Ecological Resilience at Semi-arid and Temperate Boundaries of the Mediterranean-type Fynbos Biome, South Africa, during the Holocene

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ABSTRACT

Mediterranean-type ecosystems are amongst the most vulnerable to global change. Threats from desertification are projected due to rapid expansion of adjacent semi-arid systems. Changes in fire frequency and intensity can alter ecosystem composition and structure, and potentially facilitate transitions between alternative stable states. Given the outstanding biodiversity of the Mediterranean-type fynbos biome in the Greater Cape Floristic Region (GCFR) of South Africa, understanding of the long-term impacts of global change are particularly important. In this study, palaeoecological data are used to assess the effects of changes in climate, fire and land use on vegetation at the semi-arid and temperate margins of the fynbos biome.

Previous palaeoecological studies have shown stable fynbos during the recent geologic past, which restricts interpretation of the long-term ecological processes that determine biome resilience. This study sourced sediment cores directly from present-day fynbos-succulent karoo (semi-arid) and fynbos-afrotemperate forest biome boundaries to emphasise ecological dynamics. Fossil pollen, spores and charcoal were extracted from radiocarbon dated sediment cores to provide proxies for vegetation, hydrology, large herbivore abundance and fire. Constrained hierarchical clustering (CONISS), optimal sequence splitting by least-squares, and Non-metric Multidimensional Scaling (NMDS) was applied to the fossil data to identify distinct assemblages in the record, and to further elucidate ecosystem trajectories through time.

At the semi-arid boundary at Groenkloof (5,500 cal yrs BP - near present), decreased moisture and fire from 4,000-735 cal yrs BP allowed colonisation of fynbos by a possible ‘no-analogue’ community dominated by Asteraceae and Poaceae. From 735 cal yrs BP however, climatic amelioration allowed fynbos to re-establish. The system can therefore be viewed as resilient through a capacity for ‘recovery’ and persistence through turnover in internal composition of fynbos taxa. This sensitive response to climatic forcing reflects the dominant influence of physiological stress at the semi-arid limits of Mediterranean-type ecosystems, as well as a Gleasonian type
community composition with loose species associations. In contrast, ecosystem dynamics at the temperate boundary at Platbos were dominated by internal feedback processes that promoted remarkable between-biome stability, and the persistence of distinct biomes with strong internal organisation. Further, a phylogenetic perspective suggests the high fluidity of the fynbos-succulent karoo ecocline relative to the fynbos-afrotemperate forest ecotone reflects comparative evolutionary histories of the respective biomes.

At the within-biome scale, both sites manifest impacts of pastoralism during the past 1,500 years which, through interactions among herbivory, fire, and climate, promoted persistent alternative stable states within fynbos. The degraded states were characterised by decreased functional diversity and the dominance of a palaeo-invasive plant species.

This thesis makes a significant contribution to the understanding of fynbos resilience by explicitly investigating the expression of resilience through resistance and recovery. Moreover, the relevance of the findings have been amplified by framing the study within a bioclimatic and theoretical framework that is relevant to contemporary and future environmental and ecological change in the GCFR. By identifying when, where and why abiotic, biotic and disturbance parameters become more/less significant provides important fundamental information regarding how this and other Mediterranean-type biomes might respond to potential future change scenarios.

**Keywords:** Palaeoecology, global change, alternative stable states, resistance, recovery, succulent karoo, afrotemperate forest, Cape Flora.
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1. INTRODUCTION

Global changes in climate and land use are causing substantial changes in the distribution, structure and function of the Earth’s biota (Estes, et al. 2011; Parmesan, et al. 2011). Ecological systems may be subject to rapid, catastrophic shifts as their capacity to tolerate climate and land-use change is eroded and critical thresholds are reached (Scheffer, et al. 2001). This is particularly pertinent in Mediterranean-type ecosystems that are highly sensitive to these changes and harbour an outstanding proportion of the world’s biodiversity (Keeley, et al. 2012). The Greater Cape Floristic Region of South Africa has a higher species concentration per unit area than any of an equivalent size on the planet, and is currently threatened by climate and land-use change (Allsopp, et al. 2014).

This thesis explores the possibility that biomes in this region will change in structure, function and distribution by investigating past ecological changes evidenced in the Holocene palaeoecological record. The study is framed by the themes of alternative stable states and resilience theory (Holling, 1973; Holling, et al. 2002; Oliver, et al. 2015; Scheffer, et al. 2001). Further, it addresses fundamental debates regarding global biogeography, including the significance of abiotic, biotic and disturbance drivers and their interactions in promoting biome dynamics and conservatism (Crisp, et al. 2009; Darwin, 1859; Louthan, et al. 2015; MacArthur, 1972; Potts, et al. 2015; Verboom, et al. 2014; Schimper, 1903; Slingsby, et al. 2014). By examining vegetation dynamics at semi-arid and temperate boundaries of the fynbos biome, an evaluation of the significance of biotic, abiotic and disturbance factors - as well as life-history and plant-functional traits - can be made.

1.1. THE FYNBOS BIOME AND GLOBAL CHANGE IN CONTEXT

Mediterranean-type ecosystems provide exemplary natural laboratories to study global change. They are highly sensitive to climatic and land-use changes, as well as interactions among these and associated drivers (Doblas-Miranda, et al. 2015; Keeley, et al. 2012). Located between around 30 and 40 degrees latitude (north and south) on the southern and western continental margins of the Europe, North America, South
America, Australia and Africa (Figure 1.1), these regions are highly sensitive to global atmospheric change because they are transitional in nature between semi-arid and temperate climates (Ackerly, et al. 2014). Fire is an essential component of these systems, and is strongly tied to climate through the effect of the latter on fire fuel, conditions and ignition, as well as controlling the distribution of many fire-sensitive and dependent plant taxa. The evolution of fynbos is intricately linked to both Mediterranean-type climate and wild fire, which emerged in response to the development of the Benguela Upwelling System at least around 10 million years ago (Verboom, et al. 2009; Verboom, et al. 2014). These systems harbour some 20% of global vascular plant diversity in only 2% of total land area (Cowling, et al. 1996; West, et al. 2012).

The global distribution of the fynbos biome is restricted to the south west of South Africa (Figure 1.1). It is a megadiverse, sclerophyllous, fire-prone shrubland (Allsopp, et al. 2014; Cowling 1995). Harbouring around 8,600 species in an area of 90,000 km$^2$, fynbos holds a greater species density than any area of equivalent size on Earth (Cowling, 1995). Of conservation concern, 1,736 of these species feature on the Red Data list as ‘in danger of extinction’ (Raimondo, et al. 2009). Furthermore, it has been predicted that climate change might drastically reduce the present bioclimatic envelope of fynbos; however more localised re-shuffling of species could also occur, the forecast depending on the modelling approach used (Altwegg, et al. 2014). Predictions of how land use and fire will interact with climate change are less certain still (Kraaij, et al. 2014) and it is likely to be further complicated by invasive species. Greater understanding of the factors governing fynbos structure, function and distribution at its biogeographical, climatic and ecological limits is therefore required to develop adaptive strategies in the face of present and future global change (Slingsby, 2014).
Figure 1.1. Mediterranean ecoregions of the world (highlighted) are distributed around the Mediterranean Basin, California, Central Chile, South and Southwest Australia, and in the Cape Province. Figure from Keeley, et al. (2012).

Fynbos is considered a Mediterranean-type biome due to the physiognomy and functional ecology of its flora, as well as being associated with winter rainfall and hot, dry summers climate (Ackerly, 2014). It is characterised by predominance of sclerophyll shrubs and the prevalence of fire, the latter being fundamental to biodiversity and ecological process within all Mediterranean-type ecosystems, and its key floristic sub-types are characterised by the familial dominance of either Proteaceae, Ericaceae, Restionaceae, Asteraceae or Poaceae (Keeley, et al. 2012). True Mediterranean climate occurs only in the extreme south west around Cape Town, where mild, wet winters and hot dry summers dominate due to seasonal shifts between the winter-rain bearing temperate westerlies and the dry sub-tropical anticyclone. Northwards from this Mediterranean climate zone along the western flank of South Africa, rainfall amount, biomass production and fire prevalence decrease as the climate transitions to semi-arid (Figure 1.2). This semi-arid region is dominated by the succulent karoo, a shrubland dominated by dwarf leaf-succulents, in particular of Aizoaceae, Euphorbiaceae and Crassulaceae, as well as annuals of
Asteraceae (Desmet, 2007; Cowling, et al. 1999). In contrast to fynbos, succulent karoo is not fire prone nor adapted, and is much more tolerant of aridity. Therefore at this low latitude margin, it is expected that climate will dominate fynbos dynamics due to the increasing aridity gradient. This may occur both directly by limiting fynbos growth and persistence, but also indirectly by reducing fire prevalence through limitation of biomass production and ignition.

Along the south east coast of the fynbos biome summer rainfall increases, resulting in more aseasonal climate with year-round rainfall. The Tsitsikamma region east of George (Figure 1.2) contains the only substantial representation of afrotemperate forests, which are extremely rare in South Africa. Structurally, these are tall, multilayered temperate rainforests dominated by yellowwoods (\textit{Podocarpus} and \textit{Afrocarpus}) (Bergh, et al. 2014; Geldenhuys 1991). Most are set amongst fynbos archipelagos reflecting a relict distribution of ancient forests that dominated the region until around 10 million years ago when fynbos proliferated (Mucina and Rutherford, 2006; Verboom, et al. 2014). Afrotemperate forests are fire intolerant, and mainly occur in topographic fire refugia, though they also can expand into fynbos when fire is suppressed (Slingsby, et al. 2014). Both vegetation types can co-exist within the same climate space, and can establish and persist on the same geologic substrate. Fire is thus suggested as key in determining the relative distribution of fynbos and afrotemperate forest. While climate and fire are expected to be strongly interlinked at this biome boundary, it is also expected that vegetation itself will act to promote and/ or depress fire as reduced physiological stress facilitates stronger biotic control than at the semi-arid boundary.

These north-south and east-west bioclimatic gradients define the Greater Cape Floristic Region (GCFR), which comprises fynbos, succulent karoo, renosterveld, subtropical ticket and forest biomes (Bergh, et al. 2014) (Figure 1.2).
Climate data from the last century show that the GCFR has become significantly warmer (Haensler, et al. 2010; Hoffman, et al. 2011; Hoffman, et al. 2009; Midgley, et al. 2005; New, et al. 2006). This trend is very likely to continue and climate in the GCFR could be 1-3°C warmer by 2100 (Engelbrecht, et al. 2009; Hewitson and Crane, 2006; Tadross, et al. 2005). Rainfall trends are more spatially complex. Winter rainfall will likely be reduced leading those areas in the heart of the current winter rainfall zone (WRZ) to become drier overall. Areas associated with the year-round rainfall zone (YRZ) toward the east of the region are also likely to see decreases in winter rainfall, though this may be offset by increases in summer rainfall as the present summer rainfall zone (SRZ) is expected to become wetter (Altwegg, et al 2014; Engelbrecht, et al. 2009; Hewiston and Crane, 2006; MacKellar, et al. 2007).

Bioclimatic biome envelope modelling suggests a substantial contraction of present fynbos climate space, and poleward expansion of that associated with succulent karoo, which might lead to substantial species losses (Bomhard, et al. 2005; Hannah, et al. 2005; Midgley, et al. 2002, 2003; Rutherford, 2000). Increased aridity and associated reductions in fire prevalence might lead fynbos to be invaded by drought-tolerant, fire-sensitive succulent karoo species (Wilson, et al. 2015). In contrast,
projections employing bioclimatic species niche approaches suggest that more localised shifts and reshufflings of species will occur (Driver, et al. 2012), requiring understanding of local rather than regional processes (Gillson, et al. 2013).

Where moisture availability does not restrict biomass production in fynbos, such as in regions where afrotemperate forest occur, fire frequency and intensity are anticipated to increase as a result of hotter temperatures and increased incidence of summer drought (Wilson, et al. 2010; Southey, 2009). This scenario is complicated, however, as fire regimes result from interaction among climate, vegetation and land use, the latter of which is distinctly heterogeneous and can both promote or suppress fire. Afrotemperate forest taxa are excluded from fynbos habitat by frequent fire (Geldenhuys, 1994), therefore forests can only expand into fynbos where fire is suppressed by land use and/or natural topography. In Table Mountain National Park afrotemperate forest cover has increased by over 65 % since c. 1945 (Poulsen and Hoffman, 2015; Poulsen 2013). This has led to concerns over invasion of fynbos by forests to the detriment of biodiversity, but the trend may also reflect a recovery from historic forest clearance (Luger and Moll, 1993).

Previous palaeoecological studies in the fynbos biome (Meadows and Sugden, 1991, 1993; Meadows, et al. 2010; Valsecchi, et al. 2013; Quick, et al. 2011, 2015) have suggested that fynbos has a high capacity for resilience, which is maintained by internal adaptation through overturning among fynbos sub-types with varied capacities for resistance to climate and fire (e.g. mesic, frequent-fire loving ericaceous fynbos verses drought-tolerant, slower maturing proteoid fynbos) (Valsecchi, et al. 2013). Research on drought resistance in fynbos (Agenbag, et al. 2007; Mustart, et al. 2012; West, et al. 2012) has yielded three main findings; 1) responses to drought are highly variable among co-occurring species; 2) mature woody plants are highly resistant to drought; and 3) seasonality of drought is the primary factor determining drought response (Altwegg, 2014). Interactions among climate and fire are particularly important, pre- and post-fire conditions being sensitive to ecological processes owing to the high diversity of functional traits and the centrality of fire in the biome’s ecology (Keeley, et al. 2012). Land-use changes may interact with fire and climate and modify their effects. For example clearing and burning of forest was
prevalent in the 19th century whereas fire suppression and forest regrowth has been observed in the 20th century (Poulsen, 2013). The extent to which present fynbos-forest distributions are a product anthropogenic land-use and management practices in the historical and archaeological periods is however poorly resolved, but can be elucidated using palaeoecological records.

At present in the fynbos biome, one of the greatest threats to biodiversity is posed by invasive species (Slingsby, et al. 2014; Wilson, et al. 2014; Kraaij, et al. 2014). Invaders can be seen to promote shifts to undesirable alternative stable states (Holling, 1973; Lewontin 1969; Scheffer, et al. 2001), which often occur as a result of interactions among climate, fire and land-use change with so called ‘biotic modifiers’, or ‘ecosystem engineers’ (Linder, et al. 2012). These taxa fundamentally alter the abiotic and biotic environment and modify ecological filtering processes, which often results in the persistence of (undesirable) alternative stable states (Slingsby, et al. 2014). Some of the most prolific and well known contemporary ecosystem engineers are invasive alien species (e.g. Pinus pinaster, Acacia mearnsii) (Wilson, et al. 2014). Indigenous species too can act as biotic modifiers and, often associated with a change in land use (Slingsby, et al. 2014), can be protagonists in the development of undesirable and persistent alternative stable states (Gillson, et al., 2008). By studying past invasions through the lens of palaeoecology, greater understanding of the processes of invasion can be gained by making ecological observations before, during and after invasions, and against a backdrop of long-term environmental change relevant to the future.

1.2. FYNBOS DYNAMICS AND RESILIENCE TO GLOBAL CHANGE

Biomes were first defined as globally convergent plant structural formations along with the ecosystems and biogeochemical cycles they support (Holdridge, 1947; Schimper, 1903; von Humboldt, 1807). Climate is central to the biome concept, but it is also widely acknowledged that more than one biome type can exist within the same climate space, and that disturbance, biotic interactions and edaphic factors can all play a role in determining biome boundaries (Moncrieff, et al. 2015; Slingsby, et al. 2014; Whittaker, 1975). Ecological processes such as competition for resources, and
disturbances including fire and herbivory, may be deterministic in biome organisation and extent (Bond, 2005; Bond and Keeley, 2005; Bond, et al. 2003, 2005; Coetsee, et al. 2015; Coetsee, et al. 2013; Hoffmann, et al. 2012). In regions of scarce resources, such as deserts, biota are often dominated by abiotic stress. Where moisture resources are in superfluous supply and temperature is not limiting, such as in temperate climate regions, biotic interactions and disturbance may be more significant in biome dynamics (Brown 1995; Darwin, 1859; Dobzhansky 1950; Louthan, et al. 2016; MacArthur 1972; Merriam, 1894; Schimper, 1903; Walter, 1971; von Humboldt, 1807). There may therefore be a general tendency for semi-arid boundaries of Mediterranean-type biomes such as fynbos to be more strongly defined by climate than are temperate boundaries.

This situation is however highly complex for a number of reasons. Firstly, biomes and the functioning of their ecosystems are to varying extents a product of abiotic, biotic and disturbance parameters their complex interactions (Slingsby, et al. 2014; Wessels, et al. 2011). Moreover, the global distribution of physiological stressors is highly heterogeneous (Seddon, et al. 2016). In order to understand the impacts of global change on Earth’s biota, it is therefore a priority to understand when, where and why abiotic and biotic process, as well as their interactions, determine biome distributions. One approach to untangling this is to compare dynamics at low (semi-arid) and high (temperate) latitude edges of (Mediterranean) biomes.

Understanding of global change is framed well by the concept of resilience, and this is particularly appropriate to the study of biome boundaries which represent thresholds in some combination of biological and environmental parameters. This emphasises that ecosystems (sensu biomes) have variable capacities to maintain their fundamental nature (Holling, et al 2002; Holling, 1973). Ecosystems can be resilient by either resisting changes in response to perturbations, or by recovering their original character following a change (Hodgson, et al. 2015; Oliver, et al. 2015). If the resilience of an ecosystem is exceeded, it may reorganise into one of multiple possible alternative states, each with its own fundamental properties and associated resilience mechanisms (Holling 1973; Beisner, et al. 2003). Alternative stable states theory is suited to this study as it stresses both intrinsic biotic processes (Drake 1991; Lewontin
1969) and changes in abiotic parameters (May 1977, Scheffer et al 2001), while also facilitating understanding of interactions between these two spheres (Beisner et al 2003; Vetter 2009). Such phenomena are documented worldwide from local to global scales in a variety of systems, though it is yet to be understood how persistent these transformed states are (Dakos, et al. 2015; Petraitis, et al. 2013). In the face of global change, and with a desire to maintain ecosystem functions, biodiversity and the associated services these bring to society (Oliver, et al. 2015), it is crucial to identify where abiotic and biotic factors determine the potential for alternative ecosystem states, and what factors might trigger state shifts (Slingsby, et al. 2014).

In the Greater Cape Florist Region, multiple abiotic and biotic factors combine to create complex environmental filters determining relative biome distributions (Slingsby, et al. 2014; Cowling, et al. 2014). Prior to the Late-Miocene, afrotemperate forest (and thicket) were a consistent and prominent component of the GCFR, and are the oldest component of the flora dating from at least the Palaeogene 70 Ma. However, aridification towards the end of the Miocene, in concert with the establishment of prevalent, recurrent wildfires, likely drove a rapid decline in the abundance of forest elements and replacement with arid- and fire-adapted floras (DuPont, et al 2011). Succulent karoo evolved substantially later than did fynbos (Verboom, et al. 2009), apparently in response to the regional development of strongly aseasonal winter rainfall climate driven by intensification of the Benguela Upwelling System around 3-5 Ma (Verboom, et al. 2014). The present ecology and distributions of the GCFR flora attests to these comparative life histories.

At its semi-arid distribution limits, fynbos expansion into succulent karoo appears to be inhibited by the relatively low tolerance of aridity stress of fynbos taxa. Conversely, succulent karoo taxa are excluded from fynbos habitat by fire and competition as fynbos species have higher growth rates (Carrick 2001, 2003; Esler, et al. 2015; Jacobsen et al 2009; Lechmere-Oertel and Cowling, 2001). Only in the absence of fire might competition between fynbos and succulent karoo species become deterministic (Rebelo, et al. 2006; Wilson, et al. 2015).
At its temperate distributional limit, fynbos and afrotemperate forest are capable of living in very similar abiotic environmental conditions, surviving within the same climate and on the same geological substrate (Manders and Richardson, 1992).

Fynbos is excluded from forest on the basis that shade is high and fire uncommon in forest environments, and abundant light and fire are required for fynbos growth and reproduction (Slingsby, et al. 2014). Forest species can only expand into fynbos and persist where fire is excluded from fynbos by land use and natural topography, and aridity stress is not limiting (Geldenhuys, 1994; Luger and Moll, 1993). This exclusion must be of significant duration to allow forest pioneers to attain fire resistant traits and subsequently facilitate establishment of secondary forest taxa that might shade-out fire-prone fynbos (Coetsee, et al. 2015, 2013; Hoffmann, et al. 2012). Therefore there exists a range of processes determining biome distribution at this biome boundary, ranging from strongly abiotic in semi-arid habitat, to strongly biotic consumer control where aridity is less severe. At this relatively mesic biome boundary therefore, biotic factors tend to dominate.

It is recognised that biomes can act to maintain their character because their constituents tend to share evolutionary histories and associated life-history traits which results in alteration of the abiotic and biotic environment and niche construction (Crisp, et al. 2009; Linder, et al. 2012). This in turn modifies environmental filtering processes and restricts species immigration (Slingsby, et al. 2014). Upon arrival in a recipient community, an immigrant species is confronted with the challenges of a new environment (Potts, et al. 2015). Some level of pre-adaptation is obviously advantageous, therefore lineages derived from areas where conditions similar to the destination environment prevail are clearly at an advantage (Verboom, et al. 2014). It should therefore be expected that ecosystem resistance to colonisation is much higher at between- verses within-biome scales. Palaeoecology offers the potential to investigate past colonisations (‘palaeo-invasions’; Gillson, 2008; Gillson, 2009), and so elucidate the long-term processes and interactions governing the process on timescales of decades to millennia. Understanding of these interactions over centennial – millennial timescales here will provide a deeper understanding of long-term patterns of invasive spread (Froyd and Willis, 2008).
Biome boundaries are particularly valuable in identifying global change impacts. Being transitional areas between biotic community distribution limits, they are sensitive to environmental change and provide a microcosm to observe the interactions between biotic and abiotic processes (Altwegg, et al. 2014; Cumming, 2011; Holland, et al. 1991; Hobbs, 1986; Potts, et al. 2015; Whittaker, 1960; van Leeuwen, 1966). Gradual transitions are often controlled to some progressive change in an abiotic gradient (Curtis 1959; Gleason, 1939; Whittaker 1975) whereas zones of rapid species turnover may be indicative of ecological communities that are highly structured, discrete entities, with strong internal feedback processes akin to homeostasis (Connell and Ghedini, 2015; Collins, et al. 1992; Clements, 1936). Sharp boundaries can also result from non-gradational abiotic controls such as stark substrate contrasts. Indeed, over much of the fynbos biome the fynbos-succulent karoo ecotone occurs rapidly, but this rather reflects a modification of the climate gradient by soil texture and associated moisture availability (Esler, et al 2015). In the Kamiesberg Mountains, Namaqualand, the fynbos-succulent karoo boundary occurs in the absence of stark substrate contrasts. It therefore provides an opportunity to observe the effects of climate, fire and herbivory without the complicating factor of soils modifying the effects of climate on moisture availability. The fynbos–afrotropical forest boundary is by contrast very sharp, owing to high flammability and fire adaptation in fynbos and fire intolerance in forest, and occurs independent of differences in climate and substrate. Biotic drivers are therefore likely to be strong at this biome boundary.

The magnitude of the potential threat of climate change to biodiversity loss in the fynbos biome is dependent on the proximity of present and future ecophysiological and ecological thresholds. Therefore a temporal perspective is needed which provides insight into how dynamic or resilient biomes are to different combinations of environmental and anthropogenic factors. Previous palaeoecological analyses have indicated that fynbos has been highly resilient through the present Holocene interglacial at both at its semi-arid (Valsecchi, et al. 2013; Quick, et al. 2011) and temperate margins (Quick, et al. 2015). The biome is typically characterised in fossil pollen records by overturning within fynbos in response to climatic change, while the biome as a whole persists despite this internal turnover (Meadows and Sugden, 1991,
The resilience of Cederberg mountain fynbos since the last glacial maximum, for example, has been attributed to a climatic buffering effect associated with orographic rainfall, and strong substrate association of fynbos and succulent karoo (Meadows et al. 2010; Quick, et al. 2011; Valsecchi, et al. 2013). However, there is also a taxonomic resolution issue, whereby low fossil pollen taxonomic resolution may mask overturning of functional types within taxa, masking dynamism. Such apparent stability impedes understanding of the mechanisms underlying resilience and the nature of controls on biome distribution. It is yet to be determined whether fynbos diversity reflects resilience to climatic variability, the accumulation of species over millions of years within a climatically buffered region, or a combination of these two factors (Altwegg, et al. 2014; Verboom, et al. 2009).

1.3. AIMS AND OBJECTIVES

The central aim of this thesis is to assess the resilience of fynbos plant communities to changes in climate, fire and land use at its semi-arid and temperate distribution limits.

In light of this, the following aims are identified:

- Reconstruct vegetation change at temperate and semi-arid boundaries of the fynbos biome in the palaeoecological record.
  - Assess how climate change has impacted on fynbos at its boundaries with afrotropical forest/succulent karoo in the past.
  - Reconstruct how fire has affected fynbos at its succulent karoo/and afrotropical forest boundaries in the past.
  - Infer the effects of past land-use changes on fynbos at its afrotropical forest/succulent karoo boundaries in the past.
  - Identify interactions among climate, fire and land use at the succulent karoo/ and afrotropical forest boundaries in the past.
• Identify the resilience characteristics at boundaries of the fynbos biome in the palaeoecological record.
  ▪ What are the characteristics of the temperate and semi-arid boundaries of the fynbos biome in relation to abiotic, biotic and disturbance parameters and biome organisation?
  ▪ When/ where are biomes more/ less cohesive units/ transient assemblages?
  ▪ Does fynbos at its boundary succulent karoo/ afrotropical forest manifest resilience and, if so, is this through resistance and/ or recovery?
  ▪ Are transitions between alternative stable states evident at the fynbos-succulent karoo and fynbos-afrotropical forest boundaries in the past?
  ▪ What can be learned by comparing resilience characteristics at the between- and within-biome scales?

In order to achieve these aims, the following objectives are defined:

• Quantify fossil pollen from sediment records located at (a) fynbos-succulent karoo and (b) fynbos-afrotropical forest biome boundaries, allowing reconstruction of vegetation change through time.
• Reconstruct changes in fire through time using sedimentary micro- and macrocharcoal deposits
• Reconstruct herbivore abundance through time using sedimentary fungal spores
• Date sediment record using AMS $^{14}$C and establish high-resolution calendar-year age models to enhance temporal perspectives on ecological processes
• Compare the records generated with published palaeoenvironmental, archaeological and historical data to aid interpretation of climate and human influence on biome dynamics.
• Quantitatively identify phases in the pollen record using pollen diagram zonation and multivariate ordination. This will allow identification of periods of relative stability and change to assess ecosystem resilience through time.
• Explore links between herbivore abundance, fire and ecosystem dynamics at the respective biome boundaries.
• Assess evidence of alternative stable states within- and between-biomes.
• Evaluate and compare the dynamics of the semi-arid (fynbos-succulent karoo) and temperate (fynbos-afrotemperate forest) biome boundaries to assess their resilience to environmental change.
• Evaluate the significance of abiotic and biotic parameters and their interactions as determinants of biome organisation in relation to global environmental change.

Through addressing these aims and objectives this thesis will contribute significantly to understanding of fynbos resilience to environmental change, fire and land-use specifically the impact of herbivory. Further, it will contribute to understanding of the resilience of Mediterranean-type ecosystems, the potential for rapid ecosystem state shifts, and the role of abiotic and biotic change in Mediterranean-type ecosystems at their temperate and semi-arid margins.

1.4. THESIS STRUCTURE

The context of the study is first set by summarising the state of current knowledge of fynbos ecology, dynamics and history in relevant areas of ecology and palaeoenvironmental research (Chapter 2). The theoretical topics covered include ‘Biomes and their Boundaries’, ‘Ecological Resilience and Alternative Stable States’ and ‘Ecological Dynamics in the Palaeoecological Record’. Literature relating to the fynbos, succulent karoo and afrotemperate forest biomes, their distributions, structure and function, is then reviewed. Lastly, literature describing palaeoenvironmental change and associated palaeoecological studies are examined. The following chapter (Chapter 3) first provides detailed information on the regional study area and the sites specifically. The information presented includes relevant details of climate, vegetation, geology and land use. Secondly, Chapter 3 describes the methods used in this study, including sediment analysis, dating and age modelling; pollen, spore and charcoal extraction and analysis; data handling and statistical analyses.
Chapter 4 presents the results of the fynbos-succulent karoo boundary study, and subsequently discusses the findings in the context of the regional palaeoenvironmental record and the key ecological themes explored in this thesis. Particular attention is given to making palaeoenvironmental interpretations independent of the pollen data through use of non-pollen palynomorph indicators and sedimentology in relation to previous published analyses. The resulting reconstructions are then used as frameworks to interpret the pollen data and address the aims set out above (see section 1.2). This is similarly carried out for the fynbos-afrotemperate forest boundary in Chapter 5, though within-biome dynamics are discussed first, and between-biome dynamics of afrotemperate forest and fynbos is then discussed as evidence presented from both sites. Finally, Chapter 6 synthesises and summarises the findings of the study with particular reference to the aims (section 1.2) and compares and contrast the mechanisms of resilience at semi-arid and temperate boundaries.
2. LITERATURE REVIEW

2.1. BIOMES AND THEIR BOUNDARIES

Biomes are the most basic unit of description and classification for the Earth’s vegetation and the biota and biogeochemical cycles it supports (Olson, et al. 2001). They are defined by globally convergent plant formations with similar structural and functional properties rather than by their floristic or species composition (Moncrieff, et al. 2016). Biomes have traditionally been viewed as being in equilibrium the abiotic environment, in particular climate and soils. von Humboldt (1807) noted the occurrence of analogous vegetation formations in geographically dislocated regions with similar climatic regimes. Schimper (1903) was first to define and name the world’s biomes in a way that resembles those of modern classification. He connected the dominant physiognomies of major plant formations with functional properties selected by regional climate, which implied equilibrium with climate. Later, Holdridge (1947) proposed that formations could be mapped dependent on axis of precipitation, temperature and evapotranspiration, and took this approach further by allowing modifications for soil and topography. Whittaker (1975) similarly proposed the distribution of Earth’s major biomes as a function of mean annual temperature and mean annual precipitation (Figure 2.1). The latter system raises some intriguing ambiguities in predictive ability, suggesting that biome type is a function of more than temperature and rainfall alone.

Within a certain range of rainfall and temperature combinations, it is widely held that the dominant biome cannot be reliably predicted (Figure 2.1) (Bond, 2005; Bond and Keeley, 2005; Bond, et al. 2003, 2005; Whittaker, 1975). This results from the tendency of vegetation itself to influence the environment (Moncrieff, et al. 2016). Plants and formations can alter ecological variables including climatic phenomena such as wind, temperature and moisture availability (Hoffmann, et al. 2012), soil characteristics including both texture and nutrients (Coetsee, et al. 2015; Coetsee, et al. 2013), the availability and distribution of light, and the prevalence and natural disturbances such as herbivory and wildfire (Burger and Bond, 2015; Keeley, et al.
The latter is particularly pertinent in South Africa, where multiple fire-prone and fire-intolerant biomes occur (Mucina and Rutherford, 2006). These feedbacks create the potential for multiple possible biome states where there is little significant difference in prevailing climate and underlying geological substrate. Such states can be profoundly different in terms of biodiversity and ecosystem function (Moncrieff, et al. 2016).

![Whittaker’s biome-climate ordination](image)

*Figure 2.1. Whittaker’s biome-climate ordination. Whittaker (1975) proposed that biome distributions could be predicted by precipitation and temperature. However he acknowledged within a certain climate space, climate is not a reliable predictor of biome type (red dashed line).*

In studying global-scale vegetation dynamics it is important to understand fundamental constraints on plant species distributions. Most early work on geographical range limits have promoted the role of abiotic stress (Merriam, 1894;
Schimper, 1903; von Humboldt, 1807). Darwin (1859) first proposed in *On the Origin of Species* that physiological stress determines species ranges in abiotically stressful environments. Contrastingly, in areas where abiotic resources are more abundant, he suggested that biotic interactions play a predominant role in distributions. Dobzhansky (1950), MacArthur (1972) and Brown (1995) elaborate on this, suggesting that, at high latitude distribution limits, abiotic stress determines species range shifts, while at low-latitude distribution limits biotic interactions become more important. Despite these seminal recognitions of the importance of biotic interactions in vegetation distributions, modern perspectives continue to assume that climate is the dominant determining parameter of distributions, be it directly or indirectly (Louthan, et al. 2016). Determining how modern species range shifts might change in the future is dependent on understanding when, where and why climate, biotic interactions, and disturbance become deterministic (Parmesan and Yohe, 2003). Perhaps more intriguingly, when do such factors interact to drive ecosystem dynamics?

Two general models have been proposed to explain plant species distributions in space and time. Clements’ (1936) community unit hypothesis argued that plant communities are highly structured, discrete entities where termination of one group coincides with the beginning of another. This hypothesis is commonly explained schematically as a series of species abundance distribution curves that do not overlap along an arbitrary environmental gradient (Figure 2.2). The individualistic hypothesis, seeded by Gleason (1939) and developed by Whittaker (1975) and Curtis (1959), argues that the centres and limits of species distributions are scattered non-uniformly along environmental gradients. Thus, no distinct groups of species are predicted to exist, which precludes the recurrence of groups of species in space and time. A more accurate depiction of Clements’ hypothesis is given by clusters of species abundance curves with some species spanning more than one cluster and where overlap between communities occurs at the boundary between two communities (Collins, et al., 1993; Whittaker 1975).

Two polarised types of biome boundaries can be identified, one being ‘hard’ the other ‘soft’ (Figure 2.3.) (Cumming, 2011; Holland, et al. 1991; Hobbs, 1986; Whittaker, 1960; van Leeuwen, 1966). Hard boundaries are zones of relatively rapid change.
between two plant communities termed ‘ecotones’ here. They are typically characterised by strong biotic interactions, but can also result from abiotic controls such as stark substrate contrasts. Soft boundaries, in contrast, can be referred to as ecoclines. This type of boundary is often characterised by more gradual transitions between plant communities and typically correspond to some progressive change in an environmental or biotic gradient (Kent, et al. 1997). van der Maarel (1990) proposed a third category of boundary comprised of overturning amongst a ‘mosaic’ of sub-communities. Interestingly, Kent at al.(1997) suggest that soft ecotones are likely to be more stable than hard ones because their species distributions tend to be determined by natural gradients such as climate, rather than disturbances linked to anthropogenic land use.

Figure 2.2. Schematic representations of (A) Clements’ community-unit hypothesis where two discrete communities can clearly be identified and are separated by a ‘hard’ boundary around point (i); (B) Gleason’s individualistic perspective where no discrete communities can be identified due to continuous environmental variability (ii); (C) An amalgamation of the two concepts that permits both strongly identifiable communities and individualistic distributions that overlap at the boundary.
Biomes are said to be major selective biological filters (Crisp, et al. 2009). Their constituents tend to have shared evolutionary histories, which leads to the possession of similar life-history traits and results in alteration of the abiotic and biotic environment and niche construction (Linder, et al. 2012). This in turn modifies environmental filtering processes and restricts species immigration (Slingsby, et al. 2014). Upon arrival in a recipient community, an immigrant species is confronted with the challenges of a new environment (Potts, et al. 2015). In addition to the genetic, life history and reproductive attributes that facilitate establishment of an initial population, the immigrant must rapidly adapt to the potentially novel biotic and abiotic parameters and variables. Some level of pre-adaptation is obviously advantageous, therefore lineages derived from areas where abiotic and biotic conditions similar to the destination environment prevail are clearly at an advantage (Verboom, et al. 2014). It might be expected therefore that species with similar life-history/functional traits will tend to group together forming discrete entities (i.e. Clementsian) with hard, impenetrable boundaries resulting from ecological filtering processes.
2.2. ECOLOGICAL RESILIENCE AND ALTERNATIVE STABLE STATES

The capacity of an ecosystem to absorb environmental perturbations through internal feedbacks to maintain a quasi-stable state is known as resilience. The concept of resilience has recently been dissected to emphasise the distinct ways in which ecosystems absorb or respond to environmental perturbations. Two distinct, measurable components of resilience in an ecological entity (i.e., a population, community, ecosystem, formation or biome) are recognised. First, ‘resistance’ refers to the capacity of a system to withstand a disturbance and maintain its original qualities. Second, ‘recovery’ is the capacity to return to or restore its original character following a change in response to disturbance (Oliver, et al. 2015) (Figure 2.4). As such, system ‘resilience’ can be viewed as a general concept, whereas the two components resistance and recovery represent measurable responses to environmental perturbations (Hodgson, et al. 2015).

If the resilience of an ecosystem is exceeded the system may reorganise into one of multiple possible alternative quasi-stable states, each with its own set of reinforcing negative feedbacks (Holling, 1973). Ecological thresholds define the point at which a community switches from one quasi stable state to another (Scheffer, et al. 2001). Alternative stable states can be characterised by the presence of differing plant functional types, vegetation structure, biomass and percentage cover, as well as by contrasting ecological processes (e.g. fire prone verses inflammable stands) (Anderies, et al. 2002; Beisner, et al. 2003; Gillson and Duffin, 2007). More recently, transitions between states have become known as regime shifts, where relatively long periods of stability are interrupted by large, rapid reorganisation of a system occurs resulting in a qualitatively different state (Brook, et al. 2013; Carpenter, et al. 2011; Foley, et al. 2003; Scheffer and Carpenter, 2003; Scheffer, et al 2009).
Historically, alternative stable states have been viewed from two perspectives. The ‘community perspective’ (Drake 1991; Lewontin 1969) emphasises internal changes in ecosystem populations and views the environment as fixed in some way.
Perturbations are applied to state variables by biotic processes and, if large enough, may lead to a state shift. This scenario has often been described using the ball-in-cup analogy (Figure 2.5), whereby the ball is pushed over a hill in a constant landscape to the domain of attraction of an alternative state. The ‘ecosystem perspective’ (May 1977, Scheffer et al 2001) focuses on the effects of environmental change on the state of communities. Changes in model parameters (e.g. climate) drive changes in state variables (e.g. fire), which may induce or alter propensity to a state shift (Figure 2.6). It is increasingly recognised that processes accommodated within both these frameworks may interact to determine system dynamics, whereby changes in ecosystem parameters influence the susceptibility of a system to a state shift caused by community-level perturbations (Beisner et al 2003; Vetter 2009).

Figure 2.5. Alternative stable states and the ‘ball in cup method’. The distinction between the community and ecosystem approaches to alternative stable states theory concerns the treatment of state parameters and state variables. In the ecosystem perspective (top) a parameter (P) is changed according to the vertical red arrow in response to an external factor. The community equilibrium point moves along the horizontal axis (N) driven by the parameter change. There are no interactions between the state variable and parameter. In the community perspective (bottom) the former parameter P is now a state variable included in the model, because P is subject to rapid feedback from the state variables. Perturbations caused by forces external to the variables N and P can move the community ball around on the landscape. The landscape is now defined jointly by N and P and remains fixed (Figure and caption from Beisner, et al 2003).
Figure 2.6. Classic bifurcation model of Scheffer and Carpenter (2001). The five 'stability landscapes' depicted represent the multiple alternative stable states and their basins of attraction at five different external conditions. Stable states correspond to valleys; the unstable middle section of the folded equilibrium curve corresponds to a hill. If the size of the attraction basin is small, resilience is small and a perturbation may cause a comparatively large shift to alternative stable state (Figure and caption from Scheffer, et al. 2001).

Ecologists have generally rejected the ideas of Clements, and tend to be sceptical of the idea of communities as homeostatic entities (Connell and Ghedini 2015). This seems paradoxical, given that the widely applied concepts of alternative stable states and regime shifts in ecology are underpinned by recognition for strong internal ecological organisation and feedback processes (Anderies, et al. 2002; Beisner, et al. 2003; Brook, et al. 2013; Carpenter, et al. 2011; Drake 1991; Foley, et al. 2003; Gillson and Ekblom, 2009; Holling 1973; Lewontin 1969; May 1977; Scheffer and Carpenter, 2003; Scheffer, et al 2009, 2001; Vetter 2009). Indeed, application of the alternate stable states model to vegetation change at biome boundaries incorporates an assumption that biomes are, and will remain, cohesive organisations of species through space and time due to negative feedback control. This assumption is also

2.3. ECOLOGICAL DYNAMICS AND THE PALAEOECOLOGICAL RECORD

Observations of species responses to environmental change in the fossil record have been interpreted as demonstrating that vegetation response to climatic change is individualistic, supporting the Gleasonian as opposed to the Clementsian view of community assemblage (Birks and Birks, 1980; Delcourt and Delcourt, 1988; Prentice 1992; Whittaker, 1975). For example it has been shown that, in Europe and North America, Late-Quaternary climate warming caused the distribution of individual species to change in differing rates and geographical direction (Delcourt and Delcourt, 1988; Graham and Grimm, 1990; Prentice, 1992). These differing responses resulted in dynamic community assemblage patterns and ecosystems without modern analogues (so called ‘no-analogue ecosystems’) through the Late Quaternary period in North America (Jackson, 2006) and in Europe (Bennett and Birks, 1990). Co-occurrence of species is dependent on overlap in multi-dimensional ecological and biogeographic space, making repeated overlaps less likely (Jackson and Williams, 2004).

It may seem surprising, then, that some palaeoecologists have interpreted fossil ecosystems as exhibiting evidence for the existence of alternative stable states. It is important to emphasise that the overwhelming majority of palaeoecological research used to support the Gleasonian perspective comes from Europe and North America, which were both covered by ice masses during glacial phases and re-colonised during interglacials (Lowe and Walker, 1997). Many species were forced adapt by migration on large, continental scales to refugia, which in effect emphasised individual trait differences such as differential dispersal rates (Prentice, 1992). Much of the rest of the world, particularly tropical and subtropical regions and most of the global south,
experienced comparatively less extreme environmental change (Chase and Meadows, 2007). The majority of Earth’s biodiversity may therefore possess contrasting traits and resulting dynamics. Southern hemisphere perspectives on the Clementsian/Gleasonian debate and ecosystem organisation are therefore needed.

DeBoer, et al. (2013) interpret a Late Quaternary pollen record from Mauritius as reflecting two alternative quasi-stable states interrupted by a relatively rapid regime shift between open, wet forest Last Glacial state to a stable closed, stratified, tall forest Holocene state in response to transgression of an ecohydrological threshold (Figure 2.7). Each state persisted for several millennia while the regime shift - or transition between the two alternative states - occurred over relatively shorter centennial timescales. Gil-Romera, et al. (2010) highlight two records from southern Spain (Carrión, et al. 2003; Martin-Puertas, et al. 2008) that express varying types of resilience (Figure 2.8). At Zoñar, the system closely tracked changes in aridity between 3,300 and 700 cal yrs BP. This is manifested in oscillations between
dominance of xerophytic and mesophytic vegetation where phases of stability are interrupted by relatively rapid transitions. Stabilising internal feedback processes (i.e. resilience) can be viewed as weak, however, as the system’s state varies in response to extrinsic climate forcing. In contrast, the pollen record at Gádor shows several quasi-stable phases superimposed upon a more obvious directional trend in response to aridity from around 6,000 cal yrs BP. In the latter case, each successive phase appears to show strong cohesion, but unidirectional change in ecosystem parameters (moisture) induces resilience loss resulting in successive state shifts.

The studies of both DeBoer, et al. and Gil-Romera, et al. emphasise the importance of temporal scale in describing the resilience of ecosystems. On relatively short neontological timescales (i.e. years to decades) systems may appear to be cohesive units that interact through negative feedbacks to maintain resilience. By studying plant communities and ecosystems on palaeoecological scales (i.e. decades to millennia) their deeper dynamics can be revealed (Jackson 2006; Williams and Jackson, 2004). Conversely, looking at too short a timescale might result in misleading impression of instability as erratic variability in ecological parameters (e.g. inter-annual temperature extremes) do not necessarily lead to lasting ecosystem change.

[See Figure 2.8. on following page…]
Figure 2.8. Detrended Correspondence Analysis ordinations for Zoñar (top) and Gádor (bottom). The samples are joined with a line and the oldest and youngest samples are labelled (need to give ref and accreditation here).
2.4. THE ECOLOGY OF THE FYNBOS-SUCCULENT KAROO BIOME BOUNDARY

Fynbos is a sclerophyllous shrubland composed of reed-like graminiooids, short shrubs and taller shrubs in varying combinations (DeBano 1998). The sub-types restioid, proteoid, ericaceous, asteraceous or grasy fynbos are defined by the relative dominance of the respective key families (Figure 3.9.) (Cowling 1995). Succulent karoo is dominated by dwarf leaf-succulents of the Aizoaceae, Euphorbiaceae and Crassulaceae. Also of prominence are members of the Asteraceae, Iridaceae and Hyacinthaceae. Annuals belonging to the former group contribute significantly to the spectacular springtime floral displays for which the biome is renowned (Figure 3.10) (Mucina et al 2006). The transition between these two vegetation types is almost always interrupted by a narrow zone of vegetation known as mountain renosterveld. This vegetation type is also classified as belonging to the fynbos biome (Rebelo et al 2006; Low and Rebelo 1998; Rutherford and Westfall 1986; also see Chapter 3.1). Questions of its origins, associations and status as a biome in its own right are topics of current interest (Bergh, et al. 2014, 2007; Curtis, 2013). It is often distinguished floristically by the dominance of *Elytropappus rhinocerotis*, a 1-2 m tall asteraceous shrub. Renosterveld graminoid composition also contrasts with that of fynbos where Poaceae typically forms a dense understory and Restionaceae is almost always absent (Rebelo et al 2006).

The fynbos-succulent karoo transition almost always occurs where mean annual precipitation (MAP) is around 200-300 mm, where fynbos is the relatively mesic vegetation (fynbos MAP = 287 mm to 1384 mm, succulent karoo MAP = 150 to 209 mm) (Figure 2.10) (Agenbag et al 2008, Agenbag, 2006; Rebelo et al 2006). Results from a number of studies (Carrick 2001, 2003; Jacobsen et al 2009; Lechmere-Oertel and Cowling 2001) support the assertion that fynbos expansion into karroid habitat is inhibited by relatively low tolerance of aridity stress. For example, fynbos species have been indicated as less resistant to drought induced xylem cavitation (Jacobsen et al 2009), and succulent karoo species showed less response to moisture regime variation in reciprocal transplant experiments (Lechmere-Oertel and Cowling 2001). Succulent taxa such as the Aizoaceae incorporate thick water storing tissues within
their main photosynthetic organs, which buffer against desiccation during drought (Vendramini et al 2002). Temperature change is also likely to be an important variable in vegetation distribution at the biome boundary, both independently through changing thermal stress and the proximity of thermal thresholds, and in combination with precipitation by altering the timing and extent of soil moisture availability and the vapour pressure deficit (Midgley and Thuiller 2007).

Figure 2.9. Direct ordination by climate and soil depth of fynbos sub-types and adjacent biomes in the south western Cape (figure from Rebelo, et al. 2006).
Figure 2.10 Various fynbos sub-types. A: proteoid fynbos dominated by Leucadendron xanthoconus (Proteaceae) and Phaenocoma prolifera (Asteraceae) at Potberg; B: Proteoid fynbos with tall, scattered Protea nitida (Du Toitskloof). C: Coastal asteraceous fynbos Phaenocoma prolifera (Betty’s Bay) D: grassy fynbos with Oldenburgia grandia (Asteraceae) in the foreground (Grahamstown); ericaceous fynbos dominated by Erica laeta (Cape of good hope); F: restiod fynbos with Thamnocortus spicigerus (Agulhus Plain). (Images from Rebelo, et al. 2006).
Figure 2.11. Namaqualand spring bloom. Commercial farmland in the Kamiesberg dominated by annuals of Asteraceae and Poaceae (A.J. MacPherson).

Figure 2.12. Namaqualand Mountain Renosterveld. Commercial livestock farmland in the uplands of the Kamiesberg dominated by Elytropappus rhinocerotis (‘renosterbos’). (A.J. MacPherson)
Competition has also been suggested as an important determinant in biome distribution. In the reciprocal transplant experiment by Lechmere-Oertel and Cowling (2001), karroid species showed less sensitivity to soil texture and nutrient availability, leading to the suggestion that they are outcompeted at the biome boundary where moisture availability is not limiting to fynbos growth (Lechmere-Oertel and Cowling 2001). Therefore, where moisture is ample competitive exclusion may become more deterministic at the fynbos-succulent karoo boundary. Carrick (2003) identified rooting system partitioning between karroid woody shrubs (deep rooted) and succulent shrubs (shallow rooted) in the Kamiesberg region, suggesting coexistence by differentiation (Walter 1971). The prevalence of such coexistence strategies may be indicative that biotic interactions are less important in these semi-arid systems than are abiotic stressors such as drought. Interpretations of niche separation based on models of root system partitioning in arid lands have received criticism in that they neglect root system plasticity, potential lagged response to rainfall events, the vagaries of plant phenology, and explicit precipitation thresholds that occur within highly variable soil moisture environments (Ogle and Reynolds 2004; Schwinning et al 2004). However, the effects of competition cannot be discounted altogether. Under scenarios of increasing aridity stress, the competitive advantage of fynbos species over those of the succulent karoo would be expected to diminish. Importantly, this highlights that of biotic relative to abiotic parameters become less important in determining plant distributions as aridity increases.

Fynbos is fire prone and adapted, but burning is highly destructive in succulent karoo (Bond and van Wilgen, 1997; Cowling et al 1995; Esler, et al 2015). At the boundary, fire prevalence may dominate biome boundary dynamics; only in its absence will climate, soil or competition factors become deterministic. Indeed, it has been observed that succulent karoo replaces fynbos when vegetation cover and the accumulation of combustible biomass become too low to carry fire (Rebelo et al 2006). Growth of succulents in fire-free microhabitats, such as rocky outcrops (Figure 2.13), within fynbos further suggests that fire plays a dominant role in biome boundary dynamics (Anderson 2008). The persistence of succulents in fire-free microhabitats has also been documented in other semi-arid systems (Thomas and Goodson 1992). Colonization of fynbos vegetation by succulents in the absence of
fire would greatly decrease vegetation flammability, thereby suppressing fire and fynbos regeneration, a positive feedback loop that would increase resilience of succulent karoo (Rebelo, et al. 2006). An alternative view might be that, as fynbos is drought limited, fire responds to rather than determines vegetation type at the biome boundary.

Renosterveld burns more frequently than fynbos (typical fire free intervals are 3-10 years and 15-20 years, respectively) (Rebelo et al 2006), and tends to stimulate ignition in adjacent fynbos vegetation. Kamiesberg Mountain Fynbos may require such an ignition source due to the small size of the vegetation patches and the associated low likelihood of ignition by lightning or rock falls. Renosterveld can also support a higher biomass of herbivores (particularly grazers) than fynbos because of its grassy understory. This is supported by data from rangelands in the Kamiesberg that demonstrate the potential of herbivores to significantly alter plant biomass (Anderson and Hoffman 2007). It has been hypothesised that intense grazing suppresses fire in renosterveld, allowing invasion of the transitional zone by succulents, thereby acting as a fire suppressant and potentially also removing an important ignition source for fynbos. Less frequent burning may then allow succulents to establish between senescing fynbos plants, further suppressing fire and creating a feedback loop in favour of succulence, and potentially driving a state transition between fynbos and succulent karoo (A.G. Rebelo, pers. comm.; Cowling and Holmes 1992).

A strong correlation can be observed between fynbos-succulent karoo distribution and substrate type (Quick et al 2011). Over much of their distribution, succulent karoo is distributed on soils derived from lowland shale deposits of the Malmesbury formation that are high in clay and silt content, and are relatively nutrient rich (Rebelo et al 2006). These fine textured soils have a high internal surface area, and as such greater potential to retain water, which reduces moisture availability to plants (Marshal and Holmes 1979). Fynbos is commonly distributed on nutrient leached sandy soils derived from the quartzitic sandstone mountain ridges of the Cape Fold Belt (Rebelo et al 2006). In such coarse textured soils, water is more freely extractable as it is stored in capillaries between the grains (Brady 1974). Renosterveld commonly
persists on an intermediary of shale and sandstone alluvium that is less subject to nutrient leaching than higher altitude Fynbos (Rebelo 2006). It has been hypothesised that a rainfall-induced nutrient-leaching gradient is the prime determinant in separating fynbos and renosterveld (Cowling et al 1997). There lacks consensus whether soils are most important in water retention or nutrient characteristics (Esler, et al 2015; Agenbag 2008; Lechmere-Oertel and Cowling 2001).

Boundaries between fynbos and succulent karoo are typically characterised by sharp transitions with associated oligotrophic and mesotrophic soils, respectively, as well as the aforementioned gradual climate transition. Esler et al. (2015) sought to disentangle the relative roles of climate and soil type in determining the biome boundary in a reciprocal transplant approach at Jonaskop in the Western Cape.

Their results, similar to those of (Lechmere-Oertel and Cowling 2001), suggest that succulent karoo species are neither edaphically nor climatically constrained from habitat typical of fynbos vegetation along this elevation gradient. In contrast, fynbos
species are strongly limited both edaphically and climatically from growing under conditions associated with succulent karoo. The authors therefore suggest that succulent karoo elements may be excluded from fynbos by competition or fire, and that the latter is most likely responsible for maintaining the sharp boundary. Fire would strongly exclude fire sensitive succulent karoo species from fynbos, while both mesotrophic soils and climate together would strongly exclude fynbos species from succulent karoo. The relative climate, soil and disturbance affinities might therefore provide an explanation for the relative distributions of the fynbos and succulent karoo biomes, as well as the hard ecotone type nature of the boundary. This is suggestive of Clementsian system organisation.

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**Figure 2.14. Vegetation distribution across an altitudinal gradient in the Kamiesberg. A: Succulent karoo (Kamiesberg Mountain Shrubland); B: renosterveld (Namaqualand Granite)**
The relationships between vegetation and substrate type in the Kamiesberg Mountains of Namaqualand, towards the northern extremity of fynbos distribution, are somewhat of an exception to the patterns described above. Here, similarly to across most of the GCFR, the fynbos-succulent karoo transition occurs along an increasing altitudinal gradient (Figure 2.14) where MAP = 200 to 300 mm. It is exceptional that this
transition occurs across granite-derived soils rather than those that developed from quartzitic sandstone or bokkeveld shales (Figure 2.15). While over much of the distribution the fynbos-succulent karoo boundary is characterised by a sharp boundary, likely resulting from the effects of substrate contrasts and fire (Esler, et al 2015), the interface between the two biomes in the Kamiesberg is more diffuse (Rebelo, et al. 2006). At present, there is little published data relating to soils of the Kamiesberg Mountains. Anderson (2008) surveyed soil chemistry and texture among a number of vegetation types along an altitudinal gradient in the Kamiesberg (excluding fynbos proper, which occurs only on the highest mountain tops, but including renosterveld). Upland habitats, particularly renosterveld, were characterised by high soil percentage organic carbon and nitrogen content, which is probably a function of higher vegetation cover (Anderson 2008). The diffuse nature of the boundary conforms to the ecocline type defined by Kent, et al. (1997), and is suggestive of loose system organisation where species are distributed along a climatic gradient. However, the persistence of succulents in fire-free habitat is suggestive of a hard biome boundary. Both Clementsian and Gleasonian system organisation is therefore evident in the Kamiesberg depending upon the scale of measurement.

Observations of rapid, non-linear and non-reversible changes in semi-arid rangelands as a result of grazing, drought and fire have stimulated debate as to whether such ecosystems exhibit alternate stable state characteristics (Rutherford and Powrie 2010; Vetter 2009, 2005). Rutherford and Powrie (2010) highlight how intense grazing in Namaqualand has led to the formation of resilient species pools, suggesting the existence of alternate stable states. In the Kamiesberg, alternate stable states may be characterised by shifts between fynbos and succulent karoo, as well as changes within biomes, such as a shift to dominance of Galenia africana in succulent karoo in response to heavy grazing or to Elytropappus rhinocerotis in renosterveld and fynbos (Figure 2.12) (Curtis, 2013; Keeley, et al 2012; Todd and Hoffman 2009). It is suggested here that vegetation in the Kamiesberg may be more susceptible to shifts in ecosystem state than elsewhere in the biome because (i) biome boundary transitions occur across one substrate type, reducing the resilience afforded by substrate-derived ecosystem affinities and; (ii) because the dominant ecological/physiological processes are more dynamic.
Indigenous forests of South Africa are rare, covering <1 % of the country’s land surface. Most are island archipelagos set amongst larger-scale matrices of the fynbos, albany thicket, grassland, savanna biomes and transformed biomes such as agricultural land (Mucina and Geldenhuys, 2006). Only one of the twelve forest types identified in the national vegetation classification (Mucina and Geldenhuys, 2006; also see Rutherford and Westfall, 1986) qualifies as a biome in its own right: the Southern Cape Afrotemperate Forest (Figure 2.16). These are tall, multilayered forests dominated by yellowwoods (*Podocarpus* spp.) that persist down to sea level at 34°S, and are comparable to warm-temperate forests in the northern hemisphere such as those in East Asia and the south western United States. The largest single forest patch (25,706 ha) is the Tsitsikamma Forest in the southern Cape. This forms part of a still larger complex of 60,560 ha at about 34° S, spanning 22° to 24° 30’ E (Geldenhuys 1991) in the southern Cape along the coastal plateau between Humansdorp in the east and Mossel Bay in the west.

![Figure 2.16: Distribution of forest biome sub-types in South Africana and Swaziland (Mucina and Rutherford, 2006).](image)
Forests worldwide, including those of Mediterranean and temperate climate regions, have been indicated as vulnerable to drought. Choat, et al (2012) suggest that trees are, on a global scale, vulnerable to embolism under drought conditions. Specifically, that negative pressure in the xylem results in a phase change from liquid water to water vapour, and the resulting gas globules cause vascular blockages limiting water supply for photosynthesis. They argue that embolism is a key mechanism in vegetation shifts and forest decline as this sets thresholds for stomatal closure, which limits photosynthesis, increases heat and light damage, and exhausts carbon stocks over time. There has historically been a tendency to view forests as most vulnerable to drought and, similarly, that global vegetation distribution is most influenced by climate – and the Cape flora is no exception.

February and Manders (1999) examined the effects of water availability on selected species from fynbos (Protea repens, P. nitida, P. nerifolia) and afrotemperate forest (Cunonia capensis, Kiggelaria africana) in the south western Cape by examining the relationships among plant biomass, vessel size and vessel frequency. The forest species showed lower adaptive capacity than those of fynbos, indicating absence of traits that might allow persistence in sandstone fynbos habitat that is subject to greater physiological stress than are species in forest habitat. Similarly, Manders (1990, 1992) suggests that seedlings of forest species are likely to be more vulnerable to drought than those of fynbos, possibly because they share a greater vulnerability to xylem cavitation during establishment under summer drought conditions with inadequate shade (E. February, P.T. Manders, A. Scholtz, unpublished data; Coetsee, et al. 2015). Under more favourable conditions some forest species characteristic of the ecotone, such as Kiggelaria africana or Virgilia spp., could apparently proliferate in the intermediate environmental space with adequate moisture and shade cast by forest trees. Manders (1990) concluded that moisture availability broadly determines fynbos/ forest distribution below a threshold where MAP is <600 mm. Where moisture availability exceeds this, other factors may determine the distribution forest and fynbos.

The southern Cape plateau forests are subject to less extreme summer hydrological stress than elsewhere within the fynbos biome, such as in the south western Cape that
experiences extreme summer drought, because precipitation is distributed more evenly throughout the year. In these forests the transition to fynbos occurs without strong association to climatic gradients. Afrotemperate forest persists where mean annual precipitation (MAP) can be as low as 500 mm/yr$^{-1}$ near Great Brak River, and as high as 1,200 mm/yr$^{-1}$ at Jonkersberg, Diepwalle and Storms River (Geldenhuys, 1991). In comparison, the lower and upper climatic limits of fynbos distribution in the southern Cape are MAP 310 and 1120 mm/yr$^{-1}$, respectively (Rebelo, et al. 2006). The southern Cape forests also often transition to fynbos where there is little or no difference in climate or substrate (Phillips, 1930; Adamson, 1953; Mucina and Geldenhuys, 2006; Keeley, et al. 2012; Allsop, et al. 2014). Other factors must therefore be invoked to explain the distribution of fynbos and forest in the southern Cape.

Both the structural and chemical characteristics of fynbos promote fire, and the same set of properties appear to retard fire in afromontane forest. Fynbos is characterised by a near continuous litter layer with abundant graminoids, short and medium sized shrubs, and small tree and medium sized trees, in varying combinations. This results in close coupling of biomass compartments, resulting in stand-destroying crown fires. The adjacent forests have a discontinuous understory with few graminoids, and display pronounced separation between the litter layer, understory and the canopy (Keeley, et al. 2012). Chemical properties seem to be less important. van Wilgen, et al. (1992) found that heat yields from combusted fynbos were only marginally higher than for afromontane forest species (21,900 J g$^{-1}$ and 20,700 J g$^{-1}$ respectively). This is relatively low in forest species (3%). These factors combined, fynbos is highly flammable, and forest is not.

Geldenhuys (1994) argues that forests persist in orographic refugia where fires are unlikely. He proposes that climate and soils determine the potential distribution of fynbos and forest, but the actual location of forest patches is determined by the pattern of fires in the landscape. The fire pattern is in turn determined by the interactions among prevailing winds and local geomorphology. In late summer, warm, dry air from the arid South African interior is drawn towards low pressure systems moving from west to east across the southern coast (Tyson, 1964). In combination with
lightning, these weather systems promote fire in fynbos. Afrotemperate forest islands persist in fire-free refugia formed in troughs on the lee side of in abutting mountains to the north, or in steep sided gorges where aridity stress is lower than surrounding areas. Areas without orographic protection from these winds are subject to more frequent fire than those in sheltered refugia (Figure 2.17, 2.18).

Fynbos is distributed on strongly oligotrophic soils, and forest soils are generally better developed and more nutrient rich (Cowling, 1995). The suggestion of nutrients as a limiting factor at the ecotone however has been undermined because whole forest patches in the southern Cape can be observed to transcend shale/ sandstone substrate boundaries (Geldenhuys 1994). Bond (2010) demonstrates that most fynbos soils have sufficient micronutrient stock to accommodate forest when soils are deep enough to allow development of deep root systems. Similarly, van Daalen (1981) demonstrated that forest can establish on almost any soils in the southern Cape, and that fynbos and forest soils rarely differ substantially. When differences do occur between soil nutrient content in the respective habitats, van Daalen suggests that these differences are attributable to the vegetation itself following establishment, rather than being a driver of initial vegetation change.

The boundary between fynbos and forest is often interrupted by a transitional zone dominated by the legume _Virgilia divaricata_ and/ or _V. oroboides_ (Figure 2.19) (Adamson, 1938; Phillips, 1926). Other species characteristic of this zone include _Rhus_ spp. and a number of members of Celastraceae including species of _Maytenus, Pterocelastrus_ and _Cassine_. These species have been suggested as forest expansion pioneers, their increased abundance at forest margins being an apparent precursor to woody expansion. The establishment of such species may lead to modification of the microenvironment by providing shade, reducing moisture stress and hence facilitating establishment of forest seedlings that might otherwise be susceptible to xylem cavitation during establishment (Coetsee, et al. 2013; Coetsee, et al. 2015). However, high fire frequencies in fynbos are likely to kill saplings of pioneer taxa, precluding their establishment (Midgley, et al. 1997).