). Conversely, while fire regimes are a function of climate and vegetation (fuel), fires also drive the distribution, composition and function of vegetation (Bond & Keeley, 2005), as well as contributing towards global climate through CO_2 emissions, which consequently influences fire weather (Bowman et al., 2009). In light of such a complex system of feedbacks, neither climate nor fire can be ignored as a variable in determining future species distributions, yet most climate change vulnerability assessments do not consider the role of fire, or how changes in fire regime may alter future distributions.

2.4 Distribution modelling

Understanding the distribution of flora and fauna across space and time has held the interest of ecologists and biogeographers for centuries. Distribution models are tools commonly employed in investigating species response to changes in ecological regime. Over the years, these models have been applied to numerous studies for various purposes including conservation planning and habitat selection (Araujo et al., 2004), predicting impacts of climate change on species distributions (Thomas et al., 2004; Thuiller, 2004) and identifying areas susceptible to alien species invasions (Trethowan et al., 2011).

2.4.1 Modelling approaches

Distribution models are classified as either correlative or mechanistic. Correlative models are typically referred to as species distribution models (SDMs; Elith & Leathwick, 2009), or bioclimatic envelope models (Pearson & Dawson, 2003; Thuiller et al., 2005). The correlative approach involves using statistical relationships between species occurrence and environmental factors to describe and predict species distributions. Bioclimatic envelope models are sometimes referred to as ecological niche models, however these two correlative models do differ in their construction (Newman et al., 2011; Peterson & Soberón, 2012). Ecological models are often integrated with information on the environmental tolerances of the species under study, drawn from experimental work (Newman et al., 2011). One of the major criticisms of the correlative approach in distribution modelling is that it fails to account for key dynamic processes such as

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species dispersal and biotic interactions, which mediate species responses to environmental factors (Pearson & Dawson, 2003).

An alternative to correlative models are mechanistic models which use the interactions between physiological properties and processes of a species and environmental factors to determine their distributions and abundance (Kearney & Porter, 2009). Examples of mechanistic models include gap models (Fischer et al., 2016), biogeochemical models (Sándor et al., 2016), and dynamic vegetation models (Moncrieff et al., 2015). Mechanistic models do however require large amounts time, effort, resources and data to construct and validate (Kearney & Porter, 2009; Dormann et al., 2012). Hence, correlative models, which are relatively less time consuming and data intensive, remain the cornerstone of biodiversity assessments (Evans et al., 2015). Distribution models in this study employ a correlative approach.

Although distribution models have been useful in drawing attention to the potential impacts of global and local changes (particularly climate change), it is argued that these models are inherently prone to over and under- prediction, and are unable to provide precise insights that would be useful to management and policy making (Sinclair et al., 2010). However, distribution models are one of the few existing methods that can be used to examine the potential impacts of global change, and although heuristic, they do well in giving a sense of the nature and extent to which biodiversity will be impacted (Yates et al., 2010). Furthermore, distribution models will continue to evolve and improve parallel to technological advancements (e.g. modelling software, GIS, and remote sensing) and with the development of novel modelling algorithms, e.g.: Hierarchical Bayesian Models (Wilson et al., 2010) and MLR, Multinomial Logistic Regression (Ackerly et al., 2015).

2.4.2 Model requirements

Developing a distribution model requires distribution data and environmental data (Pearson, 2007). Distribution data can be collected from sampling surveys, herbarium records, global databases (e.g. Global Biodiversity Information Facility-GBIF[1]) and published ecological studies (e.g. van Wilgen & Forsyth, 1992). Environmental data are the variables that have a direct or indirect influence on the occurrence of species. Guisan and Thuiller (2005) define environmental data in three ways: (i) limiting factors (or regulators): these are factors controlling species eco-

[1] https://www.gbif.org/

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physiology (e.g. temperature and water); (ii) disturbances: described as all types of environmental disturbances (natural or human-induced) and (iii) resources: identified as all compounds that can be assimilated by organisms (e.g. energy and water). Current technologies, particularly GIS and remote sensing have significantly improved the collection and dissemination of environmental data (Pearson, 2007; Ghisla et al., 2012).

Due to the various forms and sources used to collect data for the variables used in distribution models it is imperative that all data are carefully screened for errors, as the accuracy and robustness of the model is highly dependent on the precision of the input data (Pearson, 2007). The spatial scale (resolution) of each variable should also be considered. Firstly, it is important that the resolution of the data is suitable for capturing information regarding the species under study. Secondly, most traditional statistics are unable to handle variables of different scales (Wilson et al., 2011), therefore it is important that the variables are resampled to one matching scale before use. Another aspect that should be noted is the issue of spatial autocorrelation. Spatial autocorrelation arises in cases where the values of variables sampled at nearby locations are not independent from each other (Legendre 1993, Dormann et al. 2007), which contradicts the assumption of independence of observations used in most statistical methods (Guisan & Thuiller, 2005), and may lead to the geographic clumping of species points in the output (Elith & Leathwick, 2009).

2.4.3 Modelling algorithms

Distribution models make use of various algorithms in order to establish the relationship between species distribution data and environmental variables. The selection of an algorithm is dependent on the data available and on the objectives of the study (Alvarado-Serrano & Knowles, 2014). Each algorithm has a specific set of data requirements; some algorithms require presence only data, e.g. BIOCLIM (Booth et al., 2014), which only correlate known occurrences with a set of environmental variables. Some algorithms use presence data and background data or pseudo-absences (Pearson, 2007). These are based on the relationship between the environment associated with the known occurrences and the surrounding environment (background data), e.g. ENFA, Ecological Niche Factor Analysis (Hirzel et al., 2006) and Maxent, Maximum Entropy (Phillips et al., 2006). Other algorithms use both presence and absence/pseudoabsence (assumed absence) data to compare sites where species were, and were not, observed, e.g. ANN, Artificial Neural Networks (Pearson et al., 2002); GLM`s, Generalised Linear Models (Lehmann et al., 2003); GAM`s, Generalized Additive Models (Hastie & Tibshirani, 1986).

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Another aspect that should be considered in selecting modelling algorithms is their ability to input categorical environmental data, which is data divided into discrete classes, e.g. vegetation types. Most model output comes in the form of continuous data, for example, a probability of species presence ranging between 0 and 1, while others are expressed in binary, e.g. 0 indicates presence, 1 indicates absence (Pearson, 2007). Therefore, it is imperative to establish which form of output is relevant to the goal of the study before selecting a model algorithm. A sensitivity analysis may also be required if determining the relative influence of the variables in improving predictive accuracy is necessary to achieving the objectives of the study (Alvarado-Serrano & Knowles, 2014). In such cases, black box model algorithms, such as ANN, may be ill suited as they work 'behind the scenes' and do not identify the specific contributions of each variable so may require additional analyses (Pearson, 2007).

2.4.4 Model validation

A critical aspect of species distribution modelling lies in assessing the predictive accuracy of the model (Alvarado-Serrano & Knowles, 2014). Methods of validating SDMs vary and are dependent on the model algorithm and input data (Pearson 2010). Statistical tests are commonly used in cases where the purpose of the model is to explain processes or generate a hypothesis. If the aim of the model is to predict distributions, data splitting methods (e.g. K-fold cross validation, jacknifing and bootstrapping) are commonly employed (Elith & Leathwick, 2009). When data splitting, the occurrence data are split into calibration data and validation data, or in some cases the validation data are independent from the original data set (Peterson et al., 2011).

The validation of a model involves quantifying performance (the level at which the model fits the observed occurrences) and testing the significance of modelled predictions versus random predictions). Two categories of performance exist (Fielding & Bell 1997): those that are threshold-dependent (designed for use with binary predictions) and those that are threshold-independent (non-binary predictions e.g. continuous or ordinal). A method commonly used in the threshold-dependent category (binary model) is the confusion matrix, which uses simple row-column what? set up to identify true cases of presence and absence (Pearson, 2007). Threshold-independent predictions may be evaluated using the AUC: area under the receiver operating characteristic curve (Hanley & McNeil, 1982). The receiver operating characteristic curve results from plotting sensitivity (absence of omission error) against specifity (absence of commission error) (Peterson et al., 2011). Kappa statistics and other correlation coefficients are also applied in validating non-binary models (Elith & Leathwick, 2009).

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2.5 Conclusion

This chapter served to provide a synopsis of fynbos ecology, specifically highlighting the roles of fire, climate and soils as key determinants of fynbos species distributions. Potential implications of projected changes in climate and fire regime for the persistence of fynbos were also discussed. As a foundation to the methods employed in the proceeding data chapters, key aspects of distribution modelling were reviewed, highlighting the advantages and disadvantages of different modelling approaches (i.e. correlative versus mechanistic), as well as considerations to take note of in selecting data, algorithms and methods of validating distribution models.

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CHAPTER 3

3. FIRE AND LIFE HISTORY AFFECT THE DISTRIBUTION OF PLANT SPECIES IN A BIODIVERSITY HOTSPOT[2]

3.1 Abstract

Aim: Species distribution models (SDMs) provide valuable insights into species-environment relationships and potential climate change impacts on diversity. Most vulnerability assessments do not consider the role of natural disturbance regimes such as fire in determining current and future species distributions, or how species traits mediate their response to these stressors. Here, we investigate the importance of fire in determining the distributions of species in fire-prone fynbos vegetation, and how species' responses are affected by their life history traits (growth form and fire-response strategy).

Location: Cape Floristic Region, South Africa

Methods: We modeled the distribution of 104 plant species with different life history traits, using Maxent. The model included five climatic variables, one edaphic and one fire variable. Post-hoc analyses of model output and permutation procedures were conducted to assess variable importance and the effect of life history traits on species' responses to fire. We accounted for phylogenetic autocorrelation using sister species comparisons.

Results: Permutation importance scores identified fire return interval as a major determinant of fynbos species' distributions. Linear mixed effect analyses revealed that seeder species were significantly more sensitive to fire than resprouters. The response curves indicated that the occurrence of species across all life histories were negatively associated with longer fire return intervals.

Main conclusions: Fire and life history traits governing species' response to fire are key factors determining species distributions in our study system. SDMs that ignore potential changes in fire regime and differences among species in their sensitivity to these changes compromise our ability

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to predict responses to environmental change in fire-prone ecosystems. There is great need for better spatial data describing historical, current and future fire regimes, and for models that can incorporate different responses based on species life histories, to improve vulnerability assessments for fire-prone ecosystems.

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3.2 Introduction

Fire is a pervasive natural disturbance that drives species distributions and community composition in many ecosystems (Cowling, Holmes & Rebelo, 1992; van Wilgen, Richardson, Kruger & van Hensbergen, 1992; Bond & Keeley, 2005; Pausas & Verdú, 2008; Bowman, Balch & Artaxo, 2009), yet is rarely considered in species-level, climate change vulnerability assessments (Moretti, Conedera, Moresi & Guisan, 2006; Keith et al., 2008; Tucker, Rebelo & Manne, 2012). Fynbos, the dominant vegetation type in the Cape Floristic Region (CFR), is under threat from climate change (Midgley, Hannah, Millar, Rutherford & Powrie, 2002; Midgley, Hannah, Millar, Thuiller & Booth, 2003; Slingsby et al., 2017). Projected climate trends for the CFR suggest an increase in temperature (Niang et al., 2014), coupled with a decrease in winter rainfall in the south-west section of the CFR, and an increase in rainfall inland and towards the east (Hoffman, Carrick, Gillson & West, 2009; MacKellar, New & Jack, 2014). Beyond direct effects on plant species growth and survival, these changes in climate may lead to alterations in the fuel load, fire weather and ignition probability, consequently altering the fire regime (Mouillot, Rambal & Joffre, 2002; Wilson, Latimer, Silander, Gelfand & de Klerk, 2010; Kraaij, Cowling & van Wilgen, 2013a) and impacting on the distribution, composition and function of vegetation (Bond & Keeley, 2005). A sound understanding of the complex relationship between climate, fire and plant species distributions is required to ensure effective conservation and management of fire-prone vegetation, especially in Global Biodiversity Hotspots like the CFR (Myers, Mittermeier, Mittermeier, Fonseca & Kent, 2000).

Species distribution models (SDMs) enable us to understand and project the effects of climate change on biodiversity, helping guide conservation strategies and policies. To date, most SDMs studies use only abiotic variables such as climate and soils (Midgley et al., 2003; Parmesan & Yohe, 2003; Guisan & Thuiller, 2005) and/or do not consider the biology of the species being modeled. This limits their ability to detect or predict potential nonlinear ecosystem responses, such as the complex feedback between climate, vegetation and fire. Fortunately, there has been rapid development of SDMs that incorporate species biology over the past decade (e.g. Keith et al., 2008; Franklin, 2010; Csergő et al., 2017), and studies in fire-prone ecosystems are increasingly incorporating fire information into SDMs (Keith et al., 2008; Tucker et al., 2012; Crimmins, Dobrowski, Mynsberge & Safford, 2014; Merow, Smith & Silander, 2014), yet there is still much to be learned. While there is ample observational and experimental evidence regarding the importance of fire in determining the survival of plant species with different life history traits at

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local sites (Brown, 1993; Keeley, Pausas, Rundel, Bond & Bradstock, 2011; Kraaij, Cowling, van Wilgen & Schutte-Vlok, 2013b; Shryock, DeFalco & Esque, 2014), few studies have scaled up to explore the implications for species global geographical distributions. In particular, studies that include fire data and compare the influence of fire on the distributions of multiple species with different life history traits (e.g. Keith et al., 2008; Lawson, Regan, Zedler & Franklin, 2010; Crimmins et al., 2014) are rare.

The importance of traits in determining species responses to environmental change in distribution studies is well acknowledged (Syphard & Franklin, 2010; Dobrowski et al., 2011; Wiens, 2011; Kharouba, McCune, Thuiller & Huntley, 2013). Life history traits describe the adaptations employed by an individual during different stages in its life cycle (i.e. growth, reproduction and survival) in response to environmental conditions (van Wilgen & Forsyth, 1992). Fire response strategies are a key component of the life history of plants in fire prone environments such as the CFR. They are often simplified into three categories: obligate seeders, that are killed by fire and recruit from seed in the post-fire environment; facultative resprouters, that both resprout and recruit seedlings from fire cued seed banks post fire; and obligate resprouters, that do not have fire resistant seedbanks and regenerate after fire by sprouting from dormant buds (Bell, Hopkins & Pate, 1984; Keeley, Bond, Bradstock, Pausas & Rundel, 2012; Pratt, Jacobsen, Jacobs & Esler, 2012; Marais, Pratt, Jacobs, Jacobsen & Esler, 2014). All three fire response strategies are observed in the five growth forms widely used to describe plant species in the CFR, i.e. trees, shrubs, herbs, geophytes and graminoids (Goldblatt & Manning, 2000).

Fire response strategy determines the survival of fynbos species under varying fire regimes. For example, seeder species are killed by fire, but recruit rapidly and in typically in large numbers from fire-resistant seed banks (soil or canopy) in order to persist (Le Maitre & Midgley, 1992). Recruitment after a fire significantly depletes these seed banks. For example, Pierce & Cowling (1991) found that more than half of the seed banks belonging to six fynbos shrubs were depleted after a fire. This makes seeder species highly dependent on post fire conditions (e.g. weather; Slingsby et al., 2017) and fire-free intervals long enough for individuals to germinate, reach maturity and sufficiently replenish their seed banks before the next fire occurs (Pausas, Bradstock, Keith & Keeley, 2004; Pratt et al., 2012, Pausas & Keeley, 2014). In contrast, obligate and facultative resprouters typically possess defensive structures (bark, buds and storage tissue) that enable them to survive and regenerate after a fire, making fire free periods less important for individual persistence. However, investment in protective structures and storage tissues, often

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combined with short-lived fire-sensitive seeds (Keeley, 1997), means that resprouters tend to be slower growing and require longer maturation periods than seeders (Pausas et al., 2004; Lamont, Enright & He, 2011). Therefore, the stability of resprouter populations may require long fire free periods so that individuals can establish and transition into adults mature enough to resist fire (Keeley, 1992). In light of this, we expect that species response to different environmental covariates, particularly fire, should differ according to their respective life histories.

Previous studies that have explored the influence of fire response strategies on species distributions found that fire response strategies affect the accuracy of SDMs, with obligate seeders exhibiting greater model accuracy than resprouters (Syphard & Franklin, 2010; Crimmins et al., 2014). These findings are indicative of the mediating effect of fire response strategies on species-environment responses (Keith et al., 2008; Lawson et al., 2010). Here, we explore the importance of fire in determining the distribution of fynbos species with different life history traits (growth form and fire response strategy). We model the distributions of 52 closely related fynbos plant species pairs (104 species), classified across two growth forms (graminoids and shrubs) and their respective fire response strategies (seeder versus resprouter). We address the following questions: (1) to what extent does fire determine species distributions relative to climate and soils? (2) Does the importance of fire vary between species of differing life histories? To address these two questions, post-hoc analyses of model output and permutation procedures were employed.

3.3 Methods

3.3.1 Study area

Our study focuses on fynbos vegetation within the CFR, a Global Biodiversity Hotspot (Myers et al., 2000; Cowling, Pressey, Rouget & Lombard, 2003) located on the south-western tip of Africa. Approximately 70% of the ±9000 plant species found in the CFR are endemic to the region (Goldblatt, 1978; Linder, 2003). Fynbos accounts for almost 80% of the vegetation in the CFR and is characterized by four major growth forms: graminoids (restioids), tall shrubs (proteoids), sub-shrubs (ericoids), and geophytes (Cowling & Richardson, 1995). The geology of the CFR is dominated by layers of sandstone and shale, which gave rise to distinct soil types ranging from poor nutrient sandy soils to richer clay soils (Goldblatt & Manning, 2000).

The CFR falls within a predominantly Mediterranean climate (Köppen, 1931), with the west experiencing wet winters and hot, dry summers, and bimodal rainfall peaking in March and September in the east (Schulze, 2007; Southey, 2009; van Wilgen et al., 2010). Fynbos is fire-

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prone (Bond & Keeley, 2005), with natural fires mainly occurring during the dry, hot summer period (Cowling et al., 1992). The average fire return interval ranges between 10-30 years, with few stands surviving beyond 40 to 50 years without burning (Keeley et al., 2012).

3.3.2 Data

3.3.2.1 Species occurrence data

Species occurrence data were acquired from the National Herbarium Pretoria Computerised Information System database (PRECIS, Russell, 1985). All non-indigenous species were removed from the PRECIS dataset, and only perennial species with more than 15 records within intact fynbos, with a location accuracy of <2km, were retained. The data were classified into growth forms and fire response strategy using information from the Plants of South Africa database (POSA, Germishuizen & Meyer, 2003). Here, obligate seeder species were classified as seeders, while obligate and facultative resprouter species were combined into one class as resprouters. To account for potential phylogenetic autocorrelation, pairs of species within the same lineage, but with contrasting life history traits, were selected. Phylogenetic autocorrelation is a potential confounding factor when making comparisons among multiple species, because closely related species tend to share similar traits and ecological behaviour, potentially biasing statistical inferences in multi-species models (Felsenstein, 1985, Blomberg, Garland & Ives, 2003, Peres-Neto, 2006). It is therefore necessary to account for phylogenetic autocorrelation when comparing among species so as to avoid potential type I errors (detection of a relationship between variables that does not exist), or type II errors (not detecting a relationship between variables that does exist) (Abouheif, 1999). As a result, a total of 52 species pairs were selected for the study (see Appendix 3-1).

The data set was examined for spatial sampling bias, a common limitation found in presence-only data where some areas in the landscape are sampled more intensively than others, which could lead to misrepresentation of the real distribution of species (Reddy & Dávalos, 2003; Kadmon, Farber & Danin, 2004). We compared the species occurrence data and a random sample of points, finding the majority of both to be located within a 1km of a road (see Appendix A for details and Appendix 3-2). These results are reflective of the very dense network of roads that exists within the study area, and it is unlikely that our sample is biased with respect to the environmental covariates used in the study.

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3.3.2.2 Environmental variables

Environmental variables were selected based on their capacity to reflect the relationship between species prevalence and the environment, giving due consideration to appropriate scale (Alvarado-Serrano & Knowles, 2014, Table 3-1). These consisted of five climatic variables: mean annual precipitation, mean January precipitation, Markham`s precipitation concentration (Markham, 1970), mean maximum January (summer) temperature, mean minimum July (winter) temperature; one soil variable, representing pH, fertility and texture, and one fire variable, representing fire return interval (Table 3-1).

Table 3-1. Details of environmental variables selected for modelling.

Variable	Range	Biological significance
Fire return interval (FRI)	0.6 – 32.7 years	Fire destroys above ground biomass, exterminating species that cannot resprout or do not have a strategy for regenerating from seed (Bond & Midgley, 2001; Altwegg et al., 2014). Fire stimulates various reproductive strategies amongst fynbos species, many of which are dependent on fire for flowering, seed release or germination (Cocks & Stock, 1997; Brown et al., 2003; Southey, 2009; Keeley et al., 2012). Ash from fire acts as a mineralizing agent for fynbos (Stock & Lewis, 1986a).
Mean annual precipitation (MAP) Mean January precipitation (Summer PPT)	20 – 3198 mm 0 – 111 mm	Distribution of fynbos species closely linked to rainfall regime and gradients (Goldblatt & Manning, 2000; Cowling et al., 2005).
Mean maximum January temperature (Summer Tmax)	13.1 – 35.1 ºC	Temperature affects physiological functioning (e.g. water and nutrient assimilation, as well as growth processes such as germination and bud break (Midgley et al., 2002).
Mean minimum July temperature (Winter Tmin)	-4.9 – 10.6 ºC	

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Markham`s precipitation concentration (PPT seasonality)	0.5 – 51.5%	Rainfall seasonality is closely linked to the persistence of fynbos seeder and resprouter species in response to fire events (Ojeda, 1998; Ojeda et al., 2005; Altwegg et al., 2014)
Soils (Soil)	-0.48 – 0.55 (PCA axis 1 scores, see Appendix 3-7)	Fynbos is associated with sandy nutrient poor soils (Cowling & Holmes, 1992; Cramer et al., 2014), and many species are strongly limited by soil texture and pH (Esler et al., 2015)

Climatic variables were derived from long-term (1950-2000) mean climate data from the South African Atlas of Agrohydrology and Climatology (Schulze, 2007). Markham`s precipitation concentration represents precipitation seasonality and ranges from 0% to 100%. A value of 0% indicates equal rainfall throughout the year, while 100% indicates that all precipitation falls in a single month (Markham, 1970; Wilson et al., 2015). The soil variable was derived from a 1:250 000 geological map from the Council for Geosciences for which each lithology was classified by experts into fertility (4 classes), texture (4 classes) and pH classes (3 classes) and rasterized (Latimer et al., 2006). We reduced the dimensionality of the soil data by performing a principal coordinate analysis (PCoA) and retaining only the first PCoA axis, which captured 56% of the variance (see Appendix A for details). Low axis scores represent nutrient poor, coarse-textured, acidic soils, while high axis scores represent fertile, fine textured, alkaline soils.

Our fire variable was derived from a hierarchical Bayesian statistical framework that modelled post-fire recovery based on ten years (2000-2010) of remotely sensed Moderate Resolution Imaging Spectroradiometer (MODIS) 500m resolution 16-day gridded Normalized Difference Vegetation Index (NDVI) data (Wilson, Latimer & Silander, 2015). The variable represents the time required for the vegetation to recover to the point where it can once again carry a fire and has been used in other species distribution modelling studies (e.g. Merow et al., 2014). Wilson et al., (2015) corroborated that it is a good proxy for fire return interval by comparing it with a survival model fit with observed fire return times (see Appendix A for more details). While other components of the fire regime may also affect species' distributions (e.g. severity/intensity, timing), no such data were available. Fire return interval is perhaps the most important component of the fire regime in the CFR, as most seeder species depend on fires for seed release and/or

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germination, and require long fire-free intervals to flower and develop seed before the next fire, but not so long that they begin to senesce (Forsyth & van Wilgen, 2008; van Wilgen et al., 2010; Altwegg, de Klerk & Midgley, 2014).

A test for collinearity (level of dependence) amongst the selected variables established that none of the variables were correlated at r >|0.7| (see Dormann et al., 2013), therefore all seven variables were retained. All data were trimmed to the extent of untransformed fynbos in the CFR (40 966.1km^2), because our fire variable could not be derived for transformed areas and because our species locality information was likely biased towards untransformed areas. All data were resampled to 1min (~1.55 x 1.85 km) to match the lowest resolution data source; the soil data.

3.3.3 Model settings and outputs

The Maxent (maximum entropy) software package (http://www.cs.princeton.edu/~schapire/Maxent/; (Phillips, Dudik & Schapire, 2004; Phillips, Anderson & Schapire, 2006) was used to develop species distribution models (SDMs), and to measure the relative contribution of each variable for predicting each species' distribution (Phillips et al., 2006). Maxent is a machine-learning model that was preferred over other approaches due to its robust method in handling presence-only, non-stratified data. The Maxent algorithm estimates the probability distribution with the maximum entropy, i.e. the distribution that is most spread out, or closest to uniform after all constraints are taken into consideration (Phillips et al., 2006), by contrasting environmental conditions at the locations of presence data against those at the background location points where presence/absence is not measured.

We fitted the model with seven predictor variables (i.e. map, Summer PPT, PPT seasonality, Winter Tmin, Summer Tmax, Soil and FRI) and ran ten replicates of the model. Using a random split, 70% of the occurrence records were set aside to train the model, and 30% as test data. Background samples were set at the default of 10000 points. Only linear features were selected, as the use of simple models is more suitable when investigating the importance of predictors (Merow, Smith & Silander, 2013). It avoids complex interactions among variables and the response curves are easier to interpret, making the models more suited to hypothesis testing about key drivers of species distributions. Excluding quadratic features (i.e. unimodal relationships between species occurrence and covariates) was justified because comparison of AIC from logistic regression models, where each covariate was fitted as a linear feature only versus as a quadratic

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feature for each species, indicated preference for the linear model (ΔAUC>2) or did not distinguish between models (ΔAUC<2) in >90% of comparisons (see Appendix 3-3).

3.3.3.1 Jack-knife test scores and permutation importance

To evaluate the importance of fire in predicting species distributions relative to climate and soil, we considered Maxent's jack-knife analysis of the area under the receiver operator curve (AUC) and permutation importance values. These outputs measure the extent to which each variable contributes to the model outcome i.e. indicates the strength of the relationship between a particular variable and the distribution of the species (Phillips et al., 2006).

The jack-knife test estimates the change in AUC when each variable is removed from the model, and when each variable is used in isolation. The AUC value indicates the effectiveness of each variable in predicting species presence in the model. These values range from 0 to 1, where < 0.5 indicates a relationship worse than random, 0.5 indicates that the model has no predictive power (no better than random), and 1 signifies a perfect model (Elith et al., 2006). Models with AUC values > 0.9 are considered to be of high accuracy, while those with values in the range 0.7–0.9 are useful; and those < 0.7 fairly accurate (Swets, 1988). Models with AUC <0.5 were excluded from our study.

Maxent provides other estimates of variable importance in the form of percent contribution and permutation importance. Percent contribution is a heuristically defined estimate that depends on the path that the Maxent code uses to get to the optimal solution. With each different path, a different percent contribution is given (Kalle, Ramesh, Qureshi & Sankar, 2013). We preferred the use of permutation importance as is based on the final model rather than the path used to obtain it, although the results for both estimates of variable importance were very similar. Permutation importance is measured by randomly permuting the values of each environmental variable against training presence and background data (Phillips, 2009). The resulting decrease in training AUC indicates the extent to which the model depends on that variable, i.e. the greater the decrease in training AUC, the greater the explanatory capacity of the variable. Permutation importance scores are normalized and expressed as percentages (Phillips et al., 2006).

3.3.3.2 Response curves

To establish the direction of the effect of fire on species across the different life histories (over and above the importance), we assessed the slope of the curves of the response to each

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environmental variable for each combination of growth form and life history, based on the lambda values from the Maxent model runs.

3.3.3.3 Statistical analysis of outputs

We performed an ANOVA test for significant differences among variables in their permutation importance and slopes of the relationship for all species. To test whether species responses to each environmental variable depends on their life history traits, we fitted linear mixed effect models using the 'lme4' package (Bates, Mächler, Bolker & Walker, 2014) in R (R Core Team, 2015). Permutation importance values were extracted from the Maxent output and modelled as a function of species life history traits. Growth form and fire response were assigned as fixed effects with an interaction term, while contrasting species pairs were set as the random effect to account for phylogenetic autocorrelation. Linear mixed effect models were fit separately for each environmental variable due to sample size constraints.

3.4 Results

3.4.1 Jack-knife scores

The full model (all seven variables) achieved good accuracy (median AUC = 0.88, interquartile range = 0.8 – 0.94) in determining the distribution of species across all four life history types, despite variability among species within and between life history types (Figure 3-1). The AUC remained generally high across all life histories regardless of the omission of any of the seven variables. While this may vary by species, the lack of trend suggests that no variable consistently contributed important unique information across all species within a life history type that was not already present in the other six. The observed AUC values when the model is based on a single variable, however, do show variation in the relative strengths of each variable as a predictor of fynbos species distributions (Figure 3-1). Most univariate models had AUC scores > 0.5, suggesting that almost all variables have some power to predict the distribution of our focal species.

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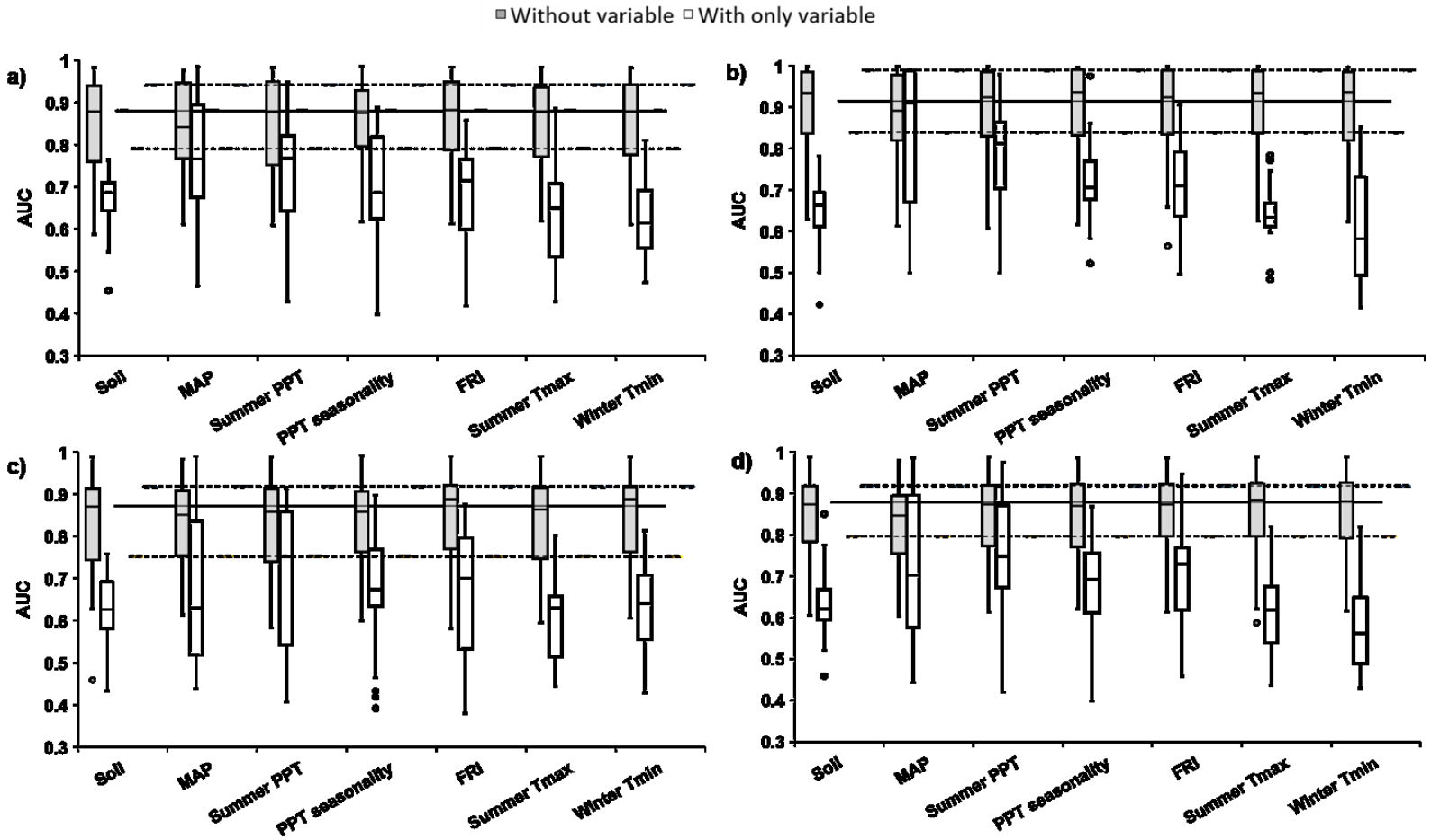

Figure 3-1. Relative importance of predictor variables as described by AUC scores for (a) resprouter graminoids, (b) seeder graminoids, (c) resprouter shrubs and (d) seeder shrubs. Grey and white bars represent models where each variable was withheld, and where each variable was used in isolation, respectively. Horizontal line indicates the median AUC, while stippled lines show interquartile ranges for each life history.

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3.4.2 Permutation importance

Permutation importance, representing the normalized change from the AUC for the optimal model with all variables for each species, revealed that there were significant differences in the importance of variables across all species (see Appendix 3-4), with FRI, MAP and PPT seasonality, generally being the strongest determinants of fynbos plant species distributions ($F = 21.83$, $Df = 6$, $P < 0.001$), although this varied among life histories (Figure 3-2).

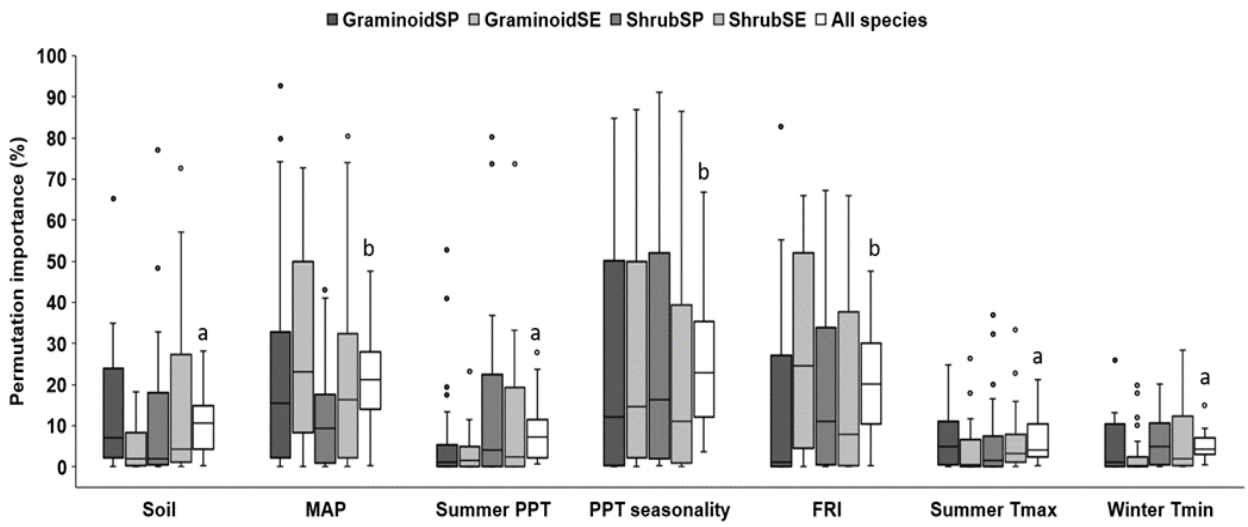

Figure 3-2. Variable importance as described by permutation importance for resprouter graminoids (GraminoidSP), seeder graminoids (GraminoidSE), resprouter shrubs (ShrubSP), seeder shrubs (ShrubSE*)* and all species. Letters indicate significant differences among variables based on an ANOVA on all species ($F = 21.83$, $Df = 6$, $P < 0.001$).

The linear mixed effects analysis exploring variation in the permutation importance scores for each variable revealed significant differences among species with different life history in response to FRI (see Appendix 3-5). Seeders were significantly more sensitive to fire than resprouters ($P < 0.05$), likely driven by the large difference between seeder graminoids (median = 24.5%) and resprouting graminoids (1.2%). For the climate variables, shrub species were significantly less sensitive to MAP than graminoids ($P \leq 0.05$). For soils, seeders were significantly ($P < 0.05$) less sensitive to soil properties than resprouters, but there was a significant ($P \leq 0.05$) interaction between the shrub growth form and seeder strategy, suggesting that seeder shrubs are more sensitive to edaphic conditions than resprouter shrubs.

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3.4.3 Response curves

The response curves indicate the direction of the relationship between species and the different environmental variables used (Figure 3-3). We observed that species across all life histories have a negative response to increasing fire return interval (Figure 3-3); i.e. a longer fire return interval results in the reduced probability of occurrence of all species. This negative relationship was also apparent for Soil, Summer PPT, Winter Tmin and Summer Tmax (i.e. hotter, more fertile conditions with higher summer rainfall), while a positive relationship was noted for MAP (higher rainfall) and PPT seasonality (stronger seasonality), generally representing the dominant environmental conditions in the mountains of the CFR ($F = 8.376$, $Df = 6$, $P < 0.001$).

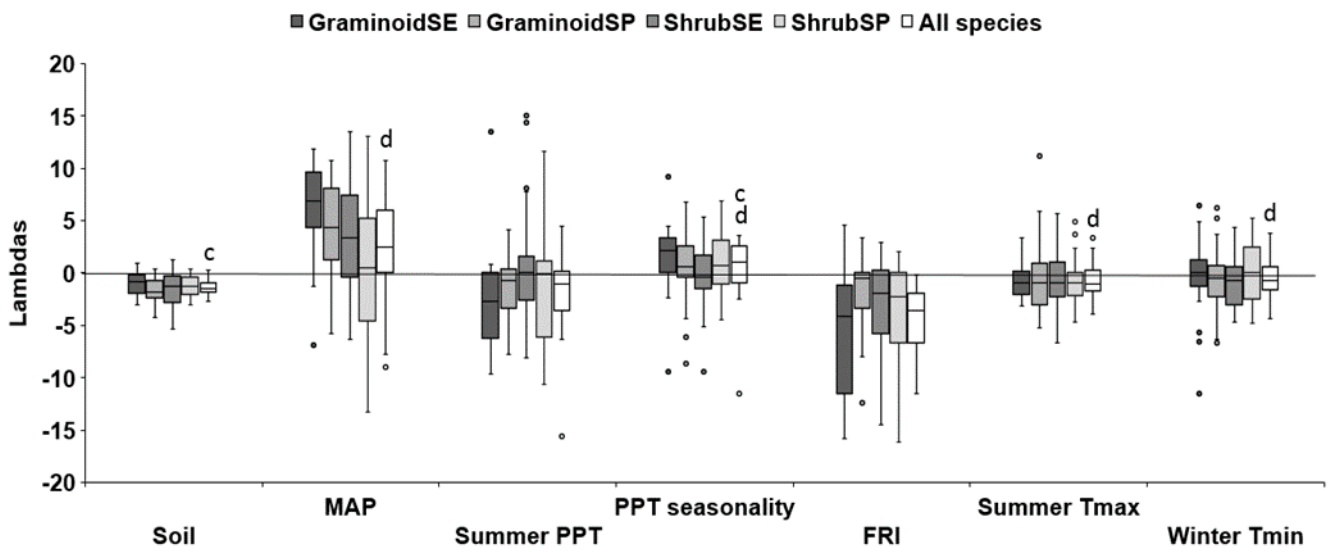

Figure 3-3. Species response to environmental variables based on slopes of the Maxent response curves for resprouter graminoids (GraminoidSP), seeder graminoids (GraminoidSE), resprouter shrubs (ShrubSP), seeder shrubs (ShrubSE) and all species. Positive lambda values indicate a positive relationship between the life history trait and corresponding variable, a negative lambda value indicates a negative relationship. Letters indicate significant differences among variables based on an ANOVA on all species ($F = 8.38$, $Df = 6$, $P < 0.001$).

The linear mixed effect analysis on the slopes of the response curves revealed that there was a significantly more negative relationship between seeders and fire return interval as compared to resprouters ($P < 0.05$, see Appendix 3-6), although the interaction term suggested that seeder shrub species were less affected. The inverse was true for the soil variable, with seeders showing significantly a less negative relationship ($P < 0.05$), but seeder shrubs showing little response. This may suggest that seeder species do better in sites characterised by more fertile soils and shorter

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fire return intervals than resprouters. There were significant ($P \leq 0.05$) interactions between the shrub growth form and seeder strategy in response to fire return interval (positive) and soils (negative), indicating that seeder shrubs are better suited to longer fire return intervals and more fertile soils than other functional types.

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3.5 Discussion

Species distribution models (SDMs) are central to improving our understanding of how species may respond to climate change. Various studies allude to the need to incorporate more non-climatic variables and consider functional trait differences amongst species when modelling their distributions (Heikkinen et al., 2006; Yates et al., 2010; Syphard & Franklin, 2010; Austin & van Niel, 2011; Enright, Fontaine, Lamont, Miller & Westcott, 2014; Franklin, Serra-Diaz, Syphard & Regan, 2016). Such modifications to traditional SDMs (typically exclusively based on climate and soils) are suggested to be necessary for the detection of underlying complex species-environment relationships, as well as the improvement of model accuracy in predicting species distributions. Given that fire is a significant driver of vegetation dynamics in Mediterranean-type ecosystems such as the CFR (van Wilgen & Forsyth, 1992; Bond & Keeley, 2005; Keeley et al., 2012), we hypothesized that fire would be a significant predictor of plant species distributions and therefore its inclusion in SDMs was warranted. We further hypothesized that the distribution of fynbos plant species would vary across life histories, with differences in the distribution of species stemming from underlying trait-driven responses to environmental conditions.

Output from our models confirm the importance of fire as a determinant of fynbos plant species distributions. The permutation importance and jackknife test scores identified rainfall, particularly annual precipitation (MAP), rainfall seasonality (PPT seasonality) and mean January precipitation (Summer PPT), followed by fire return interval (FRI) as the major determinants of the distribution of fynbos species in this study. These observations are supported by other studies that highlight the complementary roles of rainfall and fire in the reproductive and physiological processes that occur in fynbos species (van Wilgen et al., 1992; Cowling & Heijnis, 2001; Cowling, Ojeda, Lamont, Rundel & Lechmere-Oertel, 2005; Procheş, Cowling & Preez, 2005; Keeley et al., 2012). For instance, dry season fires initiate flowering and/or seed release, and break seed dormancy, in many fynbos species (Brown, 1993; Keeley et al., 2012), while winter rainfall facilitates germination and the growth of new seedlings. Furthermore, a demographic study by Treurnicht et al., (2016) found that while climate had a dominant effect on the recruitment of 26-shrub species (Proteaceae), fecundity was mostly fire-driven. In other studies; Lawson et al., (2010) and Regan, Crookston, Swab, Franklin & Lawson, (2010) used spatially explicit stochastic population models to show that changes in fire return interval have significant effects on population abundance relative to other threats such as climate change and land use. Demonstrating the influence of fire

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on the distribution of plant species further cements concerns not only for the impacts of climate change but for changing fire regimes on biodiversity in fire prone environments, and a need for models that capture the interaction of fire and climate (Abbott & Le Maitre, 2009; Yates et al., 2010).

Fire return interval was a stronger determinant of the distribution of seeder species than resprouters, confirming the variation in sensitivity of resprouters and seeders to fire regimes cited by other studies (Bond & Midgley, 2001; Keith et al., 2008; Wilson, Latimer, Silander, Gelfand & de Klerk, 2010; Enright et al., 2014). Seeder species are highly dependent on the timing and frequency of fire (Altwegg et al., 2014; Pausas & Keeley, 2014). Most seeders require fires to release seed and/or germinate and depend on fire-free intervals long enough for individuals to establish and mature, but not so long that they begin to senesce (Pratt et al., 2012). In contrast, resprouters exhibit greater resilience in their interaction with fire, with rapid regrowth and defensive structures (e.g. thick bark) facilitating continued persistence under a range of fire return intervals (Lamont et al., 2011).

While our results show that fire is an important determinant of fynbos species' distributions, models that excluded fire, and many that were based on single climatic variables, generally showed good predictive accuracy (AUC > 0.75). These results agree with those of Tucker et al. (2012), who found that fire variables did not greatly improve predictions of shrub species presence in the CFR. In a related study based in California, Crimmins and coworkers (2014) also found that fire occurrence generally did not improve model accuracy in predicting the distribution of a set of vascular plant species. The corroboration between our results and those of Tucker et al., (2012) and Crimmins et al., (2014) is not surprising given that fire is inherently a weaker determinant of fynbos distributions when compared to climate. This is likely to be due to the dependence of fire on climate, resulting in shared explanatory ability between fire and climate-related covariates (Tucker et al., 2012). Fire regimes are typically a function of rainfall seasonality, which affects the occurrence of fire weather and fuel moisture content (flammability), and precipitation (buildup of fuel load) (Wilson et al., 2010; Pausas & Paula, 2012; Ellis, Verboom, van der Niet, Johnson & Linder, 2014). Fire regime, however, holds the potential to change in a non-linear manner, with negative implications for species distributions and vegetation composition. Changes in fire regime may be affected through changes in fuel properties due to shifts in species composition (e.g. grasses or invasive alien trees), increased frequency of extreme fire weather, or direct human

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alterations in probability of ignition and fire spread (i.e. from fire suppression or habitat fragmentation). Therefore, fire information may not be essential for predicting historical fynbos distributions, but are likely to become crucial for achieving a more accurate understanding of how fynbos distributions may change in future.

Interestingly, soil texture, pH and fertility (i.e. the Soil layer) were weaker determinants of fynbos distribution. Variation in the distribution of fynbos plant species along edaphic gradients is well documented (Cowling, 1990; Richards, Cowling & Stock, 1997; Cramer, West & Power, 2014; Cowling & Potts, 2015). Proteoid fynbos, for example, generally occurs in deep fertile soils at the base of mountains, while ericoids prefer higher elevations with organic-rich fine grain soils and restioids dominate shallow dry soils on the warm north facing slopes (Cowling & Holmes, 1992a; Cowling, Richardson & Mustart, 1997). Hence, a stronger association between the edaphic layer and fynbos species in our study was expected. The low variable importance scores observed for edaphic conditions (Soil) in our study may be a result of the exclusion of higher nutrient/finer texture soils in the Soil layer, as these areas have largely been transformed by agriculture. This may have led to insufficient variation in edaphic conditions for the model to detect strong relationship between the species occurrence and soil properties. It is also possible that the ordinal classification of soil properties and the spatial resolution of the soil data (~1.75km) were too coarse to distil a stronger relationship between species occurrence and edaphic conditions (Guisan & Thuiller, 2005; Austin & van Niel, 2011; Bucklin et al., 2015).

Species across all life histories were shown to be largely associated with conditions typical of mountain fynbos; shorter fire return intervals, low summer rainfall, cool winters and summers, high annual rainfall, strong rainfall seasonality, and sandy, acidic, nutrient poor soils. Within these bounds, seeder species were significantly limited in their distribution by fire return interval, while edaphic conditions had greater influence on resprouters. This finding supports other studies that allude to the dominance of either resprouters or seeders along fire and edaphic gradients (Wisheu, Rosenzweig, Olsvig-Whittaker & Shmida, 2000; Wuest et al., 2016). For example, Wisheu and coworkers (2000), found that there was a dominance of resprouters on fertile soils, while seeders dominated sites with nutrient-poor soils and frequent fires. The dominance of seeder species was attributed to their ability to make use of nutrients (released by the fire) just below the surface that resprouters, with deeper root systems, were not able to access.

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While our study only focuses on fire return interval, we do acknowledge the ecological importance of other components of the fire regime in driving plant species distributions in fire-prone ecosystems. For example, Altwegg et al. (2014) highlight the differential effects of fire seasonality and fire intensity on resprouters and seeders, that result in the dominance of one life history over the other in a given space. In their study, Altwegg and coworkers (2014) predict resprouters to have greater resilience against out of season fires, or fires followed by unfavorable conditions for establishment (e.g. unpredictable rainfall), while high intensity fires are predicted to favor seeder species. In light of this, there is a need for better estimates of more components of the fire regime for input into SDMs. Such estimates would provide a more holistic understanding of species responses to fire regime, and ultimately improve predictions of how changes in fire regime will influence future species distributions.

Anticipating the impacts of climate change on biodiversity in fire-prone ecosystems requires an approach where not only the interactions between plant species and climate, but also disturbance factors such as fire, form the basis of vulnerability assessments. Furthermore, the role of life history traits in driving the sensitivity of plant species to changes in ecological regime should also be considered. Despite the general assumption that species distributions are more strongly limited by climate as compared to edaphic conditions and or disturbance, our study indicates that disturbance variables such as fire have the capacity to add to our understanding of plant species distributions in fire-prone ecosystems, particularly in the case of seeder graminoids and shrubs. The variation in species' response to environmental covariates across different growth forms and fire-response strategies shows that life history traits are crucial to the identification of vulnerable species. By accounting for disturbance factors such as fire, and functional differences among species that may affect their response to disturbance, SDMs become better equipped to generate more accurate and appropriate information to guide future biodiversity conservation. Our study further highlights the need for better spatial estimates of fire regime parameters, and how these may be altered under global change, to support vulnerability assessments of vegetation in fire-prone ecosystems.

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3.6 Appendix A: Supplementary methods

3.6.1 Sampling bias in species occurrence data

We generated a set of random points in ArcGIS 10.2 (ESRI, 2013) to act as a proxy for a normally distributed sample. We then compared the proximity of the sample points to roads to that of the random points using the near tool in ArcGIS (ESRI, 2013), and also the distributions of both the sample points and the random points using Kolmogorov Smirnov and Mann-Whitney U tests in SPSS version 20 (IBM Corp, 2011). It was established that a majority of both the sample points and random points were located within a 1km of a road. These results are reflective of the very dense network of roads that exists within the study area (see Appendix 3-2), and it is unlikely that our sample is biased towards the environmental covariates used in the study.

3.6.2 Soil data

The soil data was acquired in the form of a raster with 11 data layers i.e. fertility (4 layers), texture (4 layers) and pH (3 layers) (Latimer, Wu, Gelfand & Silander, 2006). We then reduced the dimensionality of the soil data by performing a principal coordinate analysis (PCoA) on the Bray-Curtis distances between cells based on the 11 data layers pertaining to fertility, pH and texture. Only the first PCoA axis (representing 56% of the variance) was retained as all further PCoA axes represented only 15% of the variance or less. Since PCoA is computed from a distance matrix and cannot give back the loadings of the variables we compared the scores of the PC axis with the original soil property classes (see Appendix 3-7). Low axis scores represent nutrient poor, coarse-textured, acidic soils, while high axis scores represent fertile, fine textured, alkaline soils. The soil layer showed good discrimination among the major soil types that support fynbos vegetation (see Appendix 3-8; Mucina & Rutherford, 2006).

3.6.3 Fire return interval data

The overlapping of the time periods in which all data are collected in modelling species distributions is crucial to making accurate inferences from SDMs. In this respect, we provide further description of the fire variable here, highlighting how the time periods pertaining to the fire, climate and species' observations data used to estimate the post- fire recovery parameters (from which our fire data is derived) overlap. Firstly, since the recovery rates were estimated in the context of post-fire vegetation age and not chronological time, and these ages ranged up

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to 59 years old (Wilson, Latimer & Silander, 2015), the estimates include the influence of weather for decades prior to the NDVI record and encompass the period during which the majority of our species locality records were collected (Median: 1993, Interquartile Range: 1972:2003). Secondly, only sites representing natural vegetation and for which a fire had been recorded (from records going as far back as the 1950s) were used for model fitting, which was then projected for the rest of the biome. We omitted transformed areas from our analysis, so our locality data largely correspond with areas used for model fitting. Major advantages of using estimates of post-fire recovery rate, over observed fire activity data, are that the hierarchical Bayesian model borrows across space to estimate the expected post-fire recovery for a given environment, down-weighting the influence of anomalous data, and represent the potential to burn based on natural vegetation productivity, which largely excludes the influence of fire management (or lack thereof).

3.6.4 References

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3.7 Appendix B: Supplementary tables and figures

Appendix 3-1. The 104 fynbos species selected for the species modelling, with 26 pairs each for the shrub and graminoid species. Number of samples (N) for each species indicated in brackets. A linear mixed effect model indicated that samples size had no significant (P = 0.263) effect on model fit (AUC).

Shrubs		Graminoids	
Resprouter	Seeder	Resprouter	Seeder
Protea glabra (N =674)	*Protea mundii* (N =419)	*Elegia galpinii* (N = 19)	*Elegia neesii* (N = 18)
Protea nitida (N = 4685)	*Protea laurifolia* (N =5637)	*Elegia asperiflora* (N = 31)	*Elegia persistens* (N = 39)
Metalasia lichtensteinii (N=23)	*Metalasia fastigiata* (N=17)	*Elegia capensis* (N = 27)	*Elegia spathacea* (N = 50)
Berzelia intermedia (N = 92)	*Berzelia lanuginosa* (N = 46)	*Elegia racemosa* (N = 25)	*Elegia stipularis* (N = 34)
Erica coccinea (N = 47)	*Erica curviflora* (N = 47)	*Hypodiscus argenteus* (N = 44)	*Hypodiscus albo-aristatus* (N = 66)
Erica mammosa (N = 15)	*Erica densifolia* (N = 92)	*Hypodiscus laevigatus* (N = 15)	*Hypodiscus neesii* (N = 15)
Grubbia tomentosa (N = 21)	*Grubbia rosmarinifolia* (N = 24)	*Ischyrolepis virgea* (N = 19)	*Ischyrolepis monanthos* (N = 15)
Helichrysum teretifolium (N = 42)	*Helichrysum cymosum* (N = 48)	*Ischyrolepis unispicata* (N = 25)	*Ischyrolepis ocreata* (N = 27)
Oedera sedifolia (N = 17)	*Oedera imbricata* (N = 34)	*Restio dispar* (N = 19)	*Restio versatilis* (N = 22)
Pteronia teretifolia (N = 15)	*Pteronia camphorata* (N = 19)	*Restio egregius* (N = 47)	*Restio bifarius* (N = 51)
Senecio pinifolius (N = 26)	*Senecio pubigerus* (N = 18)	*Ehrharta rupestris* (N = 15)	*Ehrharta bulbosa* (N = 15)
Erica cerinthoides (N = 35)	*Erica ericoides* (N = 36)	*Restio fragilis* (N = 15)	*Restio stokoei* (N = 20)
Erica umbelliflora (N = 20)	*Erica conferta* (N = 22)	*Restio inconspicuus* (N = 82)	*Restio purpurascens* (N = 46)
Erica strigilifolia (N = 25)	*Erica equisetifolia* (N = 29)	*Restio perplexus* (N = 22)	*Restio debilis* (N = 29)
Clutia alaternoides (N = 99)	*Clutia polifolia* (N = 46)	*Restio triticeus* (N = 87)	*Restio similis* (N = 54)
Clutia polygonoides (N = 18)	*Clutia ericoides* (N = 19)	*Staberoha distachyos* (N = 27)	*Staberoha cernua* (N = 108)
Indigofera heterophylla (N = 21)	*Indigofera sarmentosa* (N = 19)	*Thamnochortus fruticosus* (N = 24)	*Thamnochortus platypteris* (N = 22)
Muraltia juniperifolia (N = 29)	*Muraltia ciliaris* (N = 37)	*Willdenowia arescens* (N = 44)	*Willdenowia glomerata* (N = 40)
Protea tenax (N = 381)	*Protea laevis* (N = 469)	*Ehrharta rehmannii* (N = 43)	*Ehrharta capensis* (N = 23)
Protea acaulos (N = 1467	*Protea punctata* (N = 1631)	*Eragrostis capensis* (N = 23)	*Eragrostis obtusa* (N = 17)
Phylica imberbis (N = 30)	*Phylica lachneaeoides* (N = 27)	*Pentaschistis colorata* (N = 102)	*Pentaschistis curvifolia* (N = 58)
Phylica leipoldtii (N = 16)	*Phylica pinea* (N = 15)	*Pentaschistis eriostoma* (N = 120)	*Pentaschistis pallida* (N = 65)
Agathosma bifida (N = 15)	*Agathosma mucronulata* (N = 17)	*Pentaschistis viscidula* (N = 18)	*Pentaschistis ampla* (N = 18)
Agathosma capensis (N = 58)	*Agathosma mundtii* (N = 33)	*Calopsis hyalina* (N = 19)	*Calopsis aspera* (N = 25)
Agathosma imbricata (N = 20)	*Agathosma unicarpellata* (N = 15)	*Calopsis paniculata* (N = 16)	*Calopsis monostylis* (N = 15)
Gnidia geminiflora (N = 30)	*Gnidia galpinii* (N = 32)	*Elegia juncea* (N = 125)	*Elegia filacea* (N = 96)

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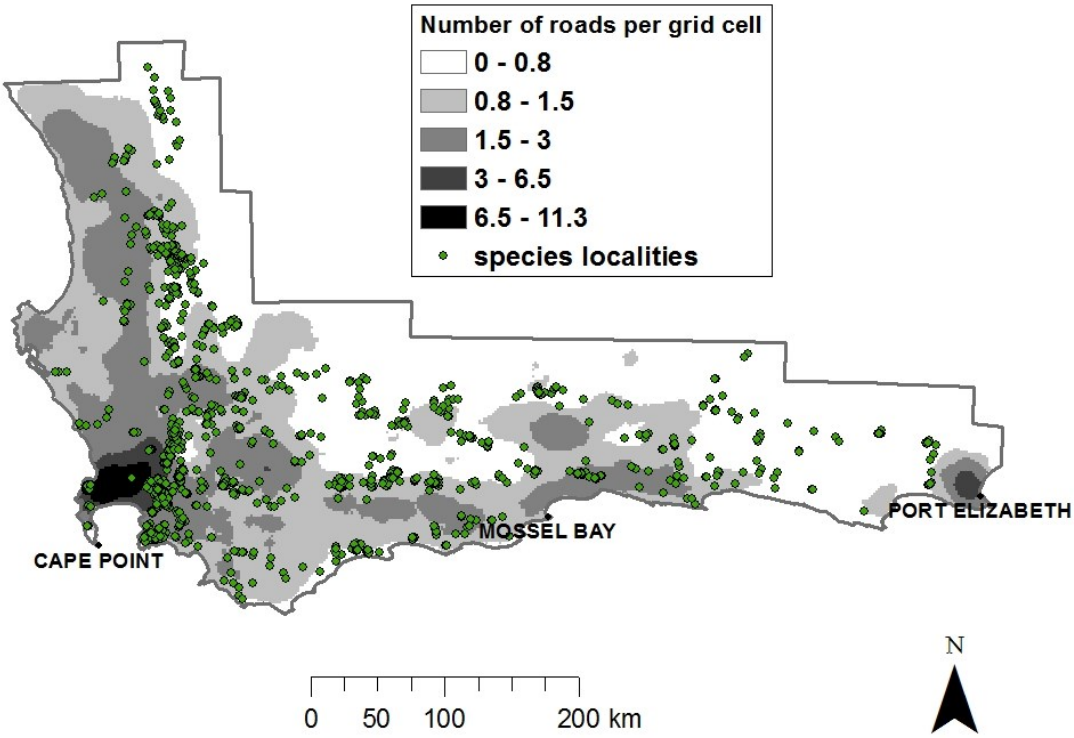

Appendix 3-2. Density of road network covering the study area (Cape Floristic Region) measured as the number of roads per grid cell and overlaid with species localities.

Appendix 3-3. Results of the logistic regression analysis showing the number of species (of 104) for which fitting each covariate as a linear feature only was preferred or not distinguished from fitting them as a quadratic feature based on AIC.

Variable	Number of species
FRI	102
MAP	98
PPT seasonality	100
Soil	97
Summer PPT	95
Summer Tmax	100
Winter Tmin	101

Notes: Pseudoabsences were created for each species by sampling twice the number of samples as the focal species observations from the locations of the remaining species set.

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Appendix 3-4. Post hoc comparisons of variable importance (based on permutation importance scores) as described by the Tukey HSD test.

	diff	lwr	upr	p adj
MAP-geocombined	11.12976	3.500847	18.75868	0.000366
Summer PPT-geocombined	-2.55033	-10.1792	5.078587	0.956488
PPT seasonality-geocombined	14.73299	7.104073	22.3619	3.41E-07
FRI-geocombined	9.339046	1.710132	16.96796	0.005821
Summer Tmax-geocombined	-5.31161	-12.9405	2.317302	0.37876
Winter Tmin-geocombined	-6.11974	-13.7487	1.509171	0.21213
Summer PPT-MAP	-13.6801	-21.309	-6.05117	3.17E-06
PPT seasonality-MAP	3.603226	-4.02569	11.23214	0.803791
FRI-MAP	-1.79072	-9.41963	5.838199	0.992927
Summer Tmax-MAP	-16.4414	-24.0703	-8.81246	3.09E-09
Winter Tmin-MAP	-17.2495	-24.8784	-9.62059	0
PPT seasonality-Summer PPT	17.28331	9.6544	24.91223	0
FRI-Summer PPT	11.88937	4.260459	19.51829	9.79E-05
Summer Tmax-Summer PPT	-2.76129	-10.3902	4.867629	0.936644
Winter Tmin-Summer PPT	-3.56942	-11.1983	4.059498	0.810741
FRI-PPT seasonality	-5.39394	-13.0229	2.234973	0.359373
Summer Tmax-PPT seasonality	-20.0446	-27.6735	-12.4157	0
Winter Tmin-PPT seasonality	-20.8527	-28.4816	-13.2238	0
Summer Tmax-FRI	-14.6507	-22.2796	-7.02174	4.09E-07
Winter Tmin-FRI	-15.4588	-23.0877	-7.82988	6.49E-08
Winter Tmin-Summer Tmax	-0.80813	-8.43704	6.820783	0.999924

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Appendix 3-5. Linear mixed effects model summary describing the importance of each environmental variable (measured as permutation importance) as a function of growth form and fire response strategy.

1

	[c]FRI			[d]MAP			[e]PPT seasonality			[f]Summer PPT			[g]Summer Tmax			[h]Soil			[i]Winter Tmin		
	B	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*
(Intercept)	**14.52**	**4.53**	***0***	**24.67**	**4.4**	***0***	**26.88**	**5.59**	***0***	**6.99**	**3.08**	***0.03***	**7.66**	**1.66**	***0***	**14.37**	**3.09**	***0***	**4.91**	**1.41**	***0***
Seeder	**15.27**	**6.41**	***0.02***	6.93	5.83	0.24	-2.6	7.9	0.74	-4	4.36	0.36	-3.68	2.13	0.09	**-10.06**	**4.37**	***0.03***	-1.87	2	0.36
Shrub	4.24	6.29	0.5	**-12.17**	**6.09**	***0.05***	3	7.75	0.7	6.57	4.28	0.13	-1.7	2.3	0.46	-2.39	4.29	0.58	2.45	1.97	0.22
Seeder - Shrub	-14.5	8.9	0.11	2.17	8.09	0.79	-4.43	10.96	0.69	1.15	6.05	0.85	3.87	2.96	0.2	**12.16**	**6.06**	***0.05***	-0.43	2.79	0.88

Appendix 3-6. Linear mixed effects model summary indicating the direction of the relationship between species and the selected environmental variables represented by the slope of the Maxent response curves as a function of growth form and fire response strategy.

	[1]FRI			[2]MAP			[3]PPT seasonality			[4]Summer PPT			[5]Summer Tmax			[6]Soil			[7]Winter Tmin		
	B	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*	*B*	*SE*	*p*
(Intercept)	**-2.07**	**0.94**	***0.03***	**4.21**	**2.19**	***0.06***	0.66	1.12	0.56	-2.17	1.8	0.23	-0.23	0.54	0.68	**-1.72**	**0.24**	**0**	-0.43	0.6	0.48
Seeder	**-3.77**	**1.34**	***0.007***	1.93	3.1	0.54	-0.89	1.5	0.56	-0.33	2.4	0.89	-0.39	0.77	0.61	**0.8**	**0.31**	***0.01***	0.02	0.85	0.98
Shrub	-1.46	1.34	0.28	*-5.15*	*3.1*	*0.1*	0.33	1.58	0.83	-2.4	2.54	0.35	-0.59	0.77	0.44	0.5	0.33	0.13	0.31	0.85	0.72
Seeder – Shrub	**3.95**	**1.89**	***0.04***	-3.26	4.38	0.46	-0.38	2.11	0.86	4.8	3.37	0.16	0.52	1.08	0.63	**-1.03**	**0.43**	***0.02***	-0.78	1.2	0.52

[c,1] Fire return interval
[d,2] Mean annual precipitation
[e,3] Markham`s precipitation concentration
[f,4] Mean January precipitation
[g,5] Mean maximum January (summer) temperature
[h,6] Soil pH, fertility and texture
[i,7] Mean minimum July (winter) temperature

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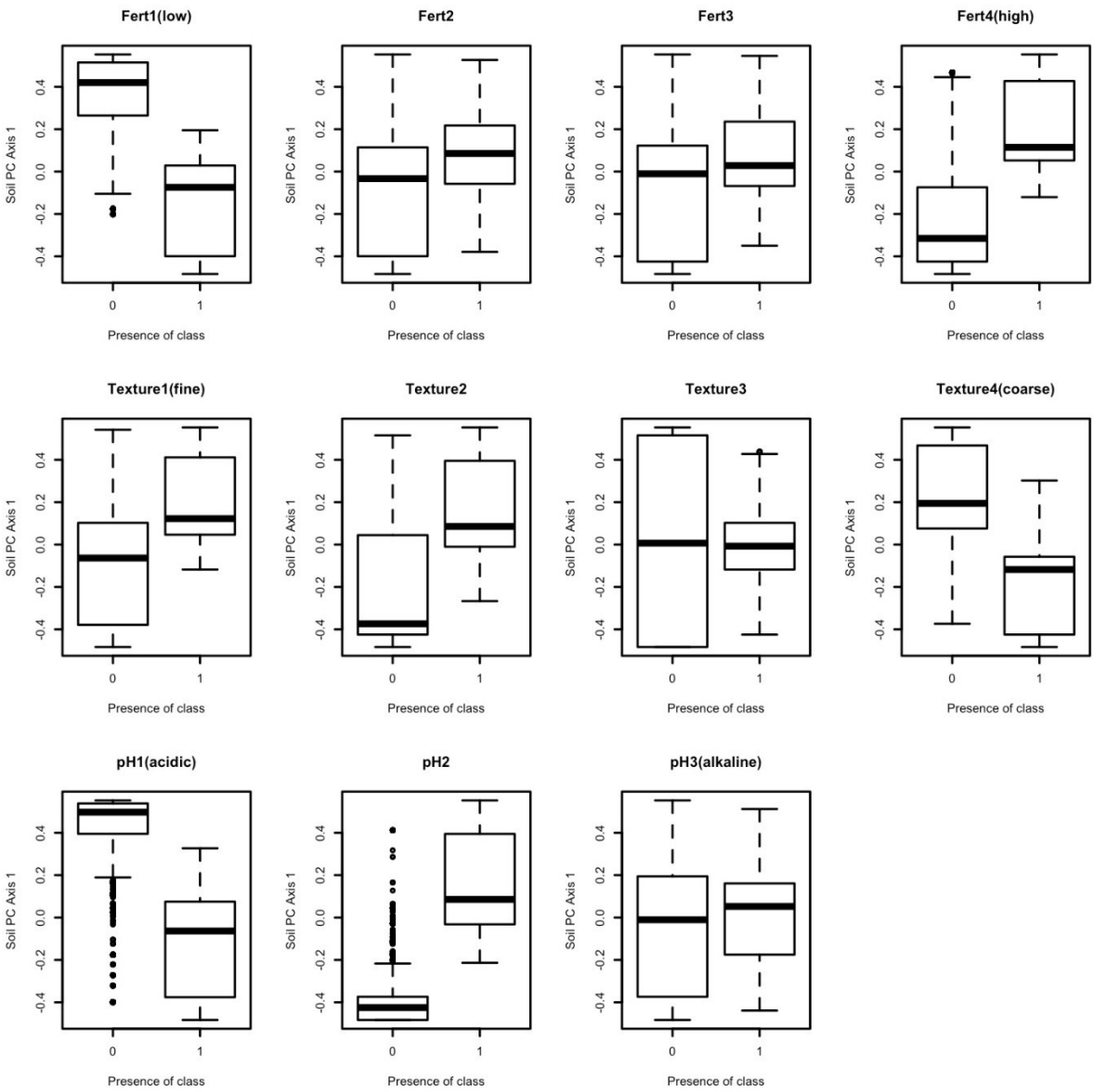

Appendix 3-7. PC Axis 1 scores from the *Soil* variable plotted against the original soil property classes as an alternative to actual loadings of the different soil layers (i.e. fertility, texture and pH) which were not available as result of the PCoA being derived from a distance matrix.

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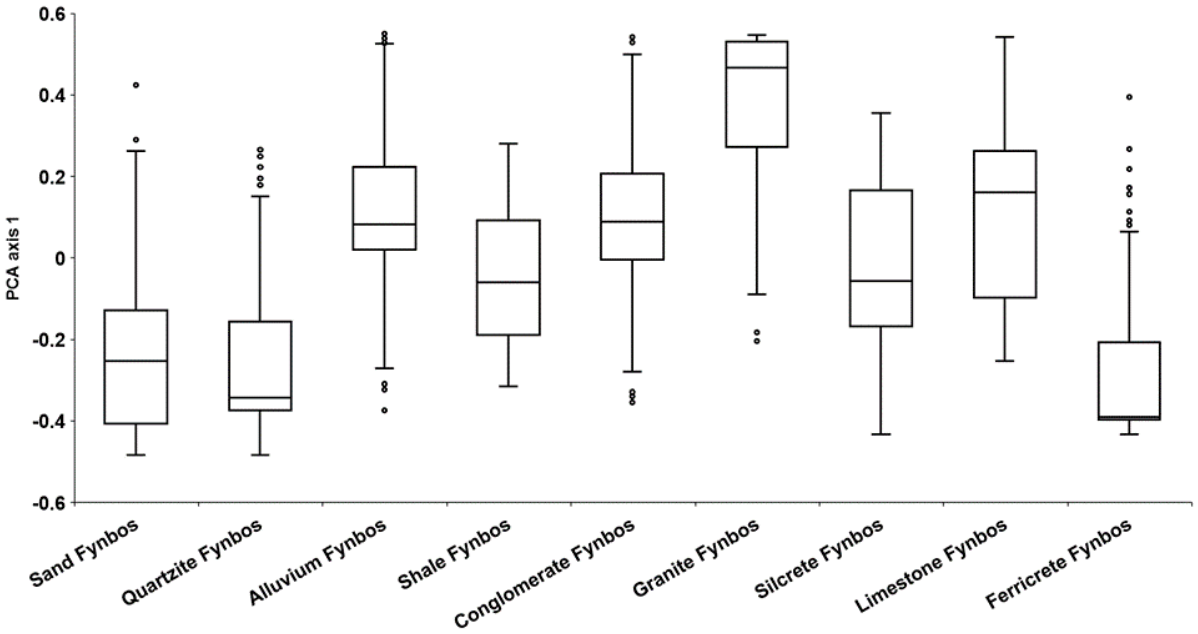

Appendix 3-8. PC Axis 1 scores from the Soil variable plotted against groupings of fynbos vegetation types based on soil type (Vegetation of South Africa, Lesotho and Swaziland Map, Mucina & Rutherford, 2006). Low PCA axis scores generally correspond with vegetation groups associated with nutrient poor, coarse-textured, acidic soils (e.g. Sand or Quartzite Fynbos), while high axis scores correspond with vegetation groups associated with fertile, fine textured, alkaline soils (e.g. Granite or Limestone fynbos).

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CHAPTER 4

4. VEGETATION RESPONSE TO PROJECTED CHANGES IN CLIMATE AND FIRE REGIME IN A MEDITERRANEAN TYPE ECOSYSTEM

4.1 Abstract

Aim: While much effort has been given to predicting potential biological responses to climate change, how changes in disturbance regimes such as fire may impact the future distribution of vegetation types remains unclear. Here, we investigate the contribution of fire in determining the distribution of fire-prone fynbos vegetation types, and the potential impacts of changes in climate and fire regime on their future distributions.

Location: Cape Floristic Region (CFR), South Africa

Methods: We modelled the current and future distribution of 22 fynbos vegetation types, using multinomial linear regression. The model was fit with five climatic variables, in conjunction with one edaphic and one fire variable. Future climate and fire data were derived from an ensemble of 11 CMIP5 general circulation models (GCMs), for the RCP4.5 and RCP8.5 scenarios, under the periods 2046-2065 and 2081-2100.

Results: As a stand-alone variable, fire return interval is the fourth strongest predictor of fynbos species distributions out of the seven covariates used in the study. However, the predictive power of the fire variable is greatly reduced when considered in conjunction with the other six variables. The areal extent of coastal vegetation types in the west is projected to increase, while higher altitude vegetation types in the east and interior are projected to decrease, in response to shorter fire return intervals. Projected changes in fire return interval and temperature are likely to have a significant impact on future vegetation distributions, with vegetation types located at sites with longer fire return intervals and warmer summer and winter temperatures being at most risk.

Main conclusions: Fire regime plays a significant role in the shaping and maintenance of vegetation distributions in fire-prone environments such as the CFR, and alterations to current

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fire regimes will likely have a greater impact on vegetation distribution than changes in rainfall regime. There is therefore a great need to develop and integrate robust estimates of historical and future fire into vulnerability assessments of vegetation in fire-prone ecosystems.

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4.2 Introduction

Fire is a key determinant of vegetation composition, structure and distribution in most Mediterranean type-ecosystems (MTEs), facilitating the recruitment and persistence of the majority of their plant species (Keeley et al., 2012). Numerous studies suggest that the predicted shift towards a warmer and drier climate in MTEs (Hennessy, 2006; Yates et al., 2010; IPCC, 2013) will result in dramatic shifts in fire activity throughout these regions (e.g. Batllori et al., 2013; Wilson et al., 2015). The coupled effect of changes in both climate and fire regimes will ultimately lead to the disruption of existing vegetation distributions as well as ecosystem functions (Gitay et al., 2001), and may result in the development of novel plant assemblages with unknown implications (Johnstone et al., 2016). An in-depth understanding of how vegetation in MTEs interacts with the environment and, more importantly, how vegetation will respond to changes in both climate and fire regimes, will be critical for mitigating and/or adapting to biodiversity loss (Bowman et al., 2009; Yates et al., 2010).

Our understanding of how climate change may impact vegetation is largely drawn from distribution models (Cramer et al., 2001; Bond et al., 2003; Moretti et al., 2006; Lötter & Le Maitre, 2014). Vegetation distribution models have been used for decades to predict future distribution patterns (Bomhard et al., 2005; Lucas et al., 2017), investigate species-environment relationships (Moretti et al., 2006), and test ecological theories (Danz et al., 2013). These models are founded on the premise that vegetation distributions are determined by the spatial distribution of environmental variables that are significantly correlated with, or limit, plant distributions (Franklin 1995). Vegetation distribution models are largely based on abiotic variables such as climate, soils and topography (Miller & Franklin, 2002; Midgley et al., 2003; Thuiller et al., 2005; Lötter & Le Maitre, 2014; Ackerly et al., 2015), while emergent properties (e.g. vegetation height, structure and fire regime) that have significant effects on the composition and distribution of vegetation are rarely incorporated.

Given that fire is a significant driver of vegetation formations and assemblages in MTEs (Bond & Keeley, 2005; Keeley et al., 2011), this study proposes that the exclusion of fire variables from

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vegetation models potentially constrains the identification of underlying ecosystem responses to changes in the environment, thus hindering our understanding of vegetation-environment linked interactions in MTEs. Although various studies advocate for the inclusion of disturbance variables such as fire in distribution models (Austin, 2002; Zhong, 2006; Franklin et al., 2016), only a few studies have investigated the efficacy of doing so (see Tucker et al., 2012; Crimmins et al., 2014). Findings from Tucker et al., (2012) and Crimmins et al., (2014) indicate that fire-related variables provide limited additional explanatory power in species distribution models (SDMs), possibly due to fire regimes largely being a product of climate (Bond & Keeley, 2005; Wilson et al., 2010). This suggests that fire-related variables may be an unnecessary addition to distribution models and climatic variables are sufficient predictors of vegetation distributions in fire-prone ecosystems. However, in the interest of conservation and management planning at larger scales, it may be useful to assess the relative importance of fire in shaping species distributions in the context of vegetation units rather than individual species.

Vegetation distributions are generally assessed at different hierarchies, i.e. as individual species (Bomhard et al., 2005; Lötter & Le Maitre, 2014), as well as at biome (Scheiter & Higgins, 2009) and community levels (Ferrier & Guisan, 2006). At the landscape scale, inferences made from SDMs are limited by the feasibility of modelling the entire range of species in the region, while the ability of ecologically significant species to act as surrogates that represent the distribution of the rest of biodiversity is also subject to uncertainty (Ferrier, 2002). On the other hand, the reduced physiological detail in biome level models results in coarse indications of potential changes in vegetation which may be too broad for landscape scale studies (Leemans, 1997). Modelling vegetation distribution at community level provides a suitable alternative for landscape scale modelling. Here, a wide spectrum of species is represented as groupings of similar species composition with a clustered position on environmental gradients across the landscape. Community level modelling does however require comprehensive species data and complex processing to derive the plant communities to be used as input for the model. In cases where plant community data may not be easily accessible, vegetation type data, which is more readily available, may be used in community level models. Vegetation types are an intermediate

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between community and biome level, they are amalgamations of similar plant communities which reflect the physiognomic and functional characteristics of vegetation across a landscape (Ackerly et al., 2015). Vegetation types are also recognised as the main biological units of measurement underpinning vegetation maps, and have been used to guide conservation planning and land management for years (NEMBA, 2004; Thorne et al., 2008; Driver et al., 2012).

This study investigates the potential impact of changes in climate and fire regime on the distribution of vegetation types in a fire-prone ecosystem, specifically focusing on fynbos vegetation found in the Cape Floristic Region (CFR). Fynbos is fire-adapted and accounts for over 56% of the floral species found in the CFR (Cowling & Richardson, 1995). Most fynbos species depend on fire for one or more of seed release, germination, supply of nutrients and regeneration (Stock & Lewis, 1986a; Brown et al., 2003; Keeley et al., 2012), and are likely to be vulnerable to the direct impacts of climate change as well as changes in fire regime. Multinomial linear regression was employed to predict the future distributions of 22 fynbos vegetation types under 44 Phase 5 Coupled Model Intercomparison Project (CMIP5) general circulation models (GCMs) and to ask:

1. What is the contribution of fire as a predictor of the current distribution of fynbos vegetation, relative to climate and soils?
2. What are the projected trends in vegetation distribution under future climate and fire regime scenarios?
3. How does the sensitivity of vegetation vary across the landscape in relation to changes in climate only versus the inclusion of fire regime?

4.3 Methods

4.3.1 Study area

Our study focuses on the remnants of fynbos vegetation found in the mountain regions of the CFR, covering an area of 36 633.26km^2. Fynbos vegetation is rich in diversity, holds high rates of endemism (Goldblatt, 1978), with approximately 70% of the ±9000 species found in the CFR

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being endemic to the region (Goldblatt & Manning, 2002; Linder, 2003). Fynbos vegetation is supported by a range of nutrient poor sandy soils to richer clay soils arising from Aeolian marine sands and underlying layers of sandstone, granite and shale (Goldblatt & Manning, 2000). The study area is largely characterized by a Mediterranean-type climate (Köppen, 1931), with wet winters and hot, dry summers in the west, transitioning into relatively temperate conditions with bimodal rainfall towards the east (Schulze, 2007; Southey, 2009; van Wilgen et al., 2010). Projected trends in climate indicate an increase in temperature (Niang et al., 2014) coupled with a decrease in winter rainfall in the south-west section of the CFR and an increase in rainfall inland and towards the east (Hoffman et al., 2009; MacKellar et al., 2014). Fires in the fynbos region mainly occur during the dry, hot summer period (Cowling, 1992), although winter fires are common in the coastal mountain ranges in the east of the CFR (Southey, 2009). Fire return interval in the fynbos ranges between 10-30 years, however these intervals are becoming shorter as a result of alterations in fire weather (Wilson et al., 2010; Kraaij et al., 2013a), increasing human populations (Forsyth & van Wilgen, 2008; van Wilgen et al., 2010), and modification of fuel loads by fauna and alien plant species (Pausas & Keeley, 2014b).

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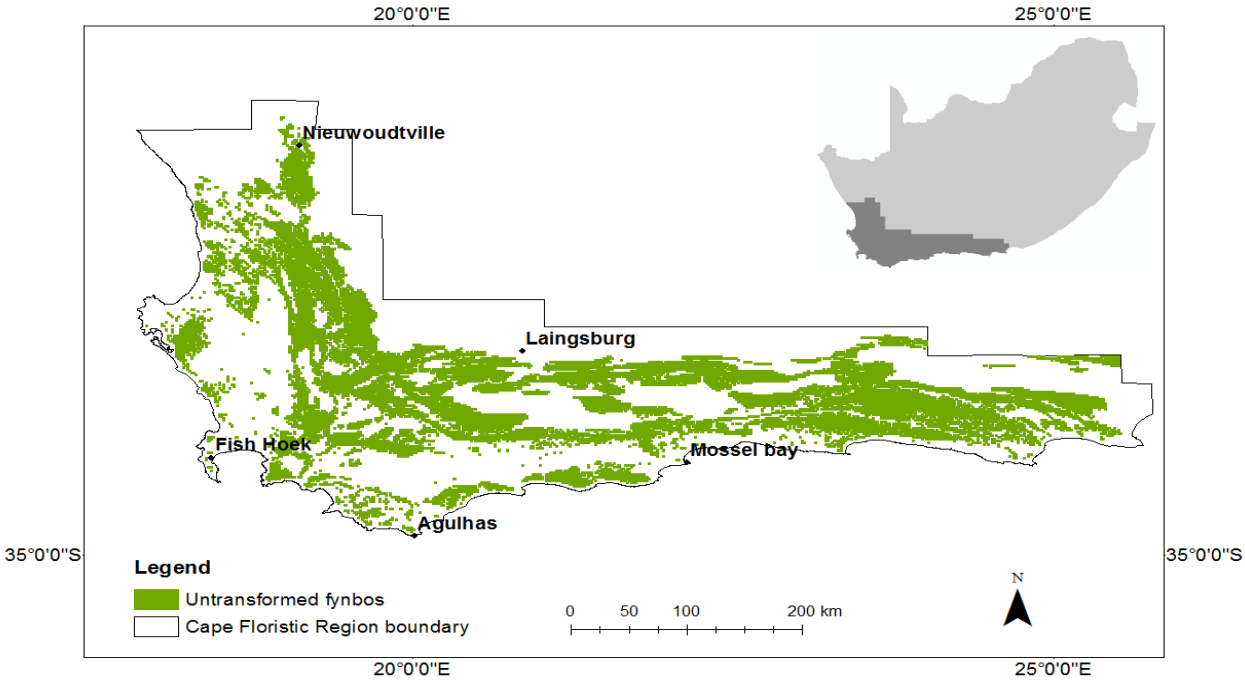

Figure 4-1: Intact (untransformed) fynbos in the CFR adapted from Wilson et al., (2015) and Mucina & Rutherford (2006).

4.3.2 Vegetation data

The Vegetation of South Africa, Lesotho and Swaziland Map (Mucina & Rutherford, 2006), also commonly referred to as the National Vegetation Map or simply the VegMap as it will be referred to in this study henceforth, was selected as our input data. The VegMap, published by the South African National Biodiversity Institute (SANBI), consists of 440 vegetation types, of which 80 are fynbos, mapped at a scale of 1:250 000 and at finer scales in some other areas. Criteria used to define these vegetation types includes: floristic similarity, vegetation structure, position along major ecological gradients and ecological preferences (e.g. alkaline soils) (Mucina et al., 2006).The VegMap is also the main ecosystem classification used for ecosystem threat assessments and environmental protection under the National Environmental Management Biodiversity Act 10 of 2004 (NEMBA, 2004). The first VegMap was produced in 2006, later updated in 2009 and further updated in 2012. The VegMap was downloaded for free from the SANBI BGIS website, http://bgis.sanbi.org/SpatialDataset/Detail/18. The VegMap was then

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rasterized to a 1min (~1.55 x 1.85 km) resolution and trimmed to regions of remnant fynbos, from which fynbos vegetation types with ≥100 pixels were extracted, thus yielding a total of 30 vegetation types.

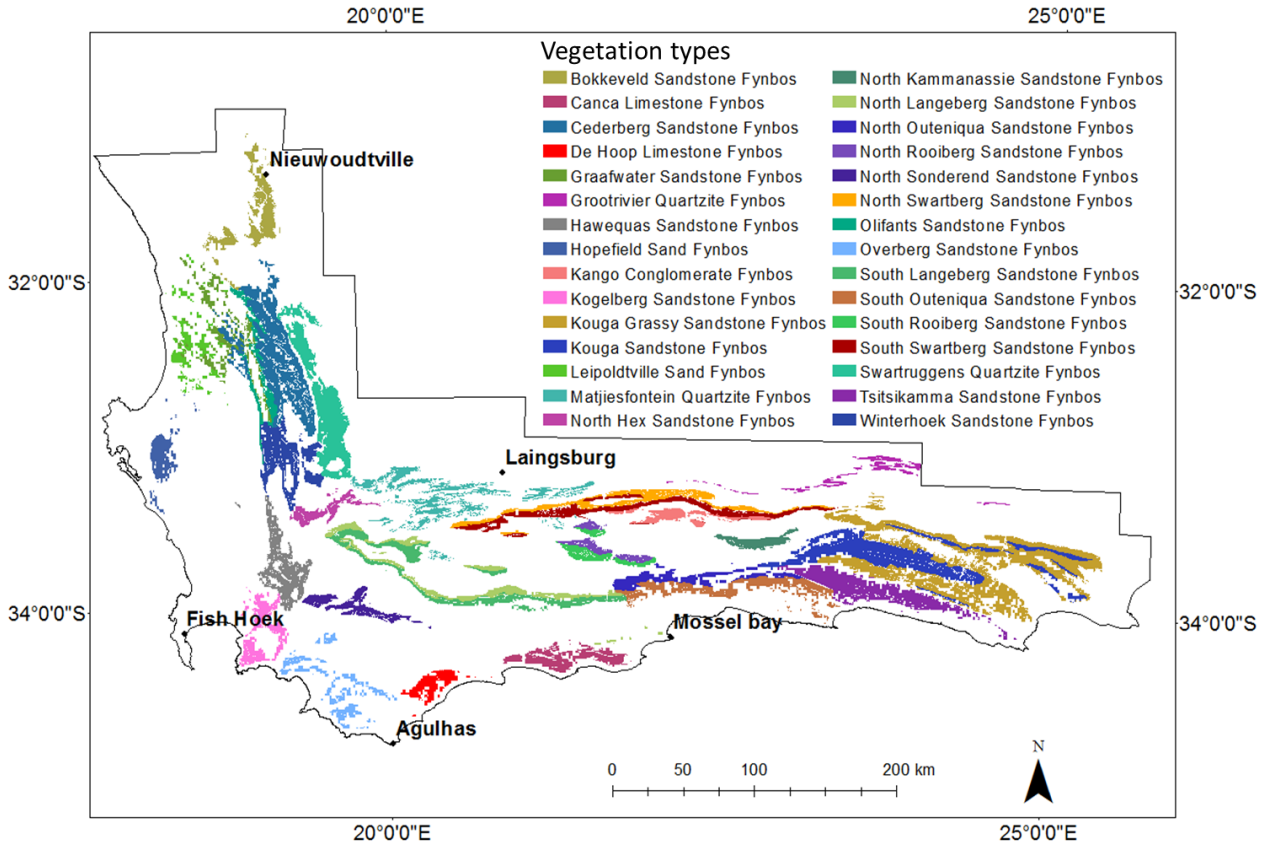

Figure 4-2: Distribution of the 30 fynbos vegetation types retained for the study extracted from the VegMap (Mucina & Rutherford, 2006).

4.3.3 Predictor variables

Predictor variables were selected following those used for modelling species in the CFR and other fire-prone ecosystems in previous studies (Midgley et al., 2006; Moretti et al., 2006; Syphard & Franklin, 2010; Lötter & Le Maitre, 2014). These consisted of five climatic variables: mean annual precipitation (*map*), mean January precipitation (*mmp01*, the driest month of the year), Markham`s precipitation concentration (*pptconc*, Markham, 1970), mean maximum January temperature (*tmax01,* summer), mean minimum July temperature (*tmin07*, winter); one

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soil variable representing pH, fertility and texture (*geocombined*), and one fire variable representing fire return interval (*fri*).

Climatic variables were derived from long-term (1950-2000) mean climate data from the South African Atlas of Agrohydrology and Climatology (Schulze, 2007). Markham`s precipitation concentration represents precipitation seasonality and ranges from 0% to 100%. A value of 0% indicates equal rainfall throughout the year, while 100% indicates that all precipitation falls in a single month (Markham, 1970; Wilson et al., 2015). The soil variable was derived from a 1:250 000 geological map from the Council for Geosciences, rasterized and reclassified into fertility (4 classes), texture (4 classes) and pH classes (3 classes) by experts (Latimer et al., 2006b). The soil data were reduced by performing a principal coordinate analysis (PCoA) on the Bray-Curtis distances between cells based on the 11 data layers. Only the first PC axis (representing 56% of the variance) was retained as all further axes represented only 15% of the variance or less. The fire variable was derived from a combination of burned area maps dating from the 1950s (Wilson et al., 2010) and ten years (2000-2010) of remotely sensed Moderate Resolution Imaging Spectroradiometer (MODIS) 500m resolution 16-day gridded Normalized Difference Vegetation Index (NDVI) data (Wilson et al., 2015). Using a hierarchical Bayesian statistical framework, these data were used to model post-fire recovery rates of vegetation in the CFR. The resultant estimates of post fire recovery rates were found to be highly correlated with fire return intervals derived by Wilson and coworkers (2010) for the CFR, and therefore adopted as the fire variable in our study (Wilson et al., 2015).

The "cor" function in R (R Core Team, 2015) was used to test for collinearity (level of dependence) amongst the selected variables. None of the variables were correlated at a level sufficiently high enough to be of concern, $r > |0.7|$ (see Dormann et al., 2013, Appendix 4-1), therefore all seven variables were retained. All data were spatially trimmed to the extent of the remnant fynbos in the CFR (Figure 4-1). The climate and fire data were resampled from 0.5 km resolution to 1min (~1.55 x 1.85 km) resolution to match the resolution of the soil data.

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4.3.4 Future climate and fire regime projections

Future climate and fire data were obtained from Wilson et al. (2015). These data are based on their seven predictor variables projected under an ensemble of 11 Phase 5 Coupled Model Intercomparison Project (CMIP5) general circulation models (GCMs), for two Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway (RCPs) scenarios (RCP4.5 and RCP8.5), in two time periods 2046-2065 and 2081-2100. This resulted in a total of 44 future climate futures. Projections of fire return interval are based on predicted changes in vegetation recovery time across the 44 downscaled CMIP5 GCMs for the CFR (Wilson et al., 2015). The RCP4.5 represents a moderate future scenario, it is described by a global population that peaks mid-century and declines thereafter, while economic structures rapidly change towards a service and information economy, with clean and resource-efficient technologies (Smith & Wigley, 2006; Clarke et al., 2007). The RCP8.5 scenario is the worst case scenario of the RCPs, representing a world characterised by high energy demand and green house gas emissions resulting from an absence of climate change policies, high population, slow income growth, and modest technological advancements and energy intensity improvements (Riahi et al., 2011).

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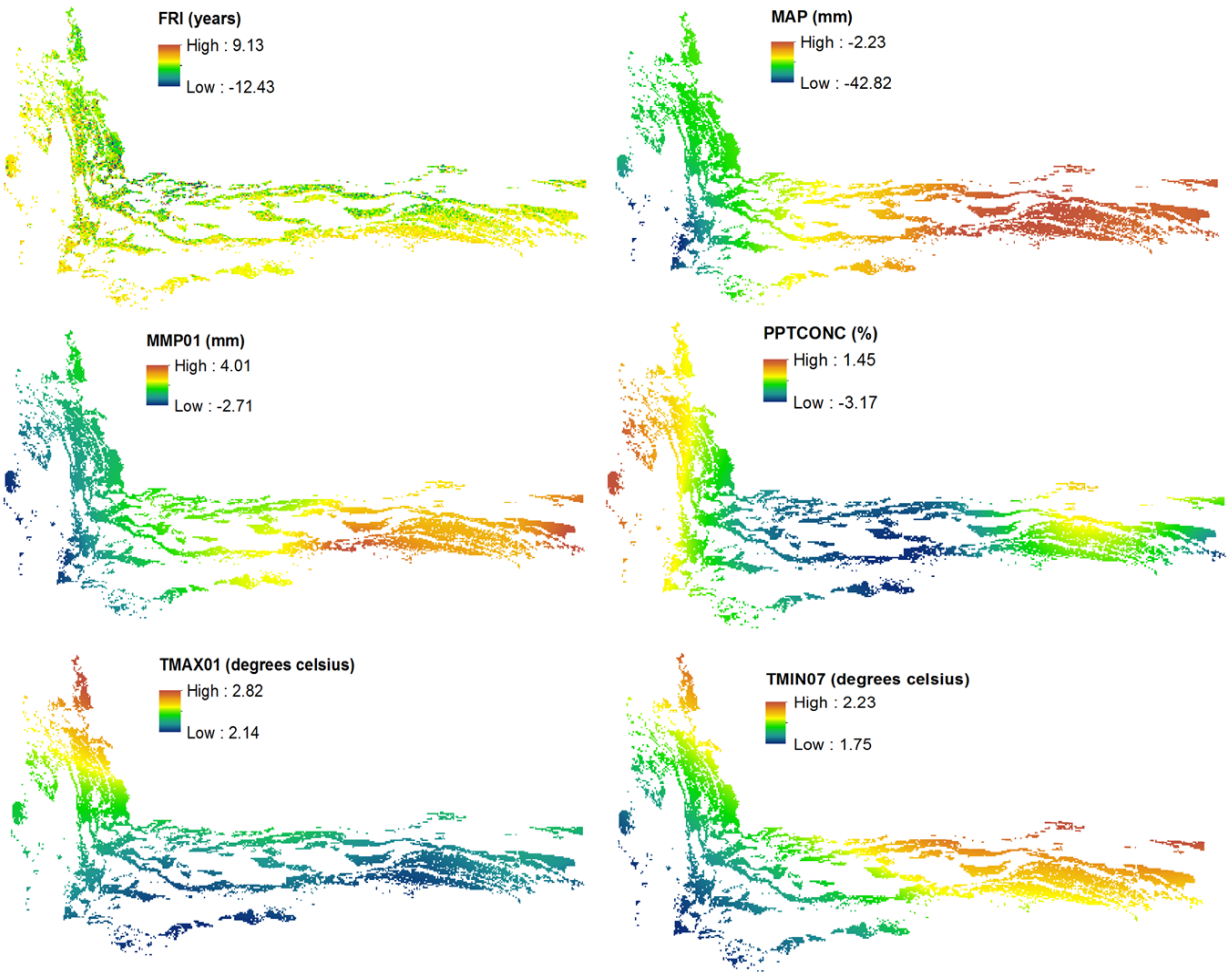

Figure 4-3: Mean projected change from the baseline estimates for the six predictor variables: mean annual precipitation (MAP), mean January precipitation (MMP01), Markham`s precipitation concentration (PPTCONC), mean maximum January (TMAX01) temperature, mean minimum July (TMIN07) and fire return interval (FRI), based on averaged values of the 44 downscaled CMIP5 GCMs.

It should be noted that the distribution models in this study are based on the assumption of equilibrium vegetation response to each climate future (model + emissions scenario), where other ecosystem processes or feedbacks that contribute to changes in the vegetation, as well as lags in vegetation response, are not included. In other words, the projected vegetation responses are

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strictly a function of the magnitude of climate change. They do not draw any time related inferences or rely on the chronology of the climate futures.

4.3.5 Distribution modelling - Multinomial linear regression

Conventional vegetation distribution models predict the most likely vegetation type to occur under a given set of environmental conditions prevailing at a particular point. Such an output overlooks the fact that alternative vegetation types can exist under the same location and set of conditions, with factors such as disturbance regime or land use determining the probability of these vegetation types occurring in that given area (Johnstone et al., 2016). Alternatively, multinomial logistic regression allows one to build a probabilistic vegetation model (PVM) to predict vegetation distribution. Multinomial logistic regression is a form of logistic regression in which there are more than two outcome categories (Field, 2009). This probabilistic approach measures the likelihood of each vegetation type in the study occurring at a given point, offering an appropriate alternative to modelling vegetation distributions and facilitating further investigation into the distribution of vegetation types of interest or rare vegetation types that may be overlooked in conventional vegetation distribution models (Ackerly et al., 2015). Multinomial logistic regression has been used in soil mapping (Zeraatpisheh et al., 2017), land use/cover change (Millington et al., 2007) and modelling vegetation distributions (Levavasseur et al., 2013; Ackerly et al., 2015). The PVM measures the probability of occurrence for all the vegetation types at each pixel, therefore the vector of probabilities is based on a scale of 0 – 1 (i.e. low to high probability). The PVM is a zero sum model where a reduction in the probability of one vegetation type is balanced by an increase in another vegetation type. This means that the model is not able to predict the development of novel assemblages of species under selected future scenarios (Ackerly et al., 2015).

Two models were run for each vegetation type: one fitted with six variables (i.e. *map, mmp01, pptconc, tmin07, tmax01 and geocombined*), and a second model fitted with *fri* as an additional variable. Vegetation distributions were modelled by overlying a rasterized layer of the 30 vegetation types with rasters of current and projected predictor variables, and extracting the corresponding values to produce 45 matrices. These matrices were used as input to predict

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vegetation distributions using the "multinom" function (Venables & Ripley, 2002) in the R software (R Core Team, 2015). The "train" function from the *caret* package (Kuhn, 2008) was used to produce a confusion matrix from which the overall accuracy of the model, as well as prediction accuracy for each vegetation type, was evaluated. Cohen's kappa coefficient (Cohen, 1968), derived from a k-fold cross-validation of the data carried out over 10 iterations, was used to estimate model accuracy. The Kappa statistic varies from 0 to 1, where 0 represents agreement equivalent to random chance, and 1 represents perfect agreement (Landis & Koch, 1977; Monserud & Leemans, 1992). Model accuracy was further evaluated using the "auc" function, which outputs area under the receiver operator curve (AUC) values as indicators of goodness of fit. AUC values range from 0 to 1, where <0.5 indicates a relationship worse than random, 0.5 indicates that the model has no predictive power (no better than random), and 1 signifies a perfect model (Elith et al., 2006). Prediction accuracy for each vegetation type was calculated as the proportion of matching pixels between the predicted and observed vegetation type. Estrada-Pena & Thuiller (2008) highlighted that similarities between response variables in models tend to lead to low accuracies. Consequently, a hierarchical cluster analysis of the current vegetation types was carried out using the *pvclust* package (Suzuki & Shimodaira 2006) in R. Here, cluster analysis is used to identify groupings of vegetation types, based on their similarities in niche characteristics, which may affect the predictive accuracy of the model.

The importance of each predictor variable in determining the distribution of the vegetation types was measured using the "dredge" function in R (Barton 2015). The dredge function estimates the change in the Akaike Information Criterion (AIC, Akaike 1973) values from the full model under all possible combinations of the predictor variables. For this study, changes in AIC values, when each of the seven predictor variables was withheld from the model, and when each of the predictor variables were used in isolation to model vegetation distribution, were considered in assessment of variable importance. As a general rule of thumb, delta AIC >2 represents a model with significant explanatory predictive power. The greater the change in AIC the greater the importance of the variable (Burnham & Anderson, 2002).

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Having established the accuracy of the model and quantified the importance of the seven predictor variables, vegetation distributions were then projected across all 44 climate futures. The projected areal extent of each vegetation type was used to describe potential vegetation responses to changes in climate and fire regime. This was achieved by calculating the proportion (expressed as a percentage) of the area covered by each vegetation type, relative to the total current areal extent of the 22 vegetation types. These proportions were subsequently plotted against the mean projected change in fire return interval (Figure 4-4) and mean annual precipitation (Figure 4-5) from their respective baseline estimates.

We further assessed the sensitivity of vegetation to changes in climate alone and to changes in both climate and fire. To achieve this, vegetation types exhibiting maximum probability of occurrence at each cell were used to map the spatial distribution of vegetation sensitivity across the study area. Vegetation sensitivity was measured as the number of times a given pixel was projected to change from the baseline vegetation type to another vegetation type in response to the 44 climate futures, and is expressed as a percentage. Hence, 0% indicates no change in vegetation type under any of the 44 climate futures at a given cell, thus signifying low sensitivity, while 100% indicates a change from the baseline vegetation type under all 44 climate futures, therefore high sensitivity. We also examined how vegetation sensitivity derived from the two models (with and without fire) differed by calculating the difference in sensitivity between the two resultant maps using raster calculator in ArcGIS 10.2 (ESRI, 2013). Finally, in order to understand the extent and direction in which the vegetation under study is sensitive to changes in climate and fire, multiple linear regression was used to model the spatial variation in vegetation sensitivity as a function the baseline climate and fire variables (Table 4-4).

4.4 Results

4.4.1 Model accuracy

Overall model accuracy in predicting the current distribution of fynbos vegetation types was fairly good, achieving a Kappa estimate of 0.65 and an AUC of 0.88. Prediction accuracy for the individual vegetation types was measured as the proportion of pixels in which the most likely

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vegetation type matched the observed vegetation type. Prediction accuracy ranged between 0 (North Rooiberg Sandstone Fynbos) and 0.97 (Hopefield Sand Fynbos). Eight of the 30 vegetation types had a prediction accuracy of less than 50% and were subsequently removed from further analyses in the study (Table 4-1, Appendix 4-1). The low accuracy in these eight vegetation types may be due to a shared similarity in ecological niche space with other vegetation types (Estrada-Pena & Thuiller, 2008). A cluster analysis of the vegetation types highlighted substantial similarities between the poorly predicted vegetation types, and the respective vegetation types in which errors of commission occurred (Appendix 4-2). For example, in the case of similar vegetation types, Kouga Sandstone Fynbos and Kouga Grassy Sandstone Fynbos, 265 pixels out of the 665 pixels belonging to Kouga Sandstone Fynbos were incorrectly predicted as Kouga Grassy Sandstone Fynbos (Table 4-1). The remaining 22 vegetation types cover 74,3% of the extent the study.

Table 4-1: Prediction accuracy for each vegetation type, based on the proportion of correctly assigned pixels; poorly predicted types shaded in grey.

Vegetation type	No. of pixels	Proportion correct	Vegetation Type	No. of pixels	Proportion correct
Bokkeveld Sandstone Fynbos	235	0.88	North Kammanassie Sandstone Fynbos	104	0.56
Canca Limestone Fynbos	209	0.94	North Langeberg Sandstone Fynbos	273	0.20
Cederberg Sandstone Fynbos	630	0.87	North Outeniqua Sandstone Fynbos	198	0.26
De Hoop Limestone Fynbos	115	0.92	North Rooiberg Sandstone Fynbos	100	0
Graafwater Sandstone Fynbos	163	0.57	North Sonderend Sandstone Fynbos	170	0.61
Grootrivier Quartzite Fynbos	107	0,96	North Swartberg Sandstone Fynbos	297	0.57
Hawequas Sandstone Fynbos	283	0.82	Olifants Sandstone Fynbos	151	0.23
Hopefield Sand Fynbos	130	0.97	Overberg Sandstone Fynbos	152	0.95
Kango Conglomerate Fynbos	122	0.90	South Langeberg Sandstone Fynbos	370	0.35
Kogelberg Sandstone Fynbos	177	0.88	South Outeniqua Sandstone Fynbos	304	0.75
Kouga Grassy Sandstone Fynbos	1053	0.77	South Rooiberg Sandstone Fynbos	118	0.43
Kouga Sandstone Fynbos	665	0.37	South Swartberg Sandstone Fynbos	343	0.41
Leipoldtville Sand Fynbos	136	0.77	Swartruggens Quartzite Fynbos	520	0.92
Matjiesfontein Quartzite Fynbos	314	0.84	Tsitsikamma Sandstone Fynbos	406	0.73
North Hex Sandstone Fynbos	113	0,65	Winterhoek Sandstone Fynbos	328	0,74

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4.4.2 Variable importance

The AIC value for the full model was 16813.83. When each variable was excluded from the model, change in AIC ranged between 388.7 and 2485.62, where *fri* was the least important variable, while *pptconc* and *map* were the most important variables (Appendix 4-2). When used in isolation, *tmax01* and *soil* were the most important variables while *fire* was moderately important, with a change in AIC greater than that of *mmp01* and *pptconc.*

Table 4-2. Variable importance as described by a change in AIC.

Without variable	ΔAIC	With only variable	ΔAIC
pptconc	2485.62	tmax01	31820.53
map	2400.49	soil	31152.81
mmp01	2295.48	tmin07	29575.47
tmin07	2198.29	map	28067.18
tmax01	1469.95	fri	26400.66
soil	1344.73	mmp01	22816.24
fire	388.70	pptconc	21683.53

Variables arranged in order of importance (high to low)

4.4.3 Projected change in areal extent of vegetation types

A significant change in the areal extent of the vegetation types in response to changes in fire return interval was observed for ten vegetation types representing 48% of study area (Table 4-3 and (Figure 4-4) Of these, the proportion of the total study area extent covered by the coastal vegetation types (i.e. Canca Limestone, De Hoop Limestone, Kogelberg Sandstone, Leipoldtville Sand, Overberg Sandstone and South Outeniqua Sandstone) increased as fire return intervals became shorter. The opposite trend was observed for the vegetation types occurring mostly in the interior at high altitudes (i.e. Kango Conglomerate, Cederberg Sandstone, Kouga Grassy Sandstone and Tsitsikamma Sandstone), which decreased in proportion in response to shortening fire return interval.

In response to decreasing mean annual precipitation (Figure 4-5), Cederberg Sandstone and Kouga Grassy Sandstone increased in proportion, while Canca limestone, Leipoldtville sand, North Hex Sandstone and North Swartberg Sandstone decreased (Table 4-3). The strength of the relationships between changes in vegetation proportion and change in fire return interval, were

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generally higher than those of the correlation between changes in vegetation proportion and change in mean annual precipitation (Table 4-3).

Table 4-3: Correlation between change in vegetation type proportions and changes mean fire return interval and mean annual precipitation

Vegetation type	**Mean fire return interval**	**Mean annual precipitation**
	r^2	r^2
Bokkeveld Sandstone	0.01	0.06
Canca Limestone	0.29***	0.10*
Cederberg Sandstone	0.39***	0.21**
De Hoop Limestone	0.16**	0.04
Graafwater Sandstone	0.04	0.01
Grootrivier Quartzite	0.03	0.03
Hawequas Sandstone	0.02	0.07
Hopefield Sand	0.03	0.01
Kango Conglomerate	0.33***	0.06
Kogelberg Sandstone	0.36***	0.07
Kouga Grassy Sandstone	0.51***	0.14**
Leipoldtville Sand	0.10*	0.13*
Matjiesfontein Quartzite	0.01	0.02
North Hex Sandstone	0.08	0.20**
North Kammanassie Sandstone	0.02	0.04
North Sonderend Sandstone	0.04	0.00
North Swartberg Sandstone	0.05	0.11*
Overberg Sandstone	0.35***	0.06
South Outeniqua Sandstone	0.38***	0.02
Swartruggens Quartzite	0.01	0.01
Tsitsikamma Sandstone	0.35***	0.03
Winterhoek Sandstone	0.02	0.01

Signif. codes: *** = P < 0.001 , ** = P < 0.01, * = P < 0.05

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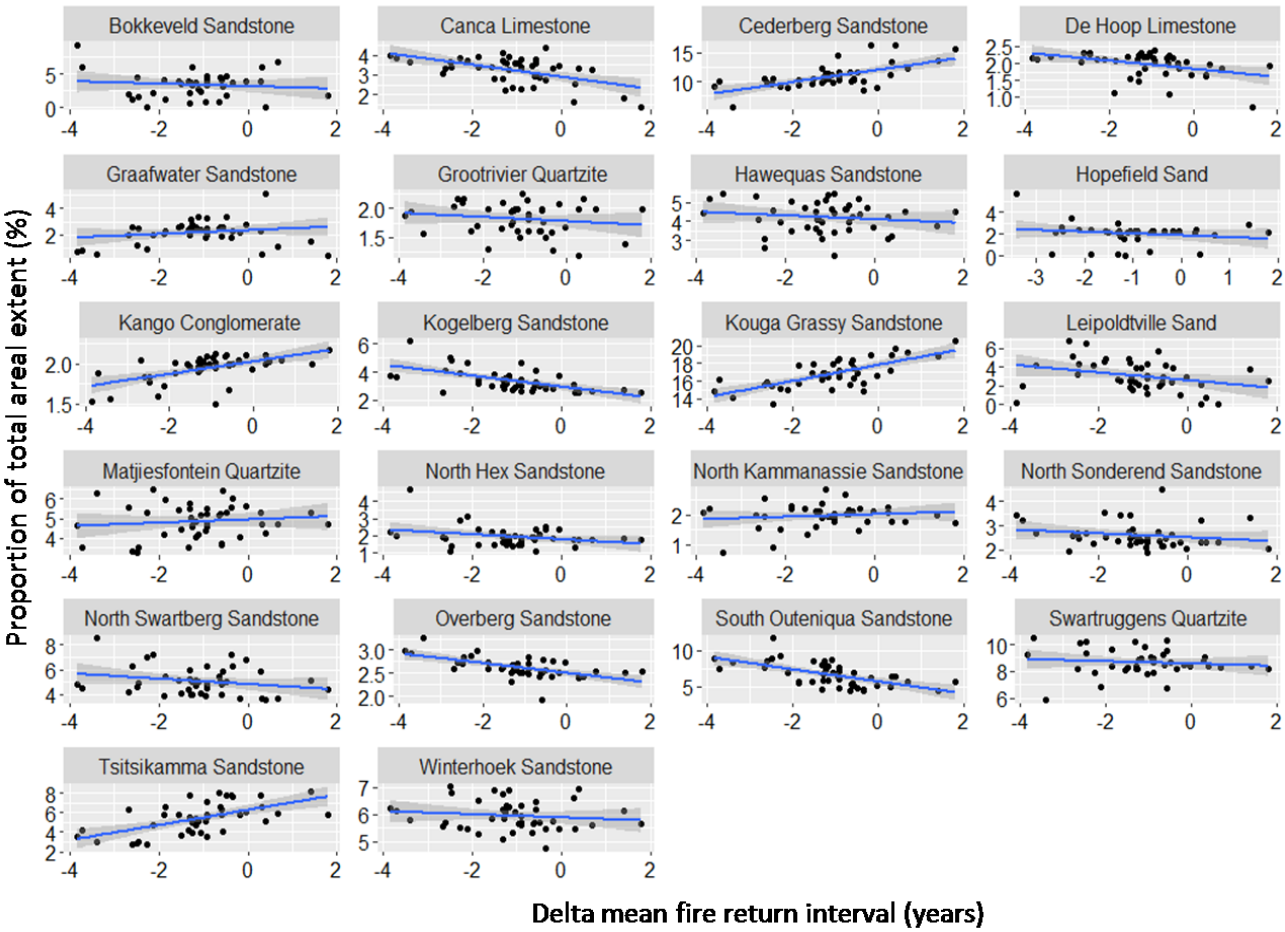

Figure 4-4: Projected areal extent of vegetation types (presented here as the proportion of the study area extent covered) across 44 climate futures in the order of change in fire return interval from the historical baseline fire return interval, regression results shown in Table 4-3.

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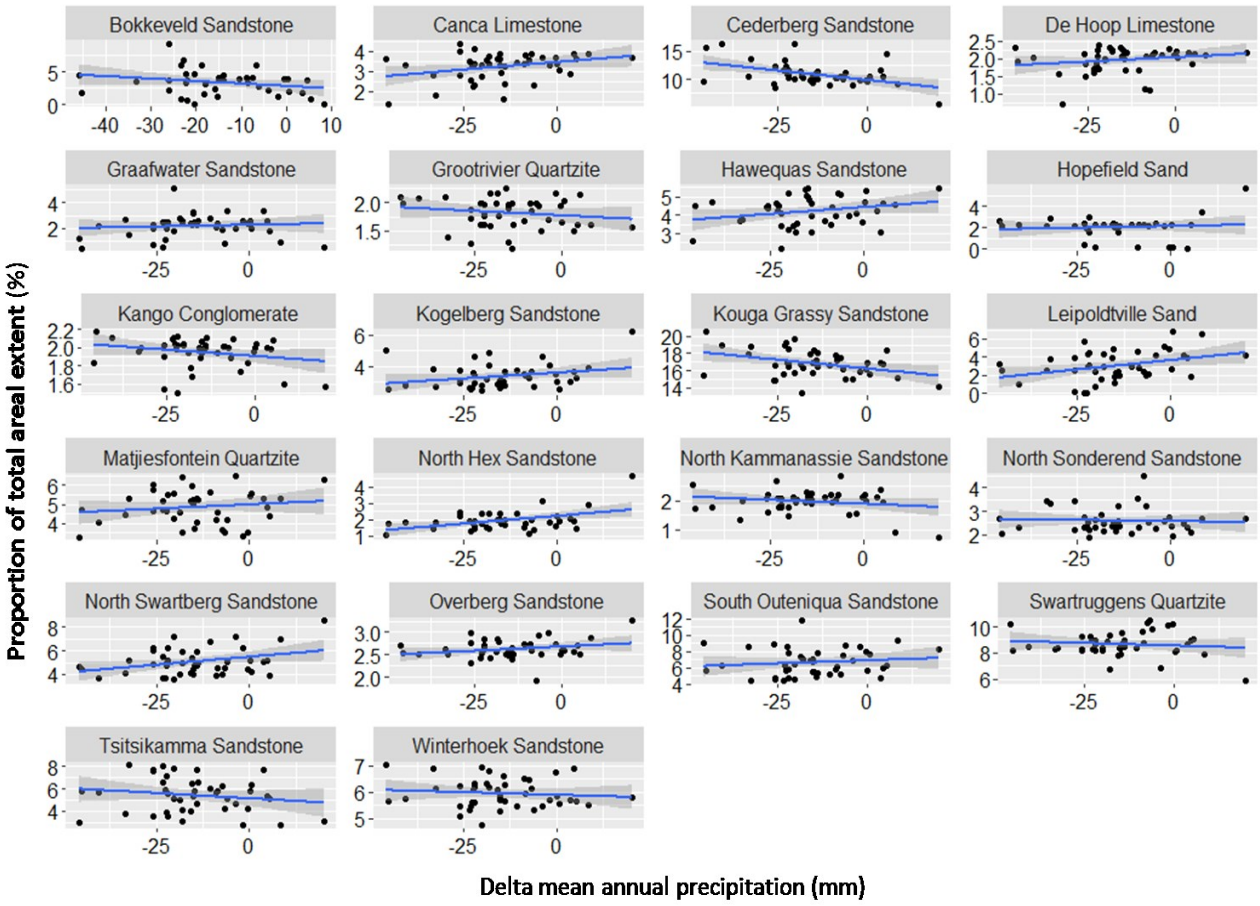

Figure 4-5: Projected areal extent of vegetation types (presented here as the proportion of the study area extent covered) across 44 climate futures in the order of change in mean annual precipitation from the historical baseline mean annual precipitation, regression results shown in Table 4-3.

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4.4.4 Vegetation sensitivity

The spatial distribution of vegetation sensitivity derived from the model with (Figure 4-6b) and without (Figure 4-6a) *fri* was highly variable and patchy. However, the vegetation types in the north-west sections (e.g. Bokkeveld Sandstone and Leipoldtville Sand) and eastern coastal sections (e.g. Tsitsikamma Sandstone) of the study area were more sensitive to changes in climate and fire regime, while other vegetation types, such as Cederberg, Kogelberg and Kouga Grassy Sandstone, exhibited less sensitivity (Figure 4-6). Changes in sensitivity in response to the additional effect of fire return interval varied across the landscape (Figure 4-6c), with 38,1% of the study area exhibiting no changes in vegetation type, while 29,6% of the area under study increased in sensitivity, as 32,3% of the area decreased in sensitivity ((Figure 4-6d). A significant relationship was observed between vegetation sensitivity and all covariates used in the model (Table 4-4) as may be expected in cases of large sample sizes. Fire return interval and temperature were highly significant ($P < 0.001$), while the rainfall variables were moderately significant ($P < 0.05$) (Table 4-4). Vegetation was projected to be more sensitive in areas with longer fire return intervals, lower mean annual precipitation and higher precipitation in January (the driest month), higher rainfall seasonality, and warmer summer and winter temperatures.

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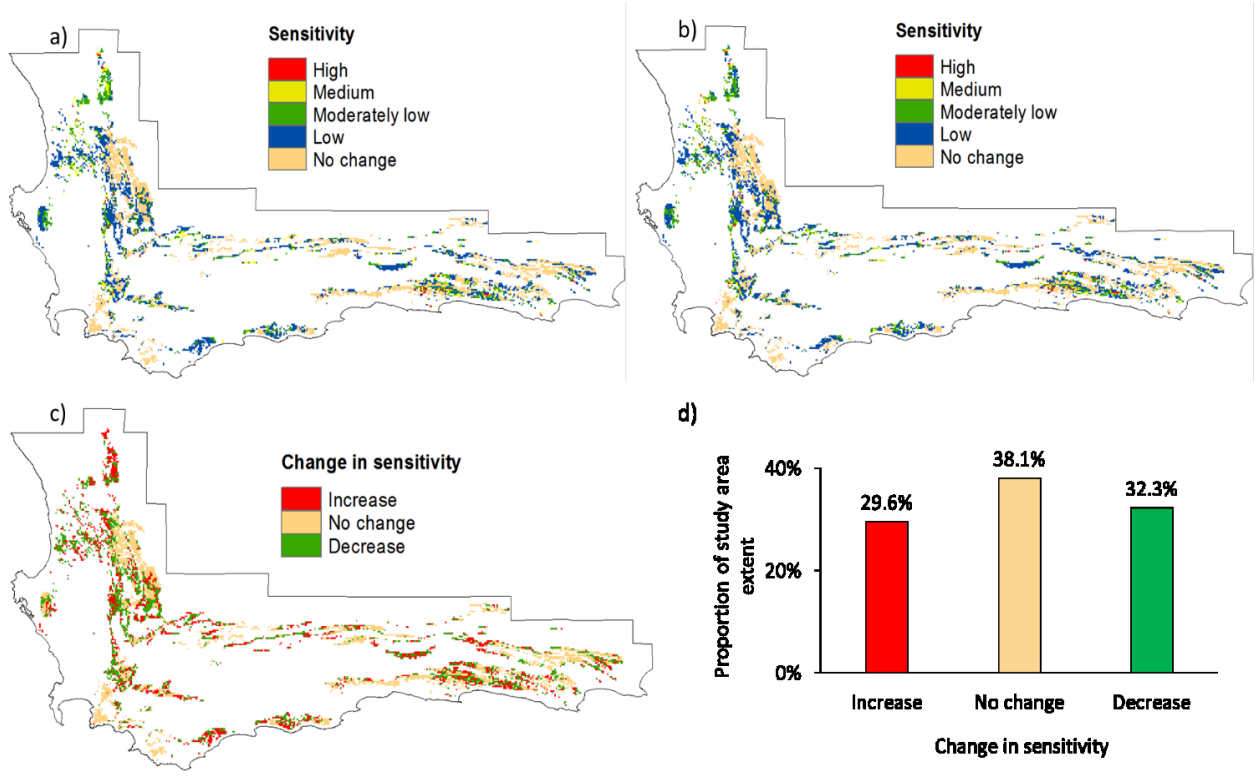

Figure 4-6: Projected sensitivity of vegetation measured by the change in vegetation type in response to changes in climate and fire regime across 44 climate futures based on a) the model excluding fire return interval (*fri*) and, b) the complete model (i.e. *fri* included). Figure 4-6c) shows the distribution of the change in vegetation sensitivity in response to the added effect of changes in fire return interval, with 6d) indicating the proportion of areal extent corresponding to the changes in sensitivity.

Table 4-4: Correlation between the spatial variation in vegetation sensitivity and the baseline climate and fire regime covariates. This indicates the extent and direction in which the vegetation under study is sensitive to changes in each of the covariates.

	Vegetation sensitivity		
	B	*SE*	*p*
(Intercept)	-20.220981	2.817207	***
fri	0.327777	0.088948	***
map	-0.003560	0.001773	*
mmp01	0.078412	0.034825	*
pptconc	0.056631	0.028678	*
tmax01	0.991729	0.105043	***
tmin07	1.096548	0.173701	***

Signif. codes: *** = P<0.001, ** = P<0.01, * = P< 0.05

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4.5 Discussion

Anticipating vegetation responses to projected changes in both climate and fire regime is crucial for the future conservation and management of vegetation in fire-prone ecosystems, such as most MTEs. The majority of vulnerability assessments rely on distribution models focused on the impacts of climate change on biodiversity (e.g. Midgley et al., 2003; Klausmeyer & Shaw, 2009; Ackerly et al., 2015), while the potential impacts of changing fire regime generally remain overlooked. The exclusion of fire covariates from distribution studies is essentially a result of the widely accepted, but limited, view that climate is the chief determinant of species distributions (Bond et al., 2005), and also a lack of fire data (Flannigan et al., 2009). However, there is growing recognition that other factors such as disturbances (e.g. fire) and biotic interactions contribute to shaping species distributions (Abbott & Le Maitre, 2009; Yates et al., 2010). Advancements in remote sensing offer an opportunity for non-climatic variables to be incorporated into distribution models (He et al., 2015). This study provides supporting evidence for the integration of fire covariates in distribution models designed for fire-prone ecosystems. We illustrate the potential of such modifications to traditional SDMs to improve our understanding vegetation distributions in fire-prone environments, and consequently, our ability to forecast vegetation responses to projected future climates and fire regime.

4.5.1 Variable importance

This study identifies fire return interval as a variable of substantial explanatory power (based on the rule of thumb AIC>2; Table 4-2), which contributes to shaping the distribution of vegetation in our study system, despite climatic influences on fire regime (Wilson et al., 2010; Kraaij & van Wilgen, 2014). When each variable is considered individually, the corresponding change in AIC (Table 4-2) indicates that fire return interval is a stronger predictor of fynbos species distributions than mean January precipitation and rainfall seasonality. However, when all variables are considered, fire return interval contributes the least towards predicting vegetation distributions in the model. This finding corroborates with observations made from our species level analysis (Chapter 3), as well as those of Tucker et al. (2012) and Crimmins et al. (2014), where fire return interval was identified as a weaker determinant of species distributions in comparison to rainfall variables. This is likely to be due to the interdependence between fire and climate, evidenced by the moderate-to-strong correlation between fire return interval and the rainfall variables in our study (Appendix 4-1). Fire regimes are typically a function of rainfall seasonality (which affects

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the occurrence of fire weather and fuel moisture content (flammability) and precipitation (buildup of fuel load) (Wilson et al., 2010; Pausas & Paula, 2012; Ellis et al., 2014). The correlative approach used in this study cannot be used to tease apart the complex roles of climate versus fire (Bond et al., 2005). Hence, while fire return interval is shown to be important in isolation, it provides little additional explanatory power relative to other variables in our model.

Discerning the relative importance of climate versus fire regime requires models that represent our mechanistic understanding of their respective roles in the ecosystem under study. This is particularly important in cases where the relationship between fire and climate is decoupled (i.e. when fire and climate act independently) either naturally (Geldenhuys, 1994) or due to human influence (Syphard et al., 2009; Regan et al., 2010), and also when fire and climate have separate but complimentary roles. For example, a demographic study on Proteaceae by Treurnicht et al., (2016) found fire to be an important driver of fecundity, while recruitment was largely determined by climate. Unfortunately, mechanistic approaches, are generally time and data intensive (Kearney & Porter, 2009; Dormann et al., 2012), and use broad scale descriptions of vegetation (e.g. biomes and plant functional types) that are not suitable at landscape scales (Leemans, 1997; Duckworth et al., 2000). Lastly, the importance of fire in this study is based on just one component of the fire regime. It is possible that a stronger influence of fire on vegetation distributions will emerge when other components of the fire regime such as fire seasonality or fire intensity are considered.

4.5.2 Projected change in areal extent of vegetation types

In response to the changing climate (MacKellar et al., 2014), fire return intervals in the CFR have decreased by an estimated four years (Wilson et al., 2010), and are expected to continue shortening in the future (Wilson et al., 2015). This study projects coastal vegetation types in the west of the CFR to increase in areal extent under shorter fire return intervals. In contrast, the areal extent of vegetation types at higher altitudes in the interior and east of the CFR are projected to decrease under shorter fire return intervals. These projected differences in vegetation response may be a result of the zero sum model used in our study, where a decline in one vegetation type is balanced out by an increase in another vegetation type. Therefore, although the impact of changing environmental conditions may, in absolute physiological terms, be negative for all the

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vegetation types, the least negatively affected may appear to show a positive response (Ackerly et al., 2015). It is further suggested that the expansion in the areal extent of some vegetation types may be indicative of their greater resilience against changing environmental conditions (Ackerly et al., 2015). Therefore, coastal vegetation types may be less sensitive to shortening fire return intervals than high altitude vegetation types. In the CFR, coastal vegetation types generally have faster post-fire recovery rates (approximately 10 years or less, Wilson et al., 2015) due to higher moisture availability, and so are likely to be less sensitive to shorter fire intervals. Contrary to coastal vegetation types west of the CFR, the coastal vegetation types in the east were observed to decrease in extent in response to shorter fire return intervals. This is despite the fact that these vegetation types have the shortest recovery rates in the CFR (Wilson et al., 2015), and thus would be expected to be less sensitive to shorter fire return intervals. Further research into the physiological tolerances of the vegetation under study would provide a clearer understanding of these potential responses to shifts in fire regime, as well as to changes in climate.

Vegetation response to decreasing mean annual precipitation varied across the landscape, with no particular trends depicted. However, we noted that vegetation distributions were more susceptible to changes in fire return interval than to changes in mean annual precipitation. It is therefore further suggested that alterations in fire regimes may have a greater influence on future vegetation distributions, than direct impacts of climate change (Nowacki & Abrams, 2015; Franklin et al., 2016; Wu et al., 2017). The projected sensitivity of vegetation to changes in climate and fire regime across the study area supports this assumption.

4.5.3 Vegetation sensitivity

Vegetation distributions showed higher sensitivity to projected changes in fire return interval and temperature, than to changes in the rainfall parameters. Vegetation types located at sites with longer fire return intervals (i.e. arid interior) and warmer summer and winter temperatures (i.e. coastal areas) were identified to be at greatest risk. This shows that the addition of fire covariates in distribution models allows for the identification of vegetation types that may not be directly affected by changes in climate, but are highly vulnerable to shifts in fire regime.

Although sensitivity to changes in climate and fire regime varied across the landscape, areas where no change in vegetation type was detected may be indicative of potential refugia sites, i.e.

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sites that are either climatically stable or predicted to be environmentally suitable for a given species or vegetation type (Morelli et al., 2016; Bonebrake et al., 2017). Protecting such sites from additional stressors (e.g. habitat fragmentation and invasive alien species) will be important for maintaining current vegetation distributions, and also providing a place where affected species or vegetation types in surrounding areas can retreat to (Keppel et al., 2012; Staudinger et al., 2012; Morelli et al., 2016). Areas where vegetation sensitivity reduced or increased as a result of the additional effect of fire may indicate sites where fire either ameliorates or exacerbates the effect of climate change. The challenge here will be to develop a mechanistic understanding to help untangle the complex feedback system between fire regime, climate change, biotic interactions and species traits in order to identify the mechanisms that determine vegetation sensitivity to changes in ecological regime. Examples of studies that have begun to address this challenge include Treurnicht et al., (2016) and Slingsby et al., (2017).

4.6 Conclusion

While much focus is given to assessing the impacts of climate change on biodiversity, the extent and manner in which changes in fire activity may affect vegetation distributions in fire-prone ecosystems requires more attention. This study has provided a basis for this recommendation through 1) quantifying the importance of fire return interval as a determinant of current vegetation distributions in the CFR, and 2) exploring potential vegetation responses to projected changes in both climate and fire regime. While the correlative approach used here is limited in its ability to separate the roles of fire and climate in shaping vegetation distributions, the study provides a foundation upon which to build future research on the importance of fire. Similarly, while the fire return interval data used is a proxy derived from vegetation recovery rates, there are few datasets of its kind and none for most flammable ecosystems. Therefore, this dataset gives us a unique opportunity to examine how changes in disturbance regimes such as fire may impact future vegetation distributions. Two key findings here are that fire provides additional information in explaining the distribution of vegetation in our model (despite the climatic control on fire), and that projected changes in fire regime are likely to have greater impacts on vegetation distribution than changes in rainfall regime would. This translates to an urgent need for robust estimates of more components of the fire regime, and how these may be altered under global change, to support vulnerability assessments of vegetation in fire-prone ecosystems.

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4.7 Appendices

Appendix 4-1 Collinearity between environmental variables as measured by Pearson`s correlation coefficient (r)

	fri	map	mmp01	pptconc	geocombined	tmax01	tmin07
fri	1.00	-0.42	-0.72	0.62	0.17	-0.16	-0.49
map	-0.42	1.00	0.66	-0.03	-0.25	-0.14	0.20
mmp01	-0.72	0.66	1.00	-0.60	-0.24	-0.04	0.17
pptconc	0.62	-0.03	-0.60	1.00	0.04	0.01	0.07
geocombined	0.17	-0.25	-0.24	0.04	1.00	0.15	-0.14
tmax01	-0.16	-0.14	-0.04	0.01	0.15	1.00	0.53
tmin07	-0.49	0.20	0.17	0.07	-0.14	0.53	1.00

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Appendix 4-2 Accuracy statistics for each the 30 selected vegetation type, poorly predicted types highlighted in grey.

	No. of pixels	Proportion of pixels (%)	Area(km2)	Proportion of area (%)	Percent correct	Sensitivity	Specificity	Pos Pred Value	Neg Pred Value	Precision	Recall
Bokkeveld Sandstone Fynbos	235	2.84	776.35	2.93	0.88	0.88	0.99	0.80	1.00	0.80	0.88
Canca Limestone Fynbos	209	2.52	655.37	2.47	0.94	0.94	0.99	0.80	1.00	0.80	0.94
Cederberg Sandstone Fynbos	630	7.60	2068.78	7.80	0.87	0.87	0.99	0.83	0.99	0.83	0.87
De Hoop Limestone Fynbos	115	1.39	371.51	1.40	0.92	0.92	1.00	0.85	1.00	0.85	0.92
Graafwater Sandstone Fynbos	163	1.97	641.65	2.42	0.57	0.57	0.99	0.52	0.99	0.52	0.57
Grootrivier Quartzite Fynbos	107	1.29	357.43	1.35	0.96	0.96	1.00	0.89	1.00	0.89	0.96
Hawequas Sandstone Fynbos	283	3.42	912.14	3.44	0.82	0.82	0.99	0.77	0.99	0.77	0.82
Hopefield Sand Fynbos	130	1.57	430.73	1.62	0.97	0.97	1.00	0.95	1.00	0.95	0.97
Kango Conglomerate Fynbos	122	1.47	383.01	1.44	0.90	0.90	1.00	0.88	1.00	0.88	0.90

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Kogelberg Sandstone Fynbos	177	2.14	584.80	2.20	0.88	0.88	1.00	0.96	1.00	0.96	0.88
Kouga Grassy Sandstone Fynbos	1053	12.71	3447.26	12.99	0.77	0.77	0.91	0.56	0.97	0.56	0.77
Kouga Sandstone Fynbos	665	8.03	2087.68	7.87	0.37	0.37	0.95	0.41	0.95	0.41	0.37
Leipoldtville Sand Fynbos	136	1.64	507.35	1.91	0.77	0.77	1.00	0.73	1.00	0.73	0.77
Matjiesfontein Quartzite Fynbos	314	3.79	1156.99	4.36	0.84	0.84	0.99	0.77	0.99	0.77	0.84
North Hex Sandstone Fynbos	113	1.36	342.47	1.29	0.65	0.65	0.99	0.63	1.00	0.63	0.65
North Kammanassie Sandstone Fynbos	104	1.26	308.64	1.16	0.56	0.56	0.99	0.56	0.99	0.56	0.56
North Langeberg Sandstone Fynbos	273	3.29	824.82	3.11	0.20	0.20	0.99	0.38	0.97	0.38	0.20
North Outeniqua Sandstone Fynbos	198	2.39	607.56	2.29	0.26	0.26	1.00	0.60	0.98	0.60	0.26

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North Rooiberg Sandstone Fynbos	100	1.21	305.11	1.15	0	0.00	1.00	NA	0.99	NA	0.00
North Sonderend Sandstone Fynbos	170	2.05	492.98	1.86	0.61	0.61	0.99	0.61	0.99	0.61	0.61
North Swartberg Sandstone Fynbos	297	3.58	821.91	3.10	0.57	0.57	0.98	0.55	0.98	0.55	0.57
Olifants Sandstone Fynbos	151	1.82	444.64	1.68	0.23	0.23	0.99	0.44	0.99	0.44	0.23
Overberg Sandstone Fynbos	152	1.83	577.79	2.18	0.95	0.95	1.00	0.91	1.00	0.91	0.95
South Langeberg Sandstone Fynbos	370	4.47	1112.77	4.19	0.35	0.35	0.98	0.51	0.97	0.51	0.35
South Outeniqua Sandstone Fynbos	304	3.67	967.17	3.65	0.75	0.75	0.99	0.78	0.99	0.78	0.75
South Rooiberg Sandstone Fynbos	118	1.42	373.90	1.41	0.43	0.43	1.00	0.58	0.99	0.58	0.43
South Swartberg Sandstone Fynbos	343	4.14	1053.37	3.97	0.41	0.41	0.97	0.40	0.97	0.40	0.41

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Swartruggens Quartzite Fynbos	520	6.28	1560.66	5.88	0.92	0.92	0.99	0.90	0.99	0.90	0.92
Tsitsikamma Sandstone Fynbos	406	4.90	1325.18	5.00	0.73	0.73	0.98	0.69	0.99	0.69	0.73
Winterhoek Sandstone Fynbos	328	3.96	1027.93	3.87	0.74	0.74	0.99	0.74	0.99	0.74	0.74

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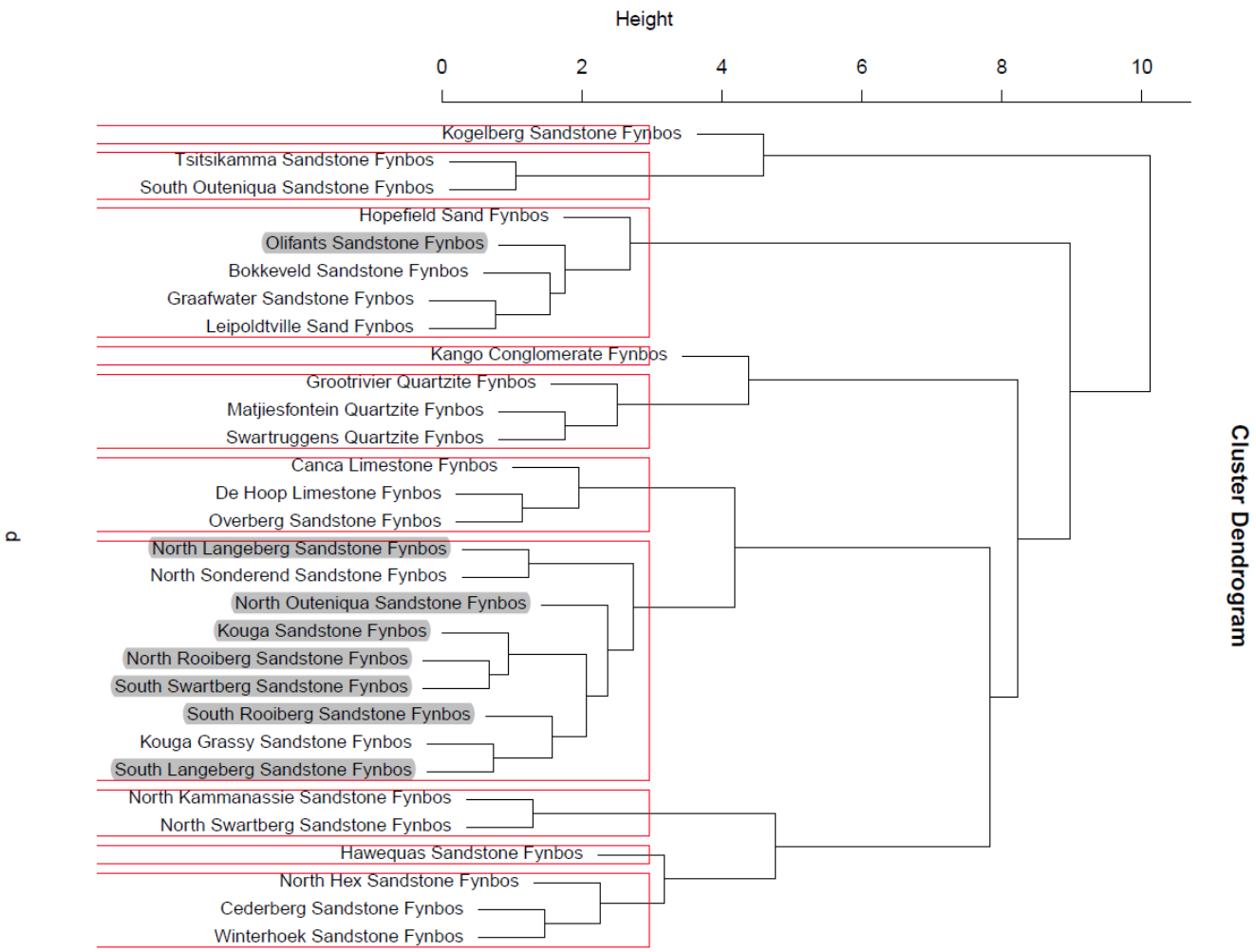

Appendix 4-3 Hierarchical clustering of 30 fynbos vegetation types, red boxes represent groups of similar vegetation types, poorly predicted vegetation types shaded in grey.

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CHAPTER 5

5. CONTRASTING SPECIES- AND VEGETATION-BASED ASSESSMENTS OF THE VULNERABILITY OF A MEDITERRANEAN TYPE ECOSYSTEM TO CHANGING CLIMATE AND FIRE

5.1 Abstract

Aim: Projected changes in climate and fire regime are anticipated to disrupt existing vegetation distributions, these changes will likely lead to the development of novel plant assemblages with unknown implications for ecosystem functions. Most vulnerability assessments rely on modelling species or predefined groupings of plant species (e.g. vegetation type) to explore changes in vegetation across landscapes. However, little consideration is given to how the underlying composition of species that define these vegetation units may also be impacted by climate change. Here, we investigate the degree to which modelled sets of individual species versus vegetation types correspond, and the implications for assessing potential vegetation responses to changes in climate and fire regime.

Location: Cape Floristic Region (CFR), South Africa

Methods: We modelled the current and future distribution of 438 fynbos species, using Maxent. The model was fit with five climatic variables, in conjunction with one edaphic and one fire variable. A *k* means clustering approach was used to select a subset of nine out of 44 future scenarios (11 CMIP5 general circulation models (GCMs), for the RCP4.5 and RCP8.5 scenarios, under the periods 2046-2065 and 2081-2100) for the modelling process. The modelled distributions of the individual species, consisting of endemic and important species, were overlaid with the projected distributions of 22 fynbos vegetation types. The overlap between these two data was used to assess the composition of the 22 vegetation types under the nine future scenarios.

Results: Pairwise Bray-Curtis dissimilarity (βBC) indicated that the species composition of all 22 vegetation types was altered by 0.05-0.3 (overall median Bray-Curtis dissimilarity (βBC)) under the nine future scenarios. The dissimilarity in the species composition of present-day and future vegetation types was largely explained by the abundance balanced variation (βBC-BAL)

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component of the Bray-Curtis dissimilarity index, i.e. individuals of some species in the present-day vegetation type were replaced by the same number of individuals of different species in the corresponding future vegetation type.

Main conclusions: Species largely respond in unison rather than as individuals to changes in climate and fire regime. Using predefined groupings of vegetation such as vegetation types in assessing vegetation response to global change drivers is particularly useful as they reflect, to a larger extent, underlying species responses within a vegetation type.

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5.2 Introduction

As the evidence of climate change and its impact on biodiversity continues to grow (Peñuelas & Filella, 2001; Parmesan & Yohe, 2003; Cavanaugh et al., 2014; Vergés et al., 2016; Slingsby et al., 2017), issues pertaining to the future management and conservation of biodiversity are evermore critical. In recent years a new field of interest, coined species redistribution, has developed amongst ecologists, conservationists and social scientists (Bonebrake et al., 2017; Pecl et al., 2017). Species redistribution focuses on the reorganisation of species distributions, i.e. shifts in species location, abundance and the resulting community composition, in response to climate change, and its consequences for both the natural system and human welfare (Bonebrake et al., 2017). Of particular concern is the impact of climate change on vegetation distributions. Shifts in vegetation distributions ultimately lead to the disruption of ecosystem functions such as water purification and carbon sequestration (Franklin et al., 2016), and present significant challenges for society, e.g. health risks, food insecurity and resource conflicts (Pecl et al., 2017). Mitigating and/or adapting to these impacts will require an enhanced scientific understanding of biological responses to climate change.

In Mediterranean type ecosystems (MTEs), where crown fires are prevalent, the distribution and composition of vegetation is likely to be altered by the combined impact of climate change and changes in fire regime, much of which is climate-induced (Mouillot et al., 2002; Batllori et al., 2013; Wilson et al., 2015). The climate in MTEs is predicted to become warmer and drier (Hennessy, 2006; Yates et al., 2010), leading to dramatic shifts in fire activity (Batllori et al., 2013; Wilson et al., 2015). The negative implications of these predictions are already being seen in MTEs such as the Cape Floristic Region (CFR), where Slingsby and coworkers (2017) observed a loss of plant species diversity partly in response to extreme post-fire weather i.e. high temperatures and drought in the first summer after fire. Anticipating vegetation responses to changes in both climate and fire regime, will be critical for the management and conservation of biodiversity in MTEs.

Projecting vegetation responses to global change drivers is typically done by modelling the distributions of species or vegetation units using either correlative or mechanistic models. Both correlative and mechanistic approaches have been used to model vegetation distributions either as individual species (Bomhard et al., 2005; Lötter & Le Maitre, 2014), or as predefined vegetation formations such as communities (Ferrier & Guisan, 2006) and biomes (Scheiter &

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Higgins, 2009). Correlative models are typically referred to as species distribution models (SDMs; Elith & Leathwick, 2009), or bioclimatic envelope models (Pearson & Dawson, 2003; Thuiller et al., 2005). The correlative approach involves using statistical relationships between species occurrence and environmental factors to describe and predict species distributions. One of the major criticisms of the correlative approach in distribution modelling is that it fails to account for key dynamic processes such as species dispersal and biotic interactions, which mediate their responses to environmental factors (Pearson & Dawson, 2003). An alternative to correlative models are mechanistic models, which make use of the morphological, behavioural and physiological characteristics of species to determine their distributions and abundance (Kearney & Porter, 2009). Examples of mechanistic models include gap models (Fischer et al., 2016), and dynamic vegetation models (Moncrieff et al., 2015). Mechanistic models do however require large amounts time, effort, resources and data to construct and validate (Kearney & Porter, 2009; Dormann et al., 2012). Hence, correlative models, which are relatively less time consuming and data intensive, remain the cornerstone of biodiversity assessments (Evans et al., 2015).

Models based on either individual species or predefined groupings of vegetation have different shortcomings. In the context of landscape scale conservation, a species level approach has significant limitations. The financial resources, computational power and time required to model the distribution of an entire range of species in a given area, on a species-by-species basis, makes such an undertaking impractical. The alternative species level approach, where only ecologically significant species are used, is also subject to uncertainty (Ferrier, 2002), as it is unclear to what extent these species are representative of the entire range of species at a given site. Furthermore, conservation and management strategies based on the requirements of a single species, or a small grouping of species, may fail to conserve other critical species or processes that contribute to the integrity and functioning of an ecosystem. Interspecific interactions such as competition and mutualism, which may be critical for the persistence of species, are also often ignored in SDMs. Such information is generally difficult to integrate into SDMs (Godsoe et al., 2017), but its exclusion may lead to an inaccurate understanding of species distributions.

Distribution models of predefined groupings of vegetation are generally based on either plant functional types (PFTs), vegetation communities or vegetation types. Plant functional types are

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non-phylogenetic groupings of species that have similar physiological, morphological or life history traits (Duckworth et al., 2000), and are typically used in dynamic vegetation models (Midgley et al., 2010). These models are however restricted to a limited number (typically <10) of plant functional types (Lavorel et al., 2007) and generally do not have a shrub PFT, a dominant feature of Mediterranean type ecosystems (Moncrieff et al., 2015). This ultimately results in a limited understanding of how vegetation, in its entirety, will respond to changes in climate and fire regime. Modelling vegetation distributions at community level involves using a wide spectrum of species represented as groupings of similar species composition with a clustered position on environmental gradients across the landscape. Community level modelling requires comprehensive species data and complex processing to derive the plant communities to be used as input for the model. In cases where plant community data may not be easily accessible, vegetation type data, which is more readily available, may be used instead. Vegetation type data contain sufficient physiological and functional detail of vegetation patterns, while being broad enough to represent a wide range of species within a landscape (Ackerly et al., 2015). Vegetation types are widely recognised as the main biological units of measurement underpinning vegetation maps, and have been used to guide conservation planning and land management for years, e.g. the Southern African Millennium Ecosystem Assessment (Bohensky et al., 2004), Succulent Karoo Ecosystem Plan (SKEP, Driver et al., 2003), National Environmental Management: Biodiversity Act (NEMBA, 2004) and the National Biodiversity Assessment (Driver et al., 2012).

However, in utilizing vegetation types as input data in modelling future vegetation distributions, the assumption is that species within a vegetation type will shift as a contiguous unit in response to changes in the environment. This implies that there exists some level of between-species coordination (sensu Clements, 1936) or similar evolutionarily-entrenched niche requirements such as particular climatic conditions, soil properties or disturbance regime which cause the species within the same vegetation type to respond in unison. If this assumption holds, then the vegetation type can be considered an appropriate unit for understanding biodiversity responses to global change as well as developing effective conservation and fire management strategies. If this assumption does not hold, then models based on vegetation types are not appropriate, species may move independently of each other (Gleason, 1926) leading to shifts in the species composition of currently described vegetation

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types, and ultimately the development of novel plant assemblages with unknown consequences for biodiversity and ecosystem processes and functions like hydrology and fire behaviour.

Despite the limitations of species- and vegetation- based models, comparing the two models offers an opportunity to gain more insight into potential species and vegetation responses to changes in climate and fire regime. In this paper, the efficacy of vegetation types as biologically meaningful entities that can be used to predict potential vegetation responses to changes in climate and fire regime is investigated. We use a correlative approach to project the distribution of 22 fynbos vegetation types, coupled with a suite of endemic and important species associated with each vegetation type, under a future climate and fire regime. Endemics are described as species` that occur exclusively in a given area. In the Fynbos biome, this definition is further expanded to include species that may have less than 10% of localities outside their respective vegetation unit (Mucina et al., 2006). Important species are those that are either high in abundance or frequency of occurrence, or predominant in a given vegetation unit (Mucina et al., 2006). We hypothesise that if species respond to changes in ecological regime in unison, the projected distributions of endemic and important species will follow the distribution of their respective vegetation types. If, however, species respond as individuals, the projected distributions of endemic and important species will not match their respective vegetation types, with some species from the current vegetation types being lost and others being gained under future climate and fire regime.

5.3 Methods

5.3.1 Study area

Our study focuses on the remnants of fynbos vegetation found in the mountain regions of the CFR, covering an area of 36 600km^2 (Figure 4-1). Fynbos vegetation is rich in diversity, holds high rates of endemism (Goldblatt, 1978), and accounts for over 7000 of the floral species found in the CFR (Cowling & Richardson, 1995). Fynbos vegetation is supported by a range of nutrient poor sandy soils to richer clay soils arising from aeolian marine sands and underlying layers of sandstone, granite and shale (Goldblatt & Manning, 2000). The study area is largely characterized by a Mediterranean-type climate (Köppen, 1931), with wet winters and hot, dry summers in the west, transitioning into relatively temperate conditions with bimodal rainfall towards the east (Schulze, 2007; Southey, 2009; van Wilgen et al., 2010).

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Projected trends in climate indicate an increase in temperature (Niang et al., 2014) coupled with a decrease in winter rainfall in the south-west section of the CFR, and an increase in rainfall inland and towards the east (Hoffman et al., 2009; MacKellar et al., 2014). These projected changes in climate are anticipated to result in drastic alterations in the regions fire regime (Batllori et al., 2013; Wilson et al., 2015). Fires in the fynbos region mainly occur during the dry, hot summer period (Cowling, 1992), although winter fires are common in the coastal mountain ranges in the east of the CFR (Southey, 2009). Fire return interval in the fynbos ranges between 10-30 years, however these intervals are becoming shorter as a result of changes in fire weather (Wilson et al., 2010; Kraaij et al., 2013a), increasing human populations (Forsyth & van Wilgen, 2008; van Wilgen et al., 2010), and modification of fuel loads alien plant species (Pausas & Keeley, 2014b).

5.3.2 Data

5.3.2.1 Vegetation type data

The 22 vegetation types which were modelled in the previous chapter (Chapter 4) and had a model accuracy (proportion of pixels correctly predicted) of greater than 50% were used in this study. These vegetation types were extracted from the Vegetation of South Africa, Lesotho and Swaziland Map (South African National Biodiversity Institute, 2006), also known as the VegMap as it will be referred to in this study henceforth. The VegMap consists of 440 vegetation types, of which 80 are fynbos, mapped at a scale of 1:250 000 and at finer scales in some other areas. Criteria used to define these vegetation types includes: floristic similarity, vegetation structure, position along major ecological gradients and ecological preferences (e.g. alkaline soils) (Mucina et al., 2006). The first VegMap was produced in 2006, later updated in 2009 and further updated in 2012. The 22 vegetation types were derived from the VegMap (version 2012) which was downloaded from the SANBI BGIS website (http://bgis.sanbi.org/SpatialDataset/Detail/18) and subsequently rasterized to a 1-minute resolution (~1.55 x 1.85 km) to match the environmental data. The rasterized VegMap was then trimmed to the extent of our study area (Figure 4-1), from which fynbos vegetation types with ≥100 pixels were extracted.

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5.3.2.2 Species occurrence data

We focused on species identified as endemic or important in each of the selected vegetation types by the VegMap (South African National Biodiversity Institute, 2006). Here, endemic species refer to species that exclusively occur within a specific vegetation type, while important species are those that are either of high abundance, frequent occurrence or prominent within given vegetation types (Mucina et al., 2006). Locality points for the selected species were derived from the Botanical Database of Southern Africa (BODATSA, South African National Biodiversity Institute, 2016). Species with less than 15 locality points were removed from the species list, yielding a total of 438 species, with 73 being endemic and 365 being important species.

The resultant species data set was examined for spatial sampling bias, a common limitation found in presence-only data where some areas in the landscape are sampled more intensively than others, which could lead to misrepresentation of the real distribution of species (Reddy & Dávalos, 2003; Kadmon et al., 2004). Here a set of random points was generated in ArcGIS 10.4 (ESRI, 2016) to act as a proxy for a normally distributed sample. We then compared the proximity of the sample points to roads to that of the random points using the near tool in ArcGIS (ESRI, 2016). It was established that >50% of both the random points and sample points were located within a 1km of a road (Figure 5-1). These results are reflective of the very dense network of roads that exists within the study area, and it is unlikely that our sample is biased towards the environmental covariates used in the study.

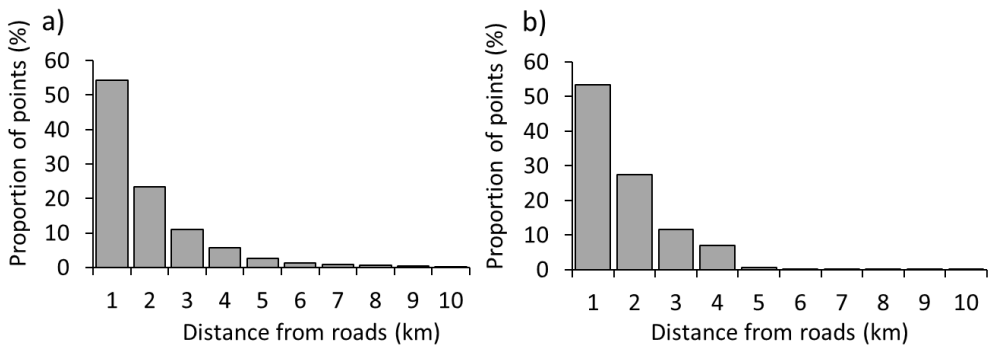

Figure 5-1: Frequency histogram indicating proximity of the a) random points and b) the study area sample points to roads.

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5.3.2.3 Predictor variables

Predictor variables were selected following those used for modelling species in the CFR and other fire prone ecosystems in previous studies (Midgley et al., 2006; Moretti et al., 2006; Syphard & Franklin, 2010; Lötter & Le Maitre, 2014). These consisted of five climatic variables: mean annual precipitation (*map*), mean January precipitation (the driest month, *mmp01*), Markham`s precipitation concentration (*pptconc*, Markham, 1970), mean maximum January (summer) temperature (*tmax01*), mean minimum July (winter) temperature (*tmin07*); one soil variable representing fertility and texture (*soil*), and one fire variable representing fire return interval (*fri*).

Climatic variables were derived from long-term (1950-2000) mean climate data from the South African Atlas of Agrohydrology and Climatology (Schulze, 2007). Markham`s precipitation concentration represents precipitation seasonality and ranges from 0% to 100%. A value of 0% indicates equal rainfall throughout the year, while 100% indicates that all precipitation falls in a single month (Markham, 1970; Wilson et al., 2015). The soil variable was derived from a 1:250 000 geological map from the Council for Geosciences for which each lithology was classified by experts into fertility (4 classes), texture (4 classes) and pH classes (3 classes) and rasterized (Latimer et al., 2006a). We reduced the dimensionality of the data by performing a principal coordinate analysis (PCoA) on the Bray-Curtis distances between cells based on the 11 data layers. Only the first PCoA axis (representing 56% of the variance) was retained as all further PCoA axes represented only 15% of the variance or less.

The fire variable was derived from a hierarchical Bayesian statistical framework that modelled post-fire recovery based on ten years (2000-2010) of remotely sensed Moderate Resolution Imaging Spectroradiometer (MODIS) 500m resolution 16-day gridded Normalized Difference Vegetation Index (NDVI) data (Wilson et al., 2015). The variable represents the time required for the vegetation to recover to the point where it can once again carry a fire and has been used in other species distribution modelling studies (e.g. Merow et al., 2014). Wilson et al., (2015) corroborated that it is a good proxy for fire return interval by comparing it with a survival model fit with observed fire return times. Since the recovery rates were estimated in the context of post-fire vegetation age and not chronological time, and these ages ranged up to 59 years old, the estimates include the influence of weather for decades prior to the NDVI record and

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encompass the period during which the majority of our species locality records were collected (Median: 1993, Interquartile Range: 1972:2003).

The climate and fire data were resampled from 0.5km resolution to 1 -minute (~1.55 x 1.85 km) resolution to match the resolution of the soil data. The "cor" function in R was used to test for collinearity (level of dependence) amongst the selected variables. None of the variables were correlated at a level sufficiently high enough to be of concern, r >|0.7| (see Dormann et al., 2013), therefore all seven variables were retained. All data were spatially trimmed to the extent of the remnant fynbos in the CFR (Figure 4-1).

5.3.2.4 Future climate and fire regime projections

Future climate and fire data were obtained from Wilson and coworkers (2015). These data are based on the six predictor variables projected under an ensemble of 11 Phase 5 Coupled Model Intercomparison Project (CMIP5) general circulation models (GCMs), for two Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathways (RCPs) scenarios (RCP4.5 and RCP8.5), in two time periods 2046-2065 and 2081-2100. This resulted in a total of 44 future climate futures. Projections of fire return interval are based on predicted changes in vegetation recovery time across the 44 downscaled CMIP5 GCMs for the CFR (Wilson et al., 2015). The RCP4.5 represents a moderate future scenario, described by a global population that peaks mid-century and declines thereafter, while economic structures rapidly change towards a service and information economy, with clean and resource-efficient technologies (Smith & Wigley, 2006; Clarke et al., 2007). The RCP8.5 scenario is the worst case scenario of the RCPs, representing a world characterised by high energy demand and green house gas emissions resulting from an absence of climate change policies, high population, slow income growth, and modest technological advancements and energy intensity improvements (Riahi et al., 2011).

5.3.3 Sub-setting future climate and fire regime scenarios

In order to account for the uncertainty associated with projected changes in climate, the (IPCC, 2014) recommends that as many future climate scenarios as possible be used in climate change impact assessments. However, the time required and enormity of projecting and analysing the distribution of multiple species, under a large ensemble of climate scenarios, can be limiting. We therefore employ a *k*-means clustering approach (Casajus et al., 2016) to select a subset of

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future scenarios that represent the range of possible future climatic and fire conditions described by the 44 climate futures available for our study. The k means clustering approach iteratively partitions *n* objects into *k* clusters using *p* variables (Casajus et al., 2016).

Following Casajus et al., (2016), a climate distance matrix describing the change in each of the 264 future climate and fire variables (6 variables x 44 future scenarios) from the baseline climate and fire return interval was created. Using the *Stats* package in R (R Core Team, 2017), hierarchical clustering, based on the Ward's minimum variance method (Ward, 1963), was applied to the standardized climate distance matrix. From the hierarchical clustering, the initial cluster centres for the k-means algorithm were identified, and clusters of similar future scenarios corresponding with the initial cluster centres were subsequently established. Using the distance between each object and the cluster centre, the remaining future scenarios were then assigned to the cluster to which they were most similar. The resultant mean for each cluster was then calculated. These cluster centres were iteratively recalculated 999 times in order to establish the optimum number of clusters. Lastly, the Rsq statistic (the ratio of the between-group sums of squares to the total sums of squares) was calculated to quantify the amount of variability between the clusters. The optimum number of clusters was further determined by repeating the entire process, from the initial clustering of the future scenarios to calculating the R^2 statistic, by varying *k* from 1 to 44. The number of clusters to be used was determined by evaluating an R^2 profile plot describing the R^2 value as a function of the number of clusters (see Appendix 5-1). This resulted in nine clusters explaining 81% of the total variance. For each cluster, the scenario that was nearest to the cluster centre was identified and formed the subset of nine future scenarios used in the study (Table 5-1).

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Table 5-1: Subset of nine out of 44 future scenarios selected using the k means clustering approach, with mean projected change from the baseline estimates for the six predictor variables: mean annual precipitation (map), mean January precipitation (mmp01), Markham`s precipitation concentration (pptconc) mean maximum January (tmax01) temperature, mean minimum July (tmin07) and fire return interval (fri). The name of each future scenario describes the scenario (RCP4.5/RCP8.5) coupled with the time period (2046-2065/2081-2100) and GCM used.

Future scenario	Δfri	Δmap	Δmmp01	Δpptconc	Δtmax01	Δtmin07
RCP45_46-65_bcccsm11	-1.05	-15.74	1.94	-0.74	1.27	1.15
RCP45_46-65_MIROCESMCHEM	1.4	-32.48	-7.12	0.88	1.99	1.23
RCP45_81-00_MIROCESM	-0.63	-13.88	-1.37	0.6	2.44	1.95
RCP85_46-65_BNUESM	-2.61	-1.84	5.16	-5.77	2.62	2.45
RCP85_46-65_MIROCESM	-1.11	-6.01	-0.14	-3.22	2.41	1.85
RCP85_46-65_CNRMCM5	0.39	-20.22	-5.39	-1.94	1.84	1.47
RCP85_81-00_bcccsm11	-2.48	-45.94	3.43	-4.19	2.97	2.75
RCP85_81-00_FGOALSs2	-3.85	-25.95	4.18	-8.96	5.8	5.41
RCP85_81-00_MIROCESM	-0.92	-15.09	-3.65	3.7	4.4	3.81

5.3.4 Modelling vegetation type distributions

The projected distributions of the vegetation types modelled (under the nine selected future scenarios) in the previous chapter (Chapter 4) were used as the basis for the species composition analysis in this study. These vegetation types were modelled using a form of logistic regression referred to as multinomial logistic regression. Multinomial logistic regression allows one to build a probabilistic vegetation model (PVM) whereby the likelihood of a vegetation type occurring at a given point is measured. The probability of occurrence for all the vegetation types at each pixel is based on a scale of 0 – 1 (i.e. low to high probability). The PVM is a zero sum model where a reduction in the probability of one vegetation type is balanced by an increase in another vegetation type. An initial set of 30 fynbos vegetation types (Figure 4-2) was modelled using the "multinom" function (Venables & Ripley, 2002) in the R software (R Core Team, 2015). The "train" function from the *caret* package (Kuhn, 2008) was used to produce a confusion matrix from which the overall accuracy of the model, as well as prediction accuracy for each vegetation type, was evaluated. Prediction accuracy for the individual vegetation types was measured as the proportion of pixels in which the most likely vegetation type matched the observed vegetation type. Prediction accuracy ranged between 0

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(North Rooiberg Sandstone Fynbos) and 0.97 (Hopefield Sand Fynbos). Eight of the 30 vegetation types had a prediction accuracy of less than 50% and were subsequently removed from further analyses (Table 4-1), resulting in the 22 vegetation types that were used in this study.

5.3.5 Modelling individual species distributions

5.3.5.1 Model settings

The Maxent (maximum entropy) software package (http://www.cs.princeton.edu/~schapire/Maxent/; (Phillips et al., 2004, 2006) was used model current and future distributions of the 438 selected species. Maxent is a machine-learning model that was preferred over other approaches due to its robust method in handling presence-only, non-stratified data. The Maxent algorithm estimates the probability distribution with the maximum entropy, i.e. the distribution that is most spread out, or closest to uniform after all constraints are taken into consideration (Phillips et al., 2006), by contrasting environmental conditions at the locations of presence data against those at the background location points where presence/absence is not measured.

Each species model was fit with the seven predictor obtained for the current period and the nine selected future scenarios (Table 5-1). Ten replicates were run for each model. Using a random split for each replicate, 70% of the occurrence records were set aside to train the model, and 30% as test data. Background samples were set at the default of 10000 points. Given the varying number of locality points for each of the selected species (median = 28, interquartile range = 15 – 72), linear features as recommended by Merow et al., (2013) for multiple species were used.

5.3.5.2 Model accuracy

Estimates of the area under the receiver operator curve (AUC) were used to evaluate model accuracy. AUC values range from 0 to 1, where < 0.5 indicates a relationship worse than random, 0.5 indicates that the model has no predictive power (no better than random), and 1 signifies a perfect model (Elith et al., 2006). Models with AUC values > 0.9 are considered to be of high accuracy, while those with values in the range 0.7–0.9 are useful; those < 0.7 fairly accurate (Swets, 1988), and those ≤ 0.5 no better than random. Models with AUC < 0.7 were excluded from our study.

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5.3.6 Assessing dissimilarity in species composition between present-day and future vegetation types

To test whether or not species respond in unison to changes in in climate and fire regime, current and projected distributions of both the individual species and vegetation types were overlaid in a raster brick using the *raster* package (Hijmans et al., 2017) in R (R Core Team, 2017). These raster bricks were then converted into community data matrices showing the probability of each species occurring within each vegetation type under the current period as well as the nine future scenarios (Table 5-1). The resultant matrices were used to compare the species composition of present-day vegetation types against that of their corresponding future vegetation types using the *betapart* package (Baselga et al., 2018) in R (R Core Team, 2017). The Bray-Curtis dissimilarity (βBC, Bray & Curtis, 1957), along with two components of the Bray-Curtis index (Baselga, 2013), i.e. balanced variation in abundance (βBC-BAL) and abundance gradient (βBC-GRA), was used to measure the dissimilarity in species composition between present-day and future vegetation types. The Bray-Curtis dissimilarity is a measure of the total change in species composition from one site to another ranging from 0 to 1, with 0 indicating that the two sites have the same composition, and 1 showing that they do not have any species in common. The summation of balanced variation in abundance (βBC-BAL) and abundance gradient (βBC-GRA) components make up the Bray-Curtis (βBC) metric (Baselga, 2013). These two components are particularly important because they highlight the underlying processes that result in a change in species composition, i.e. turnover and nestedness (Leprieur et al., 2011; Baselga et al., 2012). The balanced variation in abundance (βdBC-BAL) is representative of species turnover, indicating the replacement of species from one site (or vegetation type in this case) to another across spatial, temporal and environmental gradients (Legendre et al., 2005; Buckley & Jetz, 2008; Soininen, 2010). On the other hand, the abundance gradient (βBC-GRA) represents nestedness, where a subset of species from one site is found to occur in another site as a result of a gain and/or loss of species between sites.

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5.4 Results

5.4.1 Model accuracy

Overall model accuracy in predicting the current distribution of the 438 fynbos species was good (median AUC = 0.85, interquartile range = 0.55 – 1). Models with AUC<0.7 were removed from the study, leaving the modelled distributions of 369 species (62 endemic species, 307 important species) to be used in further analysis.

5.4.2 Dissimilarity in species composition between present-day and future vegetation types

The species composition of the 22 vegetation types under the nine future scenarios was examined using three metrics: Bray-Curtis dissimilarity (βBC), balanced variation in abundance (βBC-BAL) and abundance gradient (βBC-GRA). The change in the species composition of the selected vegetation types varied between and within each future scenario (Figure 5-2 and Figure 5-3). A unified response of species to changes in climate and fire regime (Clements, 1936) would result in 100% retention of present day species in the projected vegetation type (i.e. βBC = 0). While an individualistic response (Gleason, 1926) would result in the total replacement or loss of species between present-day and future vegetation types (i.e. βdBC = 1). Therefore, intermediate Bray-Curtis dissimilarity scores (βBC >0<1) represent both scenarios whereby some species are retained, while others are replaced or lost. The Bray-Curtis dissimilarity scores for all 22 vegetation types across the nine future scenarios is indicative of both unified and individualistic species responses to changes in climate and fire regime, with median Bray-Curtis dissimilarity (βBC) ranging from 0.05 – 0.3, (Figure 5-2), which translates to 0.7-0.95 similarity in species responses to changes in climate and fire regime.

Changes in species composition between present-day and future vegetation types stemmed from a combination of turnover and nestedness, with the median balanced variation in abundance (βBC-BAL) and abundance gradient (βBC-GRA) ranging from 0.05-0.2 and 0.05-0.1, respectively (Figure 5-2). Overall, balanced variation in abundance (βBC-BAL) accounted for most the dissimilarity in species composition across the nine future scenarios (Figure 5-2). Under future scenarios rcp45_8100_mirocesm and rcp85_8100_mirocesm (Figure 5-3b and 3i), the change in the species composition of all 22 vegetation types was largely related to balanced variation in abundance (βBC-BAL) (i.e. species replacement). The Matjiesfontein Quartzite vegetation type exhibited the greatest dissimilarity in species composition from the

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present-day vegetation type under future scenarios rcp85_8100_bcccsm11, rcp85_4665_bnuesm and rcp85_8100_fgoalss2, with a Bray-Curtis dissimilarity score of over 0.6, and balanced variation in abundance (βBC-BAL) accounting for majority of the dissimilarity (Figure 5-3d, 3e and 3g). Lastly, under future scenarios rcp45_4665_mirocesmchem and rcp85_8100_fgoalss2, some present-day vegetation types altogether disappeared, while the remaining vegetation types largely consisted of replaced species (e.g. Figure 5-3c and 5-3g).

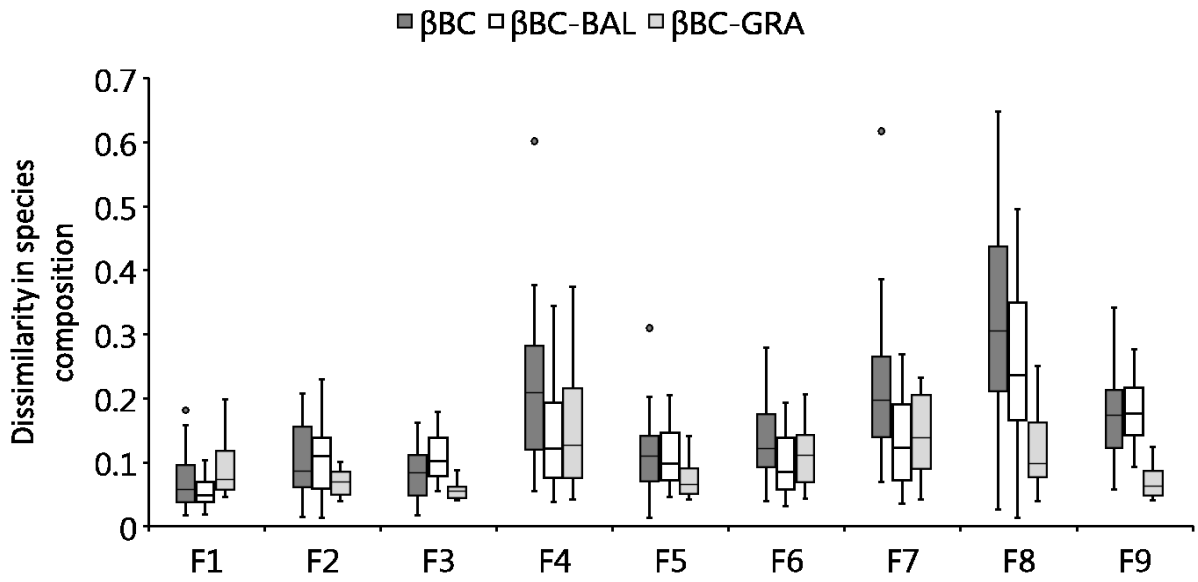

Figure 5-2. Dissimilarity in the species composition of future vegetation types from the present-day vegetation types as described by Bray-Curtis dissimilarity (βBC), balanced variation in abundance (βBC-BAL) and abundance gradient (βdBC-GRA), where F1 = rcp45_4665_bcccsm11, F2 = rcp45_4665_mirocesmchem, F3 = rcp45_8100_mirocesm, F4 = rcp85_4665_bnuesm, F5 = rcp85_4665_cnrmcm5, F6 = rcp85_4665_mirocesm, F7 = rcp85_8100_bcccsm11, F8 = rcp85_8100_fgoalss2 and F9 = rcp85_8100_mirocesm.

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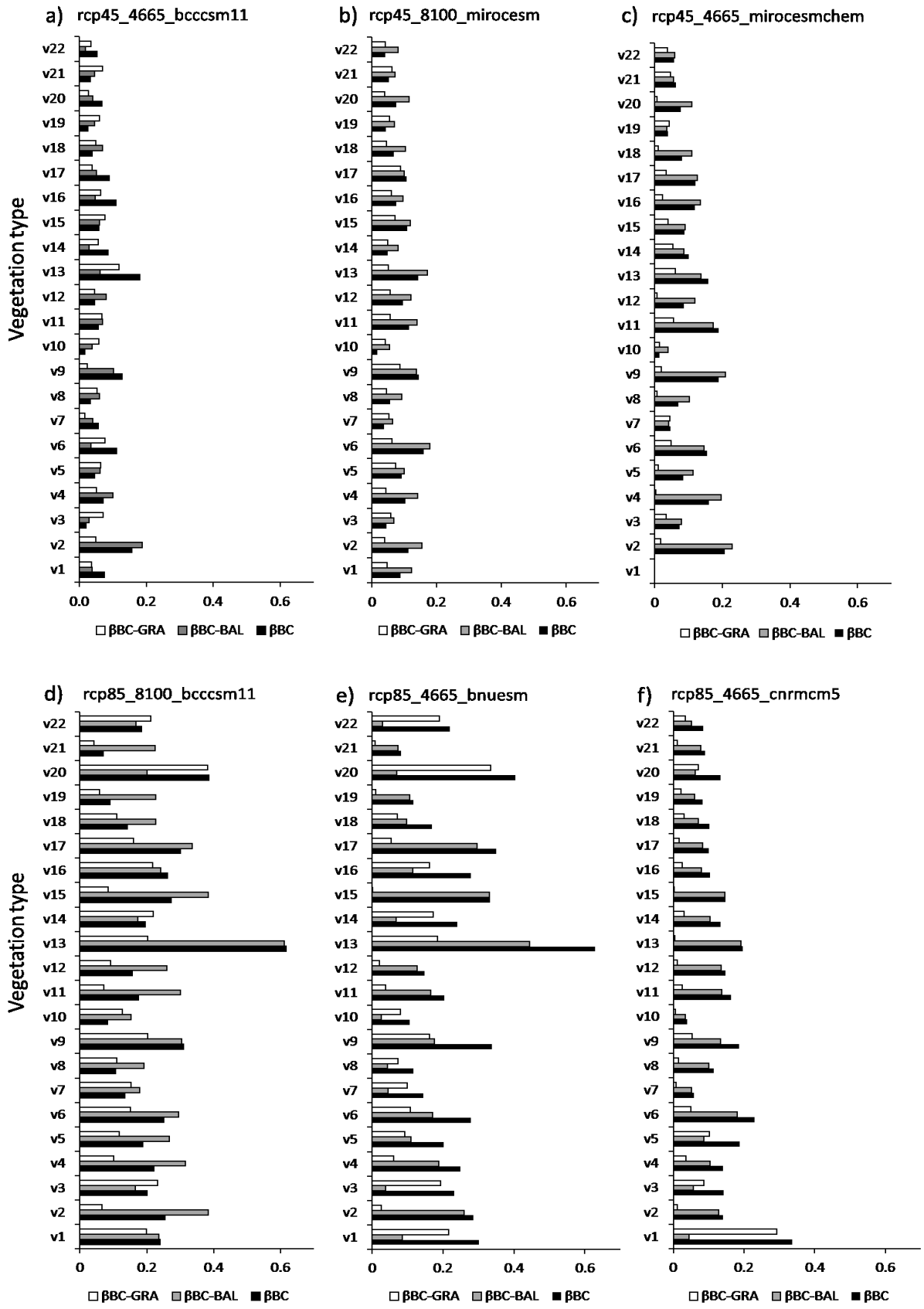

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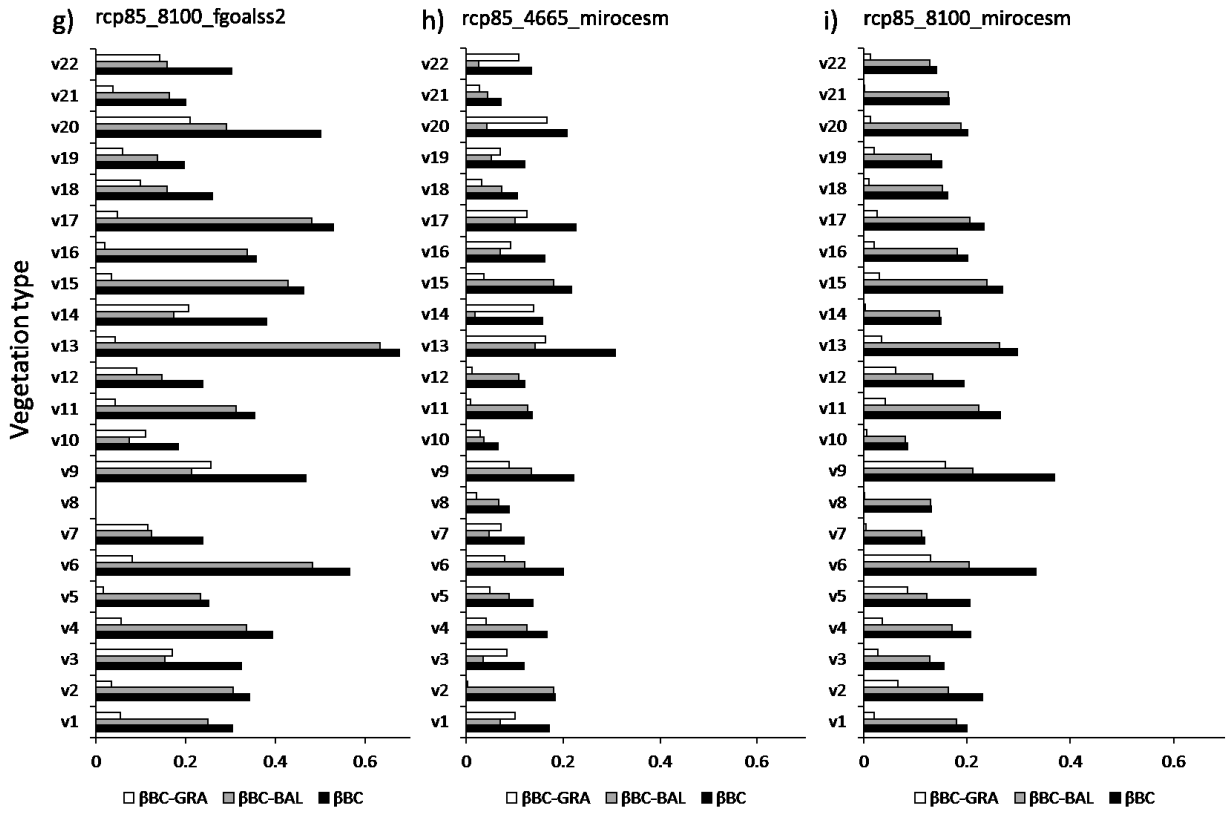

Figure 5-3: Plots a) to i) show the dissimilarity in the species composition of future vegetation types from the present-day vegetation types as measured by the Bray Curtis dissimilarity index (βBC), balanced variation (βBC-BAL) and abundance gradient (βBC-GRA) for the nine future scenarios. Abbreviations of the 22 vegetation types (v1-v22) used in the plots are explained in Table 5-2.

Table 5-2: Description of vegetation type abbreviations used in Figure 5-3

Vegetation type	Code	Vegetation type	Code
Bokkeveld Sandstone	v1	Leipoldtville Sand	v12
Canca Limestone	v2	Matjiesfontein Quartzite	v13
Cederberg Sandstone	v3	North Hex Sandstone	v14
De Hoop Limestone	v4	North Kammanassie Sandstone	v15
Graafwater Sandstone	v5	North Sonderend Sandstone	v16
Grootrivier Quartzite	v6	North Swartberg Sandstone	v17
Hawequas Sandstone	v7	Overberg Sandstone	v18
Hopefield Sand	v8	South Outeniqua Sandstone	v19
Kango Conglomerate	v9	Swartruggens Quartzite	v20
Kogelberg Sandstone	v10	Tsitsikamma Sandstone	v21
Kouga Grassy Sandstone	v11	Winterhoek Sandstone	v22

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5.5 Discussion

Anticipating potential species distributional responses to projected changes in climate and fire regime is critical for the future management and conservation of vegetation in Mediterranean type ecosystems such as the CFR. Our understanding of how climate change may impact vegetation is largely drawn from either species-based distribution models (Thuiller et al., 2005; Dobrowski et al., 2011), or models of predefined groupings of vegetation, e.g. PFTs and vegetation types (Esther et al., 2010; Ackerly et al., 2015). However, vulnerability assessments that integrate both species and vegetation based distribution models (e.g. Midgley et al., 2002), provide a unique opportunity for advancing our understanding of potential vegetation responses to various drivers of global change. In this study, the extent to which projected distributions of individual fynbos species and vegetation types correspond is investigated. Vegetation types are commonly used in conservation planning and land management (Bohensky et al., 2004; Driver et al., 2012), as they are easily accessible and allow for landscape-scale assessments of vegetation. However, inherent in the utilization of vegetation types is the assumption that species within a vegetation type will shift as a contiguous unit in response to changes in the environment (Clements, 1936). This assumption is tested by super-imposing projected distributions of individual fynbos species and vegetation types, and assessing the dissimilarity between the underlying species composition of present-day and future vegetation types.

5.5.1 Dissimilarity in species composition between present-day and future vegetation types

Bray-Curtis dissimilarity scores for the 22 fynbos vegetation types, across the nine future scenarios, indicate that less than 30% of the underlying species composition of present-day vegetation types will likely be altered in response to changes in climate and fire regime. This finding largely agrees with the assumption of a unified species response (Clements, 1936) that underpins the use of vegetation types in distribution studies, and highlights that only a small portion of species respond individualistically to changes in climate and fire regime. It is reasonable to expect such a mixed response as species that share similar functional characteristics will likely exhibit similar responses to environmental changes (Diaz & Cabido, 1997),while different adaptations and environmental thresholds may give rise to individualistic responses (Stewart et al., 2010). Changes in the species composition of present-day vegetation types under future scenarios indicates that vegetation-based models provide a limited understanding of potential vegetation response to changes in climate and fire regime. Midgley et al., (2002) highlight similar findings where a biome level approach was used to assess the vulnerability of species to climate change in

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the Fynbos Biome. This approach was found to significantly underestimate species diversity losses resulting from changes in climate. Ultimately, there is a need to integrate distributions derived from species- and vegetation- based models if predictions of vegetation response to climate change are to be improved.

5.5.2 Implications of changes in species composition

While changes in species composition between present-day and future vegetation types resulted from the combined effect of turnover and nestedness, species turnover, or more specifically, the replacement of species in present-day vegetation types by the same number of different species in future vegetation types (Leprieur et al., 2011; Baselga, 2013), accounted for much of the change in species composition observed in the study. This suggests that shifts in the relative abundance of species will likely have a greater impact on vegetation distributions than actual losses in species (Rao & Larsen, 2010). Furthermore, it is expected that changes in species composition will result the development of novel combinations of species interactions which will ultimately lead to disruptions in ecosystem functioning (Williams & Jackson, 2007; Pecl et al., 2017). For example, Cavanaugh et al., (2014) anticipate that the replacement of coastal wetland foundation species on the east coast of Florida will likely have dramatic effects on nutrient cycling, carbon sequestration and water filtration in the region. The disruption of ecosystem functions further present significant challenges for society, e.g. health risks, food insecurity and resource conflicts (Pecl et al., 2017). Therefore, efforts aimed at anticipating the impacts of climate change should also be extended towards identifying potential losses in ecological services that stem from the disruption of ecosystem functions.

Changes in the species composition of current species assemblages such as vegetation types, communities, or biomes are anticipated to give rise to ecological surprises or unexpected species responses with unknown implications (Williams & Jackson, 2007; Stralberg et al., 2009). This presents a difficult challenge for conservation managers. As conservation targets are re-shuffled and new ones emerge in unpredictable ways, identifying how, where, and which species to prioritize in conservation efforts becomes a challenge (Stralberg et al., 2009). Furthermore, it is suggested that traditional management approaches which focus on maintaining species within their known range of biotic and abiotic characteristics and processes will likely be ineffective (Seastedt et al., 2008). Therefore adaptive management, where strategies to manage novel communities are continuously revised based on rigorous research and monitoring, will be critical for future

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conservation and management of biodiversity (Stralberg et al., 2009; van Wilgen & Biggs, 2011; Westgate et al., 2013).

5.6 Conclusion

The aim of this study was to highlight the advantages of comparing the distributions of individual species versus predefined groupings vegetation (vegetation types in this case) to further our understanding of vegetation responses to changes in climate and fire regime. Using this comparative approach, it was revealed that species responses to environmental change largely conform to the Clementsian concept (Clements, 1936) that underpin the use of vegetation types, with less than 30% of the species showing individualistic responses. Therefore, the use of vegetation-based models remains a particularly useful approach in vulnerability assessments as the majority of the underlying shifts in species composition are accounted for. However, given the implications of changes in species composition on the functioning of ecosystems and the resultant emergence of novel species assemblages with unknown implications, future distribution models need to evolve towards an integrated approach, where both species level data and vegetation data are incorporated, to adequately anticipate future distributional responses to changes in climate and fire regime.

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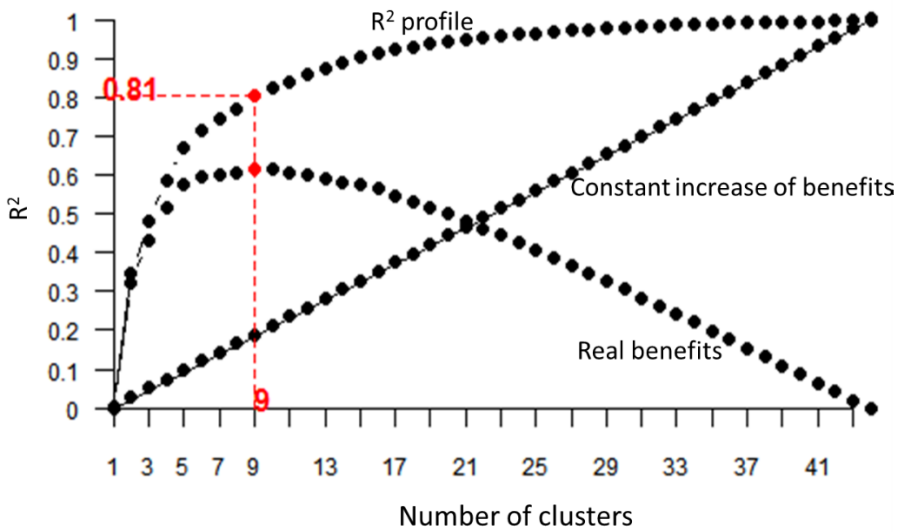
5.7 Appendices



Appendix 5-1. R^2 plot where the line plotted through the points (1,0) and (n,1), n being the maximum number of clusters, indicates a constant increase between the costs and benefits (i.e. the number of clusters and r^2 value, respectively). The curve of real benefits is then obtained by subtracting the R^2 profile from this line. The optimal number of clusters is determined by the point at which the maximum value of the curve corresponds with the inflexion point of the R^2 profile. As a result nine clusters with a total variance of 81% were identified for the study.

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CHAPTER 6

6. SYNTHESIS

The synthesis chapter highlights the significance of this study through an evaluation of the research findings drawn from the three data chapters (Chapters 3, 4 and 5). The first section of the evaluation revisits each of research objectives outlined in the introductory chapter (Chapter 1) and highlights their key findings. Thereafter, contributions to existing body of knowledge are discussed, followed by an outline of limitations and opportunities for further research are discussed, and finally the conclusion.

6.1 Introduction

The overarching aim of this research was to enhance our scientific understanding of the drivers and underlying ecosystem processes that shape vegetation distributions in the CFR, particularly focussing on the importance of fire regimes and vegetation distributional responses to changes in climate and fire regime. This aim was achieved through the implementation of the three main research objectives discussed below.

6.2 Revisiting objectives and key findings

6.2.1 Investigate the importance of fire as a predictor of plant species distributions in the CFR relative to climate and soils, and if this varies among species with different life histories.

To achieve this objective, the distribution of 104 fynbos plant species of different growth form and fire-response strategies was modelled using the Maxent (maximum entropy) software package (Phillips, Dudik & Schapire, 2004; Phillips, Anderson & Schapire, 2006). Sister species comparisons were used to account for phylogenetic autocorrelation. The model was fit with five climatic variables, in conjunction with one edaphic and one fire variable. To evaluate the importance of fire and the effect of life history on species response to fire post-hoc analyses of model output and permutation procedures were conducted. Findings from the analyses confirmed the importance of fire return interval as a determinant of fynbos plant species distributions. However, due to the dependence of fire on climate, fire was found to be an inherently weaker determinant of fynbos distributions when compared to climate. It was also observed that seeder species were more sensitive to fire return interval than resprouters.

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6.2.2 Evaluate the contribution of fire in determining the distribution of fire-prone fynbos vegetation types, and the potential impacts of changes in climate and fire regime on their future distributions.

Here, current and future distribution of 22 fynbos vegetation types were modelled using multinomial linear regression yielded probability distribution maps for each vegetation type. Data for the current distributions was fit the same seven predictor variables used in the previous data chapter. For the future distributions, future climate and fire data were derived from an ensemble of 11 CMIP5 general circulation models (GCMs), for the RCP4.5 and RCP8.5 scenarios, under the periods 2046-2065 and 2081-2100 (Wilson et al., 2015). In order to evaluate the contribution of fire as determinant of the vegetation type distributions, two sets of models were used: the first model was fitted with six variables (i.e. climate and soil), and the second model fitted with fire return interval as an additional variable. The importance of each predictor variable in determining the distribution of the vegetation types was measured using the Akaike Information Criterion (AIC) value. The sensitivity of vegetation to changes in climate and fire regime was measured by calculating the number of times a given pixel was projected to change from the baseline vegetation type to another vegetation type in response to the 44 futures scenarios.

Fire return interval exhibited substantial explanatory power in describing the distribution of vegetation in the study system, despite climatic influences on fire regime (Wilson et al., 2010; Kraaij & van Wilgen, 2014). Under future scenarios, the areal extent of coastal vegetation types in the west of the CFR is projected to increase in areal extent under shorter fire return intervals, while vegetation types at higher altitudes in the interior and east of the CFR are projected to decrease in areal extent under shorter fire return intervals. Possibly indicating greater resilience against changing environmental conditions in coastal vegetation in comparison to high altitude vegetation types. It was also noted that vegetation distributions were more susceptible to changes in fire return interval than to changes in mean annual precipitation, therefore it is likely changes in fire regimes may have a greater influence on future vegetation distributions, than direct impacts of climate change. Furthermore, vegetation types located at sites with longer fire return intervals (i.e. arid interior) and warmer summer and winter temperatures (i.e. coastal areas) were identified to be at greatest risk from changes in climate and fire regime.

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6.2.3 Compare potential species level and community (i.e. vegetation type) level responses to projected changes in climate and fire regime in the CFR.

For this objective, current and future distributions of 438 fynbos species, were modelled using the Maxent software package (Phillips, Dudik & Schapire, 2004; Phillips, Anderson & Schapire, 2006). The model was fit with five climatic variables, in conjunction with one edaphic and one fire variable. A *k* means clustering approach was used to select a subset of nine out of 44 future scenarios (11 CMIP5 general circulation models (GCMs), for the RCP4.5 and RCP8.5 scenarios, under the periods 2046-2065 and 2081-2100) for the modelling process. The modelled distributions of the individual species, consisting of endemic and important species, were overlaid with the projected distributions of 22 fynbos vegetation types modelled in the previous chapter (Chapter 4). The overlap between these two data was then used to assess the underlying species composition of the 22 vegetation types under the nine future scenarios using pairwise Bray-Curtis dissimilarity (βBC, Bray & Curtis, 1957), along with two components of the Bray-Curtis dissimilarity (Baselga, 2013), i.e. balanced variation in abundance (βBC-BAL) and abundance gradient (βBC-GRA, representing species turnover and nestedness, respectively.

Bray-Curtis dissimilarity scores for the 22 fynbos vegetation types, across the nine future scenarios, indicate that 30% (or less) of the underlying species composition of present-day vegetation types will likely be altered in under the projected future scenarios, highlighting a largely unified species responses to changes in climate and fire regime. In addition, based on the measured balanced variation in abundance (βBC-BAL) scores, it is anticipated that species turnover will be a major driver of changes in species composition under changing climate and fire regime.

6.3 Contribution to existing body of knowledge

Research findings from this dissertation do not only contribute towards a better understanding of the role of fire as a determinant of species and vegetation distributions in the CFR, but also serve to inform our decisions regarding the data and approaches we use to anticipate vegetation responses to drivers of global change.

Firstly, this study highlights the importance of fire in determining current species distributions, and the influence of life history on the sensitivity of these species, as key factors in understanding future species distributions in the CFR. While the role of fire as a determinant of species distributions is well understood (van Wilgen & Forsyth, 1992; Bond & Keeley, 2005; Keeley et

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al., 2012), and various studies allude to the need to incorporate more non-climatic variables and consider functional trait differences amongst species when modelling distributions (Syphard & Franklin, 2010; Yates et al., 2010; Austin & Van Niel, 2011; Enright et al., 2014), only a handful of studies have implemented such modifications to their species distribution models (Syphard & Franklin, 2010; Tucker et al., 2012; Crimmins et al., 2014). Chapter 3 provides comprehensive evidence of what can be learned from incorporating disturbance data (i.e. fire) and life history traits into species distribution models. A key finding that adds to that of Tucker et al., (2012) and Crimmins et al., (2014) is that the dependence of fire regime on climate tends to overshadow the importance of fire as a determinant ofspecies distributions in fire prone ecosystems. Nonetheless, an assessment of the permutation scores from the model in Chapter 3 identified fire as one of the three strongest determinants of fynbos plant species distributions. Therefore, despite the general assumption that species distributions are more strongly limited by climate as compared to edaphic conditions and or disturbance, findings from Chapter 3 indicate that disturbance variables such as fire have the capacity to add to our understanding of plant species distributions in fire-prone ecosystems. Moreover, the observed variation in species' response to environmental covariates across different growth forms and fire-response strategies in the study shows that life history traits are crucial to the identification of vulnerable species in climate change impact assessments.

Secondly, while much effort has been given to predicting potential biological responses to climate change, how changes in disturbance regimes such as fire may impact the future distribution of vegetation types remains unclear. Findings from Chapter 4, highlight two key aspects regarding potential vegetation responses to changes in climate and fire regime: 1) the addition of fire covariates in distribution models allows for the identification of vegetation types that may not be directly affected by changes in climate, but are highly vulnerable to shifts in fire regime, and 2) Projected changes in fire regime are likely to have greater impacts on vegetation distribution than changes in rainfall regime would. Therefore, the extent and manner in which changes in fire activity may affect vegetation distributions in fire-prone ecosystems such as the CFR requires more attention.

Lastly, findings from Chapter 5 contribute to the ongoing debate regarding the manner in which species respond to changes in the environment, i.e. unified versus individualistic response. There is a general agreement that species will respond to climate change individualistically, and not as communities (Stewart et al., 2010; Anadón et al., 2015). Yet, interestingly, in utilizing vegetation types as input data in modelling future vegetation distributions, the assumption is that species

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within a vegetation type will shift as a contiguous unit in response to changes in the environment. In this study, however, a comparison in between the underlying species composition of present-day and future vegetation types revealed that majority of species respond in unison, rather than as individuals, to changes in climate and fire regime.

6.4 Limitations and opportunities for further research

The correlative approach used to model the distributions of species and vegetation types (Chapters 3, 4 and 5) likely led to the underestimation of the relative importance of fire as a predictor of vegetation distributions in the CFR. This is because correlative models have a limited capacity to separate the interacting roles of fire and climate in shaping vegetation distributions. Mechanistic approaches present an effective alternative to teasing apart the relative importance of climate and fire. Such an approach would be particularly useful in cases where the relationship between fire and climate is decoupled (i.e. when fire and climate act independently) either naturally (Geldenhuys, 1994) or due to human influence (Syphard et al., 2009; Regan et al., 2010), and also when fire and climate have separate but complimentary roles (Treurnicht et al., 2016). Unfortunately, mechanistic approaches, are generally time and data intensive (Kearney & Porter, 2009; Dormann et al., 2012), and use broad scale descriptions of vegetation (e.g. biomes and plant functional types) that are not suitable at landscape scales (Leemans, 1997; Duckworth et al., 2000). Demographic and Bayesian models (Treurnicht et al., 2016; Slingsby et al., 2017) do however present alternative approaches which may aid in untangling the complex feedback system between fire regime, climate change, biotic interactions and species traits that shapes vegetation distributions.

Similarly, using fire return interval alone to represent fire regime in the study might have also led to the underestimation of the relative importance of fire as a determinant of vegetation distributions in the CFR. In addition, the fire return interval data used in this study is a proxy derived from vegetation recovery rates (Wilson et al., 2015), however there are few datasets of its kind that exist and none for most flammable ecosystems. Therefore, this dataset provides a unique opportunity in which the impacts of changes in disturbance regimes such as fire on future vegetation distributions can be examined. Nonetheless, the analyses based on this fire variable can be further built upon by incorporating other components of the fire regime. This would likely reveal a stronger influence of fire in shaping plant species and vegetation distributions in the CFR.

6.5 Conclusion

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As the impacts of changes in climate and fire regime become more apparent in fire-prone ecosystems such as the CFR, improving our capacity to anticipate these impacts in order to mitigate and/or adapt to biodiversity losses is ever more critical. While significant efforts have been made towards anticipating vegetation responses to climate change, the potential impacts of changes in fire regime are not well understood. The exclusion of fire in vulnerability assessments is largely due to lack of fire data that can be integrated into distribution models, and the long-held view of climate as the chief determinant of vegetation distributions. This study however provides evidence that: 1) fire does indeed contribute to the shaping vegetation distributions and composition, 2) changes in fire regime will likely have a greater impact on vegetation distributions than climate in the future, and lastly 3) the integration of fire covariates into distribution models facilitates the identification of species and other groupings of vegetation that are not necessarily greatly affected by changes in climate, but are highly vulnerable to changes in fire regime. Ultimately, findings from this study translate to a great need for the development of robust and easily accessible estimates of different components of the fire regime to support future vulnerability assessments in fire-prone ecosystems.

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CHAPTER 7

7. References

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