Restoration potential of alien-invaded Lowland Fynbos

by

Alexander Stuart Warren Hall

Dissertation presented for the degree of

Doctor of Philosophy (Science)

at

Stellenbosch University

Department of Conservation Ecology and Entomology, Faculty of AgriSciences

Supervisor: Prof. Karen J. Esler

Co-supervisor: Prof. Patricia M. Holmes

Co-supervisor: Dr. Mirijam Gaertner

March 2018

Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated) that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Stuart Hall

Date: March 2018

Summary

Widespread degradation of ecosystems on a global scale has led to the need for ecological restoration in order to more effectively conserve and manage threatened ecosystems. While this is an emerging field, substantial challenges remain in achieving optimal success in restoration interventions, which need to be addressed in order to improve recovery potential of degraded sites. This is especially important in highly biodiverse regions in urgent need of restoration intervention, of which the critically endangered vegetation type Cape Flats Sand Fynbos, found within the Cape Floristic Region (CFR) in South Africa is a prime example. Of particular concern in this case is the impact of invasive alien plants, especially where invasive plant removal alone does not facilitate native vegetation recovery. Use of alternative passive clearing methods, or the incorporation of active seed sowing interventions, may improve restoration success in such cases. This dissertation investigated the following aspects of restoration: (1) seed ecology and the determination of effective germination cues of structurally important species in this vegetation type (chapter 2), (2) different passive and active restoration treatments in order to determine best alien clearing and management protocols (chapter 3), (3) predicting long-term vegetation recovery trajectories under different restoration treatments and pinpointing ecological thresholds through the use of a dynamic model incorporating vegetation recovery rates under passive and active restoration treatments (chapter 4).

A seed ecology study investigated the effectiveness of smoke and heat exposure as a pre-treatment of seeds in improving germination success of species within Cape Flats Sand Fynbos. Fourteen species were exposed to a range of durations of exposure at different temperatures, in combination with exposure to smoke residue, after which seeds were germinated on agar to determine treatment success. Most species fell into one of two main groups: Seed germination in the first group (e.g. *Anthospermum aethiopicum*, *Metalasia densa* and *Watsonia meriana*) was greatest following either a lower temperature heat pulse, an extended period of mild temperature exposure, or no pre-treatment with heat. Seed germination in the second group (e.g. *Pelargonium elongatum, Phylica cephalantha* and *Trichocephalus stipularis*) was promoted after brief exposure to higher (100°C) temperatures. Species within the latter group mainly possessed physical dormancy.

Passive *Acacia saligna* clearing treatments in the field involving either burning or stacking biomass after initial alien clearing, as well as active intervention involving sowing seeds of native species either directly after burning or a year later and either with or without seed pre-treatment, resulted in very different recovery trajectories over a two year survey period. No treatment resembled a reference uninvaded vegetation condition after two years. Clearing alien biomass without burning was the cheapest method and facilitated recovery in less degraded areas, but otherwise there was very limited or no native vegetation recovery and this facilitated secondary invasion by herbaceous weeds. Burning

after clearing controlled some guilds of secondary invasive species, but stimulated mass acacia reestablishment and did not result in native vegetation recovery. The native seed bank was found to have been depleted during the period of invasion, hence the lack of autogenic recovery under passive treatments. However, while clearing without burning resulted in low acacia reestablishment, two years later the acacia seed bank was similarly reduced both with and without burning. Active seed sowing was the most expensive treatment but resulted in the highest recovery of native shrub cover and diversity. These findings suggest that a biotic threshold has been crossed where passive treatment does not result in recovery of vegetation components. Active sowing was able to partially reverse this threshold through improved recovery of total shrub cover, while pre-treatment of seeds before sowing improved establishment of some species. However, non-sprouting shrub cover was over-represented while resprouting shrubs and species of Restionaceae, which germinated successfully under greenhouse conditions, were under-represented relative to the reference condition. This suggests that barriers still exist in preventing establishment of some species from seeds sown in the field.

A dynamic model was designed to analyze the effectiveness of the different restoration methods, enabling the extrapolation of recovery trajectories over a long time span which could not be determined from short-term field surveys alone. Data for rates of vegetation recovery under different passive and active restoration treatments over the course of two years of field surveys were fed into the model. The modelled simulations showed that different treatments in similar degraded states at the time of initial clearing resulted in vastly different recovery trajectories when extrapolated over an extended period of time. Active seed sowing was initially the most expensive treatment but resulted in the highest indigenous shrub recovery, which in turn decreased the costs of longer-term follow-up alien plant clearing, as well as providing competition against establishment of secondary invasive species. Clearing without burning was the cheapest method, but resulted in limited recovery of indigenous or acacia cover over the long-term, leaving barren ground prone to secondary invasion by herbaceous weeds. The model therefore supported the finding of the field restoration experiments that ecological thresholds have been crossed which prevented recovery of certain vegetation components. Active sowing was able to partially reverse these thresholds and resulted in sustained shrub cover, but even this treatment did not resemble the reference condition in terms of restoring a balance of structural components after simulating over an extended period of time.

By synthesising the knowledge gained from the three aspects of this dissertation, and in light of what was previously known to work effectively, management recommendations were formulated to provide practitioners with more effective guidelines for best practise in future restoration of lowland fynbos vegetation. Firstly, it was concluded that biotic thresholds to restoration have been crossed within the study site, due to the lack of autogenic recovery of native cover and diversity under passive treatments as a result of a depleted native seed bank. Active interventions can partially reverse this threshold through the reintroduction of native seeds, and increase resilience of the vegetation to secondary invasive species. Secondly, the additional knowledge gained through germination tests using heat and smoke pre-treatment of seeds is highly valuable for incorporating into further restoration work. The use of species-specific pre-treatments for stimulating optimal germination can improve restoration success following active seed sowing intervention in the field. However, some species which respond well to seed pre-treatment in greenhouse conditions fail to establish from seed in the field, and these species are better restored through nursery propagation for planting into the field. Thirdly, the best treatment to use in the field was found to depend on the level of degradation at the time of initial alien clearing. A less degraded site with representative native vegetation structure i.e. more than 10% cover of both non-sprouting and resprouting native shrubs will recover after clearing without burning, while a more degraded site lacking native vegetation structure or cover will require active intervention in order to facilitate recovery of native cover and improve resilience to invasion by primary or secondary invasive species.

Since burning after clearing resulted in mass recovery of *Acacia saligna*, both in passive and active restoration treatments, two alternative treatments to those tested in the field are proposed. The most appropriate treatment would depend on the size of the secondary invasive seed bank. If this seed bank is small, clearing without burning and sowing pre-treated native seeds should be more effective than burning. If the secondary invasive seed bank is large, then clearing and waiting two years to facilitate acacia seed bank reduction, after which a management burn is conducted, should deplete the secondary invasive seed bank. Sowing native seeds after burning would result in native seedlings experiencing less competition from invasive species before establishing. It may not be feasible to restore the entire diversity found in a reference habitat, but focusing on restoring vegetation structure will provide resilience against invasive species establishment, facilitate an appropriate fire regime and provide suitable habitat for reintroduction of rare or threatened species in future once follow-up control of invasive species is more manageable.

Opsomming

Wydverspreide degradasie van ekosisteme op ‘n wêreldwye skaal het daartoe gelei dat ekologiese restourasie nodig is om bedreigde ekosisteme doeltreffend te bewaar en te bestuur. Terwyl dit 'n ontluikende gebied is bly daar groot uitdagings om optimale sukses in restourasie-intervensies te behaal. Die uitdagings moet aangespreek word om die restourasiepotensiaal van gedegradeerde terreine te te verbeter. Dit is veral belangrik in gebiede met hoë diversiteit wat dringend restourasie-intervensies benodig, waarvan die krities bedreigde vegetasietipe, Kaapse Vlakte Sandfynbos, wat binne die Kaapse Floristiese Streek (KFS) in Suid-Afrika voorkom, 'n uitstekende voorbeeld is. Van besondere belang in hierdie geval is die impak van indringerplante, veral waar indringerplantverwydering alleen nie inheemse plantegroei sal herstel nie. Die gebruik van alternatiewe passiewe skoonmaakmetodes, of die inkorporering van aktiewe saadsaai-intervensies, kan in sulke gevalle die sukses van die herstel verbeter. Hierdie proefskrif het die volgende aspekte van restourasie ondersoek: (1) saadekologie en die bepaling van effektiewe ontkiemingstoestande van struktureel belangrike spesies in hierdie veldtipe (hoofstuk 2), (2) verskillende passiewe en aktiewe restourasiebehandelings om die beste bestuursprotokolle vir uitheemse plantverwydering te bepaal (hoofstuk 3), (3) die voorspelling van langtermyn vegetasiehersteltrajekte onder verskillende restourasiebehandelings en die bepaling van ekologiese drempels deur die gebruik van 'n dinamiese model wat vegetasiehersteltempo bevat onder passiewe en aktiewe restourasiebehandelings (hoofstuk 4).

'n Saad-ekologie-studie het die effektiwiteit van rook- en hitteblootstelling ondersoek as 'n voorbehandeling van sade in die verbetering van ontkiemingsukses van spesies binne Kaapse Vlakte Sand Fynbos. Veertien spesies was aan 'n reeks tydperke van blootstellings by verskillende temperature blootgestel, in kombinasie met blootstelling aan rookresidu, waarna saad op agar ontkiem is om behandelingsukses te bepaal. Die meeste spesies het in een van die twee hoofgroepe geval: Saadkieming in die eerste groep (bv. *Anthospermum aethiopicum*, *Metalasia densa* en *Watsonia meriana*) was die grootste na 'n laer temperatuur hittepuls, 'n lang tydperk van ligte temperatuur blootstelling of geen voorafbehandeling met hitte. Saadkieming in die tweede groep (bv. *Pelargonium elongatum*, *Phylica cephalantha* en *Trichocephalus stipularis*) is na kort blootstelling aan hoër (100 ° C) temperature bevorder. Spesies in die laasgenoemde groep het hoofsaaklik fisiese dormansie gehad.

Passiewe *Acacia saligna*-skoonmaakbehandelings in die veld wat die brand of stapeling van biomassa behels ná aanvanklike uitheemse plante verwydering sowel as aktiewe intervensie waarby die saai van inheemse spesies plaasvind word, hetsy direk na brand of 'n jaar later en óf met of sonder saadvoorbehandeling, gelei tot baie verskillende hersteltrajekte oor 'n tydperk van twee jaar. Geen behandeling het na twee jaar dieselfde gelyk as vegetasie sonder indringerplantegroei. Die verwydering van uitheemse plante sonder verbranding was die goedkoopste metode en het herstel binne minder-

gedegradeerde gebiede die beste fasiliteer, maar andersins was daar baie beperkte of geen inheemse plantegroeiherstel nie en dit het sekondêre indringing deur onkruide gefasiliteer. Verbranding na die verwydering van uitheemse plante het sommige sekondêre indringerspesies beheer maar dit het ook akasia-hervestiging gestimuleer wat nie tot die herstel van inheemse plantegroei gelei het nie. Die inheemse saadbank was tydens die tydperk van indringing uitgeput, dus was daar nie outogene herstel onder passiewe behandelings nie. Alhoewel die skoonmaak sonder verbranding tot lae akasia-hervestiging gelei het, was die akasia-saadbank twee jaar later ook met en sonder verbranding verlaag. Aktiewe saadsaai was die duurste behandeling maar dit het die hoogste herstel van inheemse plantegroei en diversiteit tot gevolg gehad. Hierdie bevindinge dui daarop dat 'n biotiese drempel oorgesteek is waar passiewe behandeling nie tot die herstel van vegetasiekomponente lei nie. Aktiewe saai was in staat om hierdie drempel gedeeltelik om te keer deur verbeterde herstel van totale struikbedekking, terwyl voorbehandeling van sade voor saai, vestiging van sommige spesies verbeter. Nietemin, struikbedekking wat nie self uitloop was oorverteenwoordig, terwyl struikbedekking van self uitloop en Restionaceae-spesies, wat onder kweekhuis-toestande suksesvol ontkiem het, onderverteenwoordig was relatief tot die verwysingsvegetasie. Dit dui daarop dat daar nog struikelblokke bestaan wat oorkom moet word vir sekere spesies wat in die veld gesaai word van saad om te vestig.

'n Dinamiese model was ontwerp om die effektiwiteit van die verskillende restourasiemetodes te analiseer. Dit maak die ekstrapolasie van hersteltrajekte moontlik oor 'n lang tydperk wat nie alleen vanuit korttermyn veldopnames bepaal kon geword nie. Data vir die groeikoers van vegetasieherstel onder verskillende passiewe en aktiewe herstelbehandelings oor twee jaar van veldopnames was in die model gevoer. Die gemodelleerde simulasies het gewys dat verskillende behandelings in soortgelyke gedegradeerde state ten tye van die eerste skoonmaak tot baie verskillende hersteltrajekte gelei het wanneer dit oor 'n lang tydperk geëxtrapoleer was. Aktiewe saadsaai was aanvanklik die duurste behandeling, maar het tot die beste inheemse plantegroei gelei, wat die koste van langtermyn-opvolg uitheemse plantverwydering verminder het, asook die kompetisie vergroot het teen die vestiging van sekondêre indringerspesies. Verwydering sonder verbranding was die goedkoopste metode, maar het tot beperkte herstel van inheemse of akasia-bedekking oor die langtermyn gelei. Dit het die onbedekte grond blootgestel aan ʼn sekondêre inval deur onkruide. Die model ondersteun dus die bevinding van die veld-herstel eksperimente dat ekologiese drempels oorgesteek is wat die herstel van sekere vegetasiekomponente verhinder het. Aktiewe saadsaai kon hierdie drempels gedeeltelik omkeer en tot volhoubare struikbedekking lei, maar selfs hierdie behandeling het nie die verwysingsvegetasie weerspieël ten opsigte van die herstel van 'n balans van strukturele komponente nadat dit oor 'n lang tydperk gesimuleer is nie.

Deur die kennis wat uit die drie aspekte van hierdie proefskrif verkry word, en in die lig van wat voorheen bekend was om doeltreffend te werk, is bestuursaanbevelings geformuleer om praktisyns te voorsien met meer effektiewe riglyne vir beste praktyke in die herstel van die land se fynbosplantegroei. In die eerste plek is daar tot die gevolgtrekking gekom dat biotiese drempels vir herstel in die studieterrein oorskry is weens die gebrek aan outogene herstel van natuurlike dekking en diversiteit onder passiewe behandelings as gevolg van 'n uitgeputte inheemse saadbank. Aktiewe intervensies kan hierdie drempel gedeeltelik keer deur natuurlike sade weer in te saai, en die veerkragtigheid van die plantegroei verbeter teen sekondêre indringerspesies. Tweedens, die bykomende kennis wat verkry is deur ontkiemingstoetse wat hitte- en rookvoorbehandeling van saad gebruik, is waardevol vir die inkorporering in verdere restourasiewerk. Die gebruik van spesiespesifieke voorbehandelings om optimale ontkieming te stimuleer kan die restourasie-sukses verbeter na aktiewe saadsaai in die veld. Sommige spesies wat goed op saadvoorbehandeling in kweekhuistoestande reageer, kan egter nie van saad in die veld vestig nie, en hierdie spesies word beter gevestig deur plante te kweek om in die veld te plant. Derdens is gevind dat die beste behandeling wat in die veld gebruik kan word, bepaal word deur die vlak van degradasie ten tye van aanvanklike uitheemse plantverwyder. 'n Minder gedegradeerde terrein met 'n verteenwoordigende inheemse plantegroeistruktuur, d.w.s. meer as 10% bedekking van inheemse struike sal ná verwydering sonder verbranding herstel, terwyl 'n meer gedegradeerde terrein sonder inheemse plantegroei of bedekking aktiewe ingryping benodig om die herstel van natuurlike plantbedekking, en veerkragtigheid teen primêre of sekondêre indringerspesies te fasiliteer.

Aangesien verbranding na verwydering tot die herstel van *Acacia saligna* gelei het by beide passiewe- en aktiewe-restourasiebehandelings, word twee alternatiewe behandelings wat in die veld getoets word voorgestel. Die mees geskikte behandeling sal van die grootte van die sekondêre indringersaadbank afhang. As die saadbank klein is moet plantverwydering gedoen word sonder enige verbranding. In die geval sal die saai van voorafbehandelde inheemse sade doeltreffender wees as om te brand. As die sekondêre indringersaad bank groot is, moet daar twee jaar lank se verwydering gedoen word om die vermindering van akasia saad te vergemaklik, waarna 'n beheerde brand aangewend kan word. Die aksie sal die sekondêre indringersaadbank verwyder. Saai van inheemse sade na ‘n brand sal lei tot die vestiging van inheemse saailinge met minder mededinging van indringerspesies. Dit mag nie moontlik wees om die totale diversiteit in 'n verwysingshabitat te restoureer nie, maar om op die herstel van vegetasie te fokus sal veerkragtigheid teen indringerspesies gevestig word, 'n gepaste brandperiode fasiliteer en geskikte habitat verskaf vir die hervestiging van seldsame of bedreigde spesies in die toekoms sodra opvolgbeheer van indringerspesies meer beheerbaar is.

Acknowledgements

I wish to express my sincere gratitude and appreciation to the following persons and institutions:

- The Millennium Seed Bank Programme (MSBP), the Arcadia Fund and the Bentham Moxon Trust, the DST-NRF Centre of Excellence for Invasion Biology and Working for Water Programme through their collaborative research project on “Integrated Management of invasive alien species in South Africa”, the Table Mountain Fund (TMF), the National Research Foundation (NRF), and the German Academic Exchange Service (DAAD) are gratefully acknowledged for financial support.

- The Centre of Excellence for Invasion Biology (CIB), and the department of Conservation Ecology and Entomology at Stellenbosch University, as well as City of Cape Town Nature Conservation and the South African National Biodiversity Institute (SANBI) for institutional and logistical support.

- Suzaan Kritzinger-Klopper from CIB, Monean Jacobs and Celeste Mockey from the department of Conservation Ecology and Entomology, and Jacques Kuyler from Blaauwberg Nature Reserve for logistical support in organizing and carrying out fieldwork, Anthony and Barbara Hall for kindly providing me with accommodation on many occasions close to my field site, as well as Inez McGregor, Zoe Poulsen, Karen Merrett, Hillary Moyo, Dale Slabbert, Sam Pinzi, Clarissa Fransman, Grant Alexander and others for assistance in the field and help with seed collection.

- Stanley Snyders for use of nursery space for setting up the indigenous seed bank study.

- Prof. Martin Kidd for much patience and assistance with statistical analysis of data.

- Dr. Rosemary Newton from MSBP for support in developing and implementing the seed heat treatment study and for hosting me at the Millennium Seed Bank, as well as John Adams for lab support; Pablo Gómez and Beatrice Dewenter for help in setting up heat-treatment experiments and monitoring germination.

- Prof. João Cabral, Dr. Joana Vicente, Dr. João Honrado, Sofia Vas and Rita Bastos for support in conceptualizing and development of the dynamic model study, and hosting me at their institutions.

- My Supervisors Prof. Karen Esler, Prof. Pat Holmes and Dr. Mirijam Gaertner for their guidance, support and assistance, and providing different yet complementing and highly constructive comment and ideas throughout the development of this dissertation.

- My family and friends who supported and encouraged me to follow my passion and pursue this field of study, and helped me to persevere in completing my studies.

Preface

This dissertation is presented as a compilation of 5 chapters. **Each chapter is introduced separately and is written according to the style of the journal Austral Ecology to which Chapter 2 was submitted for publication. Each data chapter was written as a stand-alone paper, and therefore there is some content overlap between them (in particular study site description and methodology). Chapters 3 and 4 are due to be submitted for publication after further minor edits and formatting.**

Chapter 1 **General Introduction and project aims**

Chapter 2 **Effect of heat treatment on seed germination**

Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type.

Hall, S. A., Newton, R. J., Holmes, P. M., Gaertner, M., Esler, K. J. (2016) Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type. *Austral Ecology*. **42**, 354–366.

SAH contributed through conceptualization of the study, collection and analysis of data, and writing of the manuscript; RJN assisted with logistics; PMH assisted with species selection; RJN and PMH assisted with development of the methodology; RJN, PMH, MG and KJE reviewed and edited the manuscript.

Chapter 3 **Alien clearance methods (passive and active restoration)**

Assessing the effectiveness of passive and active restoration techniques in conserving a critically endangered vegetation type in a biodiversity hotspot

Chapter 4 **Modelling vegetation recovery trajectories under different restoration treatments**

Anticipating the effectiveness of invasive plant control and native vegetation recovery: An innovative dynamic tool to optimise South African fynbos management decision-making

Chapter 5 **Synthesis of findings and implications for management following alien invasion**

Table of Contents

Chapter 1: Introduction and key components of the study

1.1 Background context

1.1.1 Conservation and Ecological Restoration

Widespread degradation of ecosystems on a global scale has led to the need for ecological restoration, the process of assisting the recovery of degraded ecosystems (SER, 2002), along with traditional conservation practises in order to more effectively manage sustainable social-ecological systems. There have been advances in the science and practice of ecological restoration over the past few decades (Hobbs 2007; Gaertner *et al.* 2012), but substantial challenges remain, particularly regarding scaling-up and financing of restoration initiatives. Furthermore, successful interventions may be specific to certain ecosystems and not others, while short-term recovery may not be sustained over the long term. These challenges need to be addressed in order to improve recovery potential and save threatened ecosystems, especially in highly biodiverse regions in urgent need of restoration intervention of which the Cape Floristic Region (CFR) in South Africa is a prime example (Gaertner *et al.* 2011).

1.1.2 Threatened Mediterranean Climate Ecosystems

The vegetation of all Mediterranean Climate Regions contain a substantial proportion of the world's plant species for the area of land represented, with many of these species endemic to these regions (Cowling *et al.* 1996). However, much of the vegetation across all regions has been transformed, mainly due to clearing for agriculture and urban development, as well as from alien plant invasions. Consequently, many of the plant species across these regions is under threat (Brooks *et al.* 2002). The fynbos vegetation of the Cape Floristic Region, South Africa has extremely high levels of plant diversity and endemism for the size of the region (Goldblatt and Manning 2000). However, as with other Mediterranean Climate Regions, the region's biodiversity has been compromised by human impacts (Rouget *et al.* 2003). This is especially true for the lowlands, where vast areas have been ploughed or lost due to urban development (Heijnis *et al.* 1999). This has left natural vegetation confined to scattered fragments of land, which are mostly too small to sustain ecological processes, and are often isolated from other lowland vegetation or larger areas of natural habitat on mountains.

Although conservation areas have been proclaimed to protect some of what remains in the CFR, many entire vegetation types are not represented by a sufficiently large enough area to even nearly approach national conservation targets (Rebelo *et al.* 2006). Added to this is the fact that a number of vegetation types on the lowlands of the Cape have so little remaining intact land representative of the vegetation type found there historically that it is now impossible to fulfil national conservation targets by preventing further loss of these habitats alone (Rebelo *et al.* 2006). For this reason it is crucial to restore any degraded areas where at all feasible in order to improve the conservation value of remaining natural areas especially degraded vegetation within protected areas.

1.1.3 Invasive alien species

Invasive alien species further exacerbate the loss of natural habitat by transforming natural ecosystems (Gaertner *et al.* 2014). While invasive alien species are a huge problem across most vegetation types within the Cape Floristic Region, they are particularly problematic across the already highly degraded lowlands. In these habitats, invasive alien species have infested much of the remaining natural habitat (Rebelo *et al.* 2006), and are further degrading these remnant patches. Fragmented vegetation is prone to a larger edge effect from disturbances due to neighbouring land-use and the presence of invasive alien species associated with human-transformed landscapes (e.g. Horn *et al.* 2011), which provides these competitive species with the ability to colonize and subsequently outcompete indigenous vegetation (e.g. Sharma *et al.* 2010).

Invasive alien species such as *Acacia saligna* transform the entire ecosystem. The lack of natural predators (until recent biological control agents were established) allowed the acacias to produce large numbers of long-lived seeds that remain dormant in the soil until a fire goes through the vegetation (Van Wilgen 2009; Richardson *et al.* 2011; Le Maitre *et al.* 2011). Even under biological control, sufficient seeds can remain to propagate many more seedlings almost immediately after the first fire that goes through the vegetation (Strydom *et al.* 2017), and before most indigenous species are able to establish and compete.

Alien clearing programmes have been initiated in many parts of the CFR. However, in most cases this has only involved clearing of the alien species without any further management action other than follow-up clearing. Seed banks in mountain fynbos vegetation appear to persist for two fire-cycles under invasive alien infestation, but not in lowland sand fynbos vegetation (Holmes 2002). This suggests that abiotic or biotic thresholds (Suding and Hobbs 2009) (Figure 1), representing barriers to potential ecosystem recovery, are different in these vegetation types. Seed banks and ecological thresholds are vitally important factors to consider when attempting to clear alien species and to restore lowland vegetation.

1.1.4 Cumulative effects of invasion

Earlier restoration research within the Cape has pinpointed density and also duration of dense alien invasion as being of great importance in determining the potential for restoration (Holmes *et al.* 2000; Gaertner *et al.* 2012), and these studies highlight the importance of clearing woody alien species at an early stage of invasion. Invasive trees outcompete indigenous species and act as a barrier to restoration in various ways, both directly and indirectly. For example, the invasives may change soil nutrient levels by the addition of nitrogen-rich leaf litter (Yelenik *et al.* 2004), or fire regime by allowing hotter burns as a result of increased biomass accumulation (Richardson and Van Wilgen 1986). Rodents can be more prevalent in old field vegetation (Holmes 2008), or following removal of woody invasives, which in turn causes increased soil disturbance. These processes eventually pass a critical point, also known as an ecological threshold or tipping point (Briske *et al.* 2006; Groffman *et al.* 2006), which represents a barrier to autogenic recovery. At this point the system will no longer shift back towards resembling the historical ecological state but rather move towards an alternative ecosystem state following alien clearance (Beisner et al 2003). This could be where vegetation becomes dominated by grassland where it was previously a shrubland (Le Maitre *et al.* 2011; Gaertner *et al.* 2012). At this stage restoration will be complex and will require major management interventions, and the chances that a functional ecosystem will autogenically recover are very unlikely (Gaertner *et al.* 2012). However, the point at which restoration would be considered unfeasible may depend on the conservation status of the habitat to be restored. An ecosystem of very high conservation status, such as Cape Flats Sand Fynbos, provides greater justification for restoration of more degraded habitat than one of the less threatened or more widespread vegetation types on the mountains. However, it is vital to know when irreversible thresholds have been crossed in any ecosystem which would result in restoration efforts being futile (Aronson *et al.* 1993) (Figure 1).

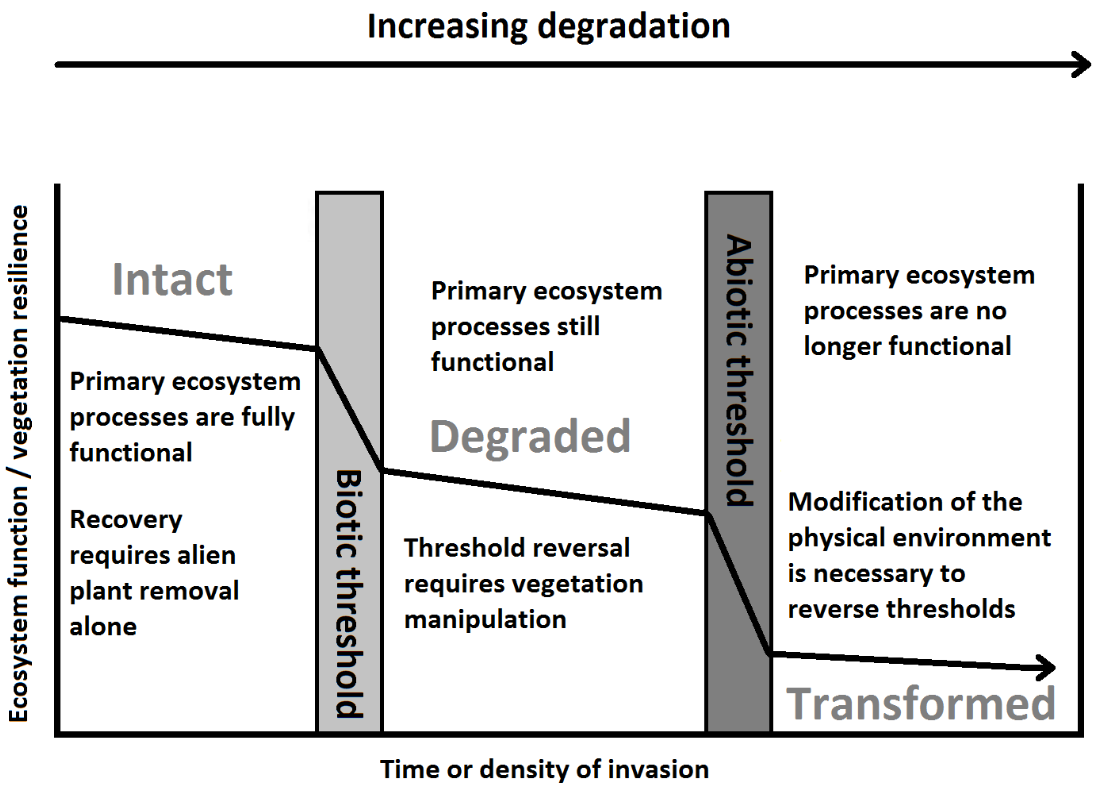


Figure 1. Conceptual framework of multiple ecological thresholds which are more likely to be crossed with increasing duration or density of invasion. Modified from Whisenant (2002).

1.1.5 Using active restoration to counteract invasive alien impact

Holmes (2002) found that long-lived obligate re-seeders did not persist well in sand fynbos seed banks following invasion. Thus resulted in changes in vegetation structure following alien clearance, similar to findings in Coastal Sage Scrub in California (Cione *et al.* 2002). In order to correct this imbalance it may be necessary to reintroduce species whose seeds are unlikely to have persisted during alien invasion. Reintroduction of indigenous plants by sowing of seeds (or planting seedlings) will thus have two added benefits that may be less successfully achieved by merely removing invasive alien species. Sowing of common (pioneer) or annual species indigenous to the site which can grow vigorously may help to outcompete invasive aliens (Herron *et al.* 2013) so that other indigenous species can come back over time without being hampered by invasive alien plant cover. This method was utilised in the Agulhas plain region of the CFR following *Acacia* invasion (Gaertner *et al.* 2012), as well as in Australia following *Chrysanthemoides monilifera* invasion (Vranjic *et al.* 2012). Introducing seeds or seedlings of species that have become rare or absent from a community and did not survive in the seed bank can help to re-establish appropriate vegetation structure (Cione *et al.* 2002; Waller *et al.* 2016). Populations of threatened species could also be introduced in order to improve their conservation status, as has been done within Table Mountain National Park where at least five threatened species have established following reintroduction (Hitchcock *et al.* 2012;

Petersen *et al.* 2007). However, in an Australian study such interventions were found to be of limited success (Morgan 1999).

Resprouting shrubs and geophytes are able to persist for a longer period of time under invasive cover as they are not solely dependent upon seeds to re-establish after fire, and have more stored resources to allow them to persist for a longer time (Holmes and Cowling 1997). However, even these plants eventually disappear from the system after lengthy invasion. The vegetation becomes dominated with acacia as well as some indigenous thicket elements appearing due to these species having bird-dispersed fruit (Holmes and Cowling 1997), for example *Putterlickia pyracantha* (Hall, personal observation). The obligate resprouting species do not readily recruit from seeds and so this guild is harder to re-establish than reseeding species once it has been lost from the system.

1.1.6 The importance of fire in fynbos ecosystems

As with most Mediterranean-type ecosystems (except Chile), fire is a vital component in sustaining vegetation, with a return interval in fynbos of 4-45 years (Van Wilgen *et al.* 1992; Keeley *et al.* 2012), although the actual return interval will depend on the vegetation type and the local climate. Most fynbos species are adapted to recruit from seeds immediately after fire (Le Maitre and Midgley 1992). Seeds produced between fire cycles will either remain in cones on the plant (in the case of serotinous species), or else are dropped into the soil where they remain dormant until one or more traits associated directly or indirectly with fire prompts the breaking of dormancy and stimulates germination. Smoke (Brown 1993) and heat pulse (Jeffery *et al.* 1988; Cocks and Stock 1997) are known to be effective cues for many fynbos species. However, studies on the effect of heat pulse are limited to a few hard-seeded species while this may be an important cue in a wider range of species, as has been found in other Mediterranean ecosystems (Reyes and Trabaud 2009; Keeley *et al.* 1985; Tieu *et al.* 2001).

Many fynbos species can also resprout after fires and so persist over successive fire intervals in this way (Kruger 1983; Van Wilgen and Forsyth 1992). If fires are too frequent then reseeding species may not have time to build up sufficient seed banks to re-establish after the fire and will thus disappear from the plant community (Van Wilgen 1982). If the fire interval is too long then obligate reseeder species will become senescent thus losing their seed bank, resulting in a shift in vegetation composition (Kruger 1983). The seed bank of such species will also become depleted as they may lack dormancy, especially in the case of serotinous proteas (Bond 1980).

1.2 Restoration in fynbos

1.2.1 Cape Flats Sand Fynbos, the focal vegetation type of this study

Cape Flats Sand Fynbos is a sclerophyllous shrubland occurring at low altitudes on oligotrophic sandy soils of low pH (Rebelo *et al.* 2006). Sand fynbos is analogous to Australian kwongan in that both vegetation types are confined to nutrient poor soils and burn frequently yet contain very high species diversity and levels of narrow-range endemism but low growth-form diversity, i.e. many species are closely related (Cowling *et al.* 1996). This vegetation contains a mix of both resprouting and non-sprouting species. Typical vegetation components are graminoid shrubs known as restios, ericoid shrubs, overstorey serotinous shrub species and geophytes (Figure 2). Within the study site the dominant restio species is *Thamnochortus punctatus* (family Restionaceae), an obligate seeder, which is therefore prone to disappearing under acacia invasion. Ericoid shrubs account for much of the remaining dominant cover. This group consists of species within the family Ericaceae, as well as a number of other families including Asteraceae, Rutaceae, Thymelaceae, Rubiaceae and Rhamnaceae. *Erica mammosa, Diosma oppositifolia, Phylica cephalantha* and *Trichocephalus stipularis* are conspicuous examples of resprouting shrubs in this vegetation, while *Ifloga repens, Passerina corymbosa* and *Anthospermum aethiopicum* are examples of non-sprouting obligate reseeder species. The overstorey serotinous shrub component, although not highly diverse, consists of *Protea repens* and *Protea scolymocephala* (family Proteaceae). Being serotinous, these species do not accumulate a seed bank in the soil. Geophytes are plants with an underground storage organ from which they can resprout after fire and most also go dormant over the dry summer season. The family Iridaceae is highly diverse within this vegetation type, including species within many genera such as *Gladiolus*, *Moraea* and *Watsonia*.

Figure 2. Structural components within pristine Cape Flats Sand Fynbos (from left to right): Restios – represented by *Restio quinquefarius*; Ericoid shrubs – represented by *Erica ferrea*; Serotinous proteas – represented by *Protea scolymocephala*; Geophytes – represented by Babiana villosula; representation of mostly structurally intact vegetation in a reference site.

Cape Flats Sand Fynbos is confined to a relatively small area of less than 40km diameter within the City of Cape Town's jurisdiction between Blaauwberg in the north, Lakeside in the south and Kraaifontein to Macassar in the east (Rebelo *et al.* 2006) (Figure 3). This area receives higher average annual rainfall than the sand fynbos found further north. This vegetation type is rich in endemic plant species (16) and Red List threatened species (108, including 5 extinct/extinct in the wild species) (Raimondo *et al.* 2009). As is the case for a number of lowland vegetation types in the Cape, only 11% of the historical area of Cape Flats Sand Fynbos remains, more than half of which is in poor habitat condition (Holmes and Pugnalin 2016). This is already far short of the national conservation target of 30% (Rouget *et al.* 2004). This vegetation type is classified as critically endangered and therefore a national conservation priority.

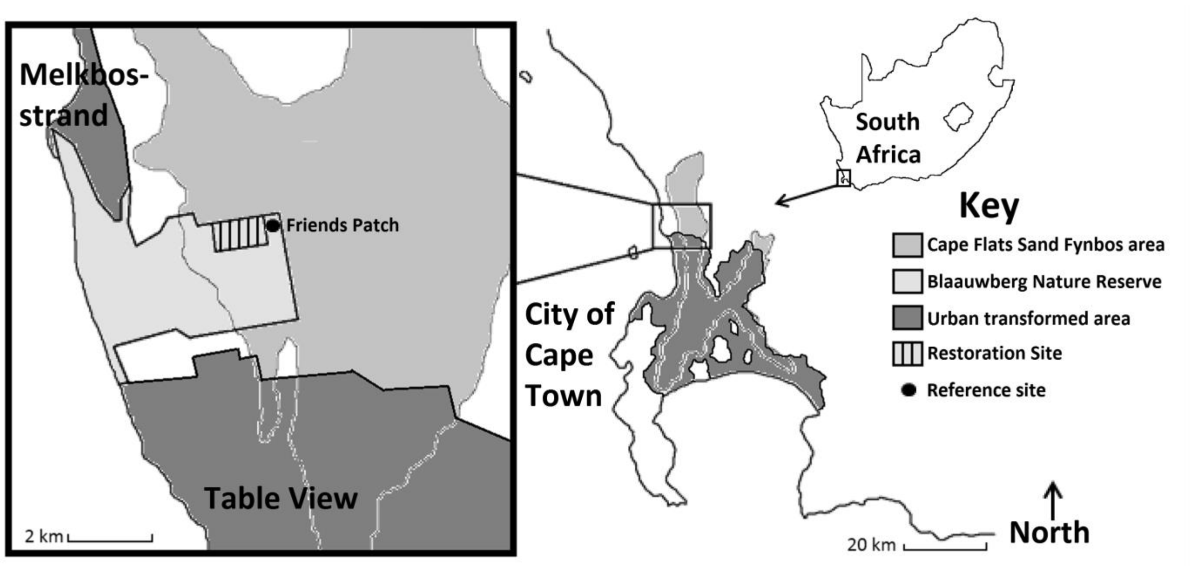


Figure 3. Location of the study area at Blaauwberg Nature Reserve north of the city of Cape Town, within the Western Cape province of South Africa.

1.2.2 Description of the field site

Blaauwberg Nature Reserve, where this project is being undertaken, contains the largest remaining area of unfragmented land within Cape Flats Sand Fynbos (approximately 400ha). Restoration of this site is therefore vital in order to approach national conservation targets. The “Friends Patch”, a relatively small area which was manually cleared by volunteers close to the study site, does contain species representing most structural components of Cape Flats Sand Fynbos (Figure 2), although missing much of the overstorey serotinous component. It is nevertheless a fairly representative example of what the vegetation should resemble following restoration, and illustrates the high conservation potential of parts of this site. Amongst the *Acacia saligna* in the study area a number of smaller patches of relatively diverse fynbos still persisted, although these consisted mostly of resprouting shrub species. In between these patches were large areas found to contain very low indigenous diversity and cover, mostly lacking even the more resilient resprouting shrub component and therefore classified as low restoration potential (Figure 4).

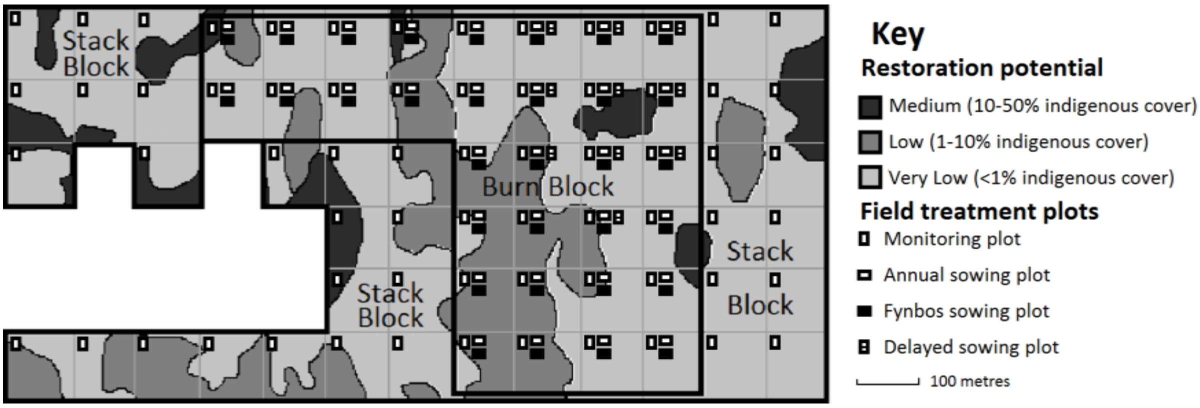


Figure 4. Mapped restoration potential within the restoration site at Blaauwberg Nature Reserve, divided into 1ha management blocks within 32ha sized passive stack-block and burn-block treatments. Active sowing treatments were set up within burn-block plots.

The history of the site was investigated in a previous study (Wotsitsa and Mgese 2012), and was of great importance to the planning of this project. At least from a social historical perspective, the most well-known historical event at this site was the 1806 Battle of Blaauwberg, in which the Batavians fought against the invading British forces (Cowell 2014). Other than this the main impact to the site has been the spread of *Acacia saligna* across the area following successive fire events.

The historical survey of the site used non-continuous, available aerial imagery from 1926 up until the present day (Wotsitsa and Mgese 2012). These images were georeferenced and used to determine acacia cover, ploughed areas, and to document any evidence of fires going through the site in order to get an idea of fire frequency in different parts of the site. A survey was done in May 2012 using 13 transects across the sand fynbos area to record remaining indigenous cover, and together with the information mapped from the land-use history study, used to quantify restoration potential (P. M. Holmes pers. com.). Although not fine-scale, the resultant map still gave an idea of the level of impact of acacia in different parts of the 400ha area. It showed that there is a high level of variation in fire frequency and length of invasion across the site, and so would explain why fynbos has persisted better in some parts than others. Areas that have been invaded for a longer period of time, or have been burnt more frequently since becoming invaded are less likely to have fynbos cover still persisting or an intact indigenous seed bank. A longer period of invasion results in increased soil nutrient levels such as soil N (Le Maitre et al. 2011), which facilitates weedy secondary invasions and negatively affects fynbos shrubs through competition (Yelenik et al 2004). Both of these factors would negatively affect restoration potential.

1.2.3 Reference site selection

It is important to identify sites against which to compare treatments in order to determine relative success of particular restoration interventions (Dorner 2002). Pristine habitats with similar environmental conditions may be considered as good reference sites, but often all habitat in a region has been degraded beyond the point of being considered pristine.

As mentioned above, the “friends patch” is itself not a pristine site due to degradation by previous invasion. Atlantis Sand Fynbos is found on the coastal plain of the Cape West Coast to the north of where Cape Flats Sand Fynbos occurs. A larger fraction of historical cover of this vegetation type still remains than in Cape Flats Sand Fynbos, and areas of intact habitat still remain within this vegetation type that have never been invaded and are still considered pristine in terms of species diversity and vegetation structure. The general vegetation structure and much of the species diversity is shared between Atlantis Sand Fynbos and Cape Flats Sand Fynbos (Rebelo *et al.* 2006). This makes it an appropriate reference for making comparisons at least with the northern limit of extent of Cape Flats Sand Fynbos at Blaauwberg Nature Reserve. Part of the area also burnt at the same time as the planned management burn at Blaauwberg, allowing the possibility of recording the rate of vegetation recovery under both pristine and invaded habitat.

1.2.4 Previous restoration interventions within the lowlands of the Cape Fynbos

Prior to this study, few restoration projects had been initiated within fynbos vegetation. However, three such projects suggest that restoration can be successful in restoring natural habitat. Tokai Park is a site near the southern limit of distribution of Cape Flats Sand Fynbos, and the only area of viable restoration potential within the southern region of the historical distribution of the vegetation type (Hitchcock *et al.* 2012). The site was previously planted with pine trees, but subsequently cleared in order to allow the recovery of Cape Flats Sand Fynbos while the seed bank was still viable. Fynbos seed banks persist better under pine trees than under acacias (Mostert *et al.* 2017; Galloway *et al.* 2017), although certain structural and compositional elements of the vegetation, especially a number of threatened species known to occur historically within the area, had been lost from the seed bank. These species were reintroduced either as seeds or as nursery-grown plants and then planted out shortly after the site had been burnt to clear the dead invasive alien biomass and stimulate indigenous seed bank to germinate. Indigenous vegetation structure and diversity re-established mostly without any large-scale reintroductions of common species. It was however fortunate that there was a historical record in the form of William Purcell’s herbarium from Bergvliet Farm (which borders Tokai) between 1902 and 1919 as a reference for what species occurred in the area (Rourke *et al.* 1981), and this was used to guide what species or structural components may need to be reintroduced from elsewhere if not recorded in the restoration site after clearing alone. Species composition is an issue to consider when attempting to restore the vegetation at Blaauwberg Nature Reserve, since the only reference sites for comparison are themselves degraded to varying extents.

A different study was done by Gaertner et al. (2012) to evaluate different restoration approaches to re-establish native fynbos communities on the Agulhas Plain. This also involved reintroducing species that have economic value for sustainable wildflower harvesting for the cut-flower industry. This can be used for additional motivation to clear invasive alien species on private land. While the restoration study at Blaauwberg Nature Reserve is purely for the purposes of conserving the highly threatened vegetation type, ecosystem service provision is of great importance when trying to motivate private landowners to clear invasive alien species in order to restore indigenous vegetation. However, the Gaertner et al. (2012) study found that active restoration treatments incur much higher costs than passive restoration, which at least in the short term outweigh the economic benefits resulting from it.

Waller et al. (2016) investigated seed-based ecological restoration in renosterveld, a different vegetation type found on the lowlands of the Cape region. This study found that renosterveld restoration in a site degraded and dominated by invasive alien grasses is possible using a combination of methods including but not limited to sowing of seeds. Indigenous seed banks were depleted due to the severity of degradation, but recovery was also hindered by invasive alien grasses unless their dominance was broken for a sufficient time period to allow for shrub recovery.

1.3 Rationale for this study

Invasive alien clearance has often been initiated where there is a desire to restore native vegetation cover. In some cases there has been good recovery of vegetation after clearing, but in some cases not. What causes this to happen is poorly understood. Additionally, success of restoration interventions has mostly only been determined from short-term studies, while long-term recovery is very seldom assessed.

While work has been done on the use of different methods of clearing and restoration in mountain fynbos ecosystems, sand fynbos communities are ecologically quite distinct in terms of seed banks and therefore also restoration potential (Holmes 2002). Invasive alien clearance has taken place across many parts of the lowlands but to date there has been little scientific work on comparing effectiveness of different methods of clearing in order to determine whether one method is most effective at restoring indigenous vegetation in this ecosystem. This is an important issue across a large region, since much remaining sand fynbos across the West and South coasts of the South-Western Cape has been invaded by *Acacia saligna* (Rebelo et al 2006).

This dissertation aimed to address these research needs, by determining effective protocols for restoring and managing a highly threatened vegetation type currently at risk of being lost due to invasion by alien acacia species. Current restoration methods appear not to be working effectively in lowland fynbos and this has highlighted a gap in the current knowledge around how to manage this ecosystem. The chapters of this dissertation cover different aspects of restoration, from seed ecology and the determination of effective germination cues of structurally important species in this vegetation type (Chapter 2), comparing different passive and active restoration treatments in order to determine best alien clearing and management protocols (Chapter 3), and predicting long-term vegetation recovery trajectories under different restoration treatments through the use of a dynamic model (Chapter 4). These results may furthermore determine whether ecological thresholds may have been crossed. By synthesising the knowledge gained from this study, and in light of what was previously known to work effectively, management recommendations are presented to provide practitioners with more effective guidelines for best practise in future restoration of lowland fynbos vegetation. Concepts investigated and developed within this dissertation are applicable on a much wider scale than in this vegetation type alone, since many of the issues discussed here are relevant in a wide variety of ecosystems facing similar threats (Le Maitre *et al.* 2011).

1.4 The objectives of this study

1.4.1 Effect of heat treatment on seed germination – Chapter 2

In a fire-prone Mediterranean ecosystem such as the fynbos region, seeds of most species only germinate in response to fires, since seed germination cues are linked to an aspect of fire such as smoke (Brown 1993) or heat (Jeffery *et al.* 1988). Sowing seeds of fynbos structural component species may therefore fail as a restoration tool if seeds are not adequately stimulated to break dormancy before sowing *in situ*. The effect of smoke on germination of certain species has been well documented (Mukundamago 2016), but heat treatment has been less well researched, both in terms of what temperature and duration of exposure is most effective and which species show positive response to this treatment. Of species that respond to heat treatment, some may respond to a different temperature and duration of exposure than others based on seed morphology, as found by Bond et al. (1999). Knowledge of the benefit of heat treatments on keystone structural component species can help to facilitate much better establishment of seeds sown as an active restoration intervention.

The objective of chapter two was therefore to determine optimal methods of smoke and heat pre-treatment for stimulating germination of a range of species to sow an as active restoration intervention.

1.4.2 Alien clearance methods (passive and active restoration) – Chapter 3

Different alien clearance methods - clearing and stacking alien biomass (Stack-block), and clearing and burning biomass (Burn-block) - were compared within the restoration site. Alien clearance is costly and will impact on the ability of the natural vegetation to recover depending on how it is implemented. Stacking of cleared biomass is the usual method of alien clearing used, and this was compared with the more novel Burn-block treatment. The most cost-effective, as well as most ecologically effective option of promoting recovery of natural vegetation was determined.

Where species representing key components of the natural vegetation structure have disappeared from the seed bank, active intervention would be necessary. This involved reintroduction of certain guilds by sowing seeds shortly before the onset of winter rains, and incorporated three aspects. Firstly, supplementation of the seed bank by sowing seeds of certain perennial plant guilds was predicted to enhance the vegetation structural composition of indigenous species over the persisting seed bank reserves. Secondly, the study explored whether augmenting propagule density by sowing seeds of native annual plants could help to outcompete invasive alien species which were anticipated to reinvade from a persistent soil seed bank (Herron et al 2013). Native annual plants could also provide protection for enhanced establishment of native perennial species germinating from the seed bank (Padilla and Pugnaire 2006). In sites with very low fynbos restoration potential, even the resprouter guild had been eliminated by invasive aliens and thus the rapid post-fire growth potential of these species had been lost. The extent to which a fast-growing pioneer seed mix may compensate for the lost function of sheltering slower growing fynbos seedlings was therefore investigated. Thirdly, it was determined whether pre-treatment of fynbos shrub seeds with a combination of heat and smoke further enhanced germination and establishment success.

The main objective of this chapter was to determine which treatments are most successful in restoring lowland fynbos, and furthermore whether thresholds have been crossed and which treatments are able to reverse these thresholds.

1.4.3 Modelling vegetation recovery trajectories under different restoration treatments to determine predictions of long-term recovery and to assess whether ecological thresholds have been crossed – Chapter 4

Short term monitoring of vegetation recovery will not necessarily determine what treatment works best over the long term. Therefore data from vegetation growth rates can be used to simulate recovery under different clearing treatments and determine long-term invasive alien and indigenous vegetation recovery as well as cost accumulation of different treatments. This can detect where thresholds have been crossed and treatments that can reverse them, in order to provide guidelines for long-term management.

The objective of this chapter was therefore to determine if dynamic models can reproduce fynbos vegetation recovery, as well as how different restoration treatments impact on recovery in the long term, and if the model can infer where restoration thresholds may have been crossed and treatments which could facilitate their reversal.

1.4.4 Synthesis of chapters into management guidelines – Chapter 5

The findings of the above chapters complement each other in determining best management practises for restoring a vegetation type such as sand fynbos (Figure 5). The results of the seed heat treatment study, in combination with studies on smoke pre-treatment (Mukundamago 2016), were used to inform most effective species-specific pre-treatments of seeds before sowing into the restoration site, in order to improve efficiency of percentage germination and diversity of species establishing in actively sown restoration plots assessed in chapter 3. Data collected to assess effectiveness of passive and active treatments in chapter 3 were used to model recovery trajectories in order to simulate long-term recovery under different treatments in chapter 4. Chapters 2 and 3 were used to infer best practice for restoration and management of fynbos after alien clearing, while chapter 4 provided further data to back up the findings of chapter 3 in terms of long-term sustainability of different treatment interventions. All three chapters therefore add to our understanding of how best to attempt restoration of degraded fynbos vegetation after alien clearing. This study is novel not only in a local context but on a global scale in terms of the combinations of treatments used as well as making use of modelling to predict long-term recovery trends. Therefore it provides insights into new methods of determining and assessing restoration projects that are applicable in an international context.

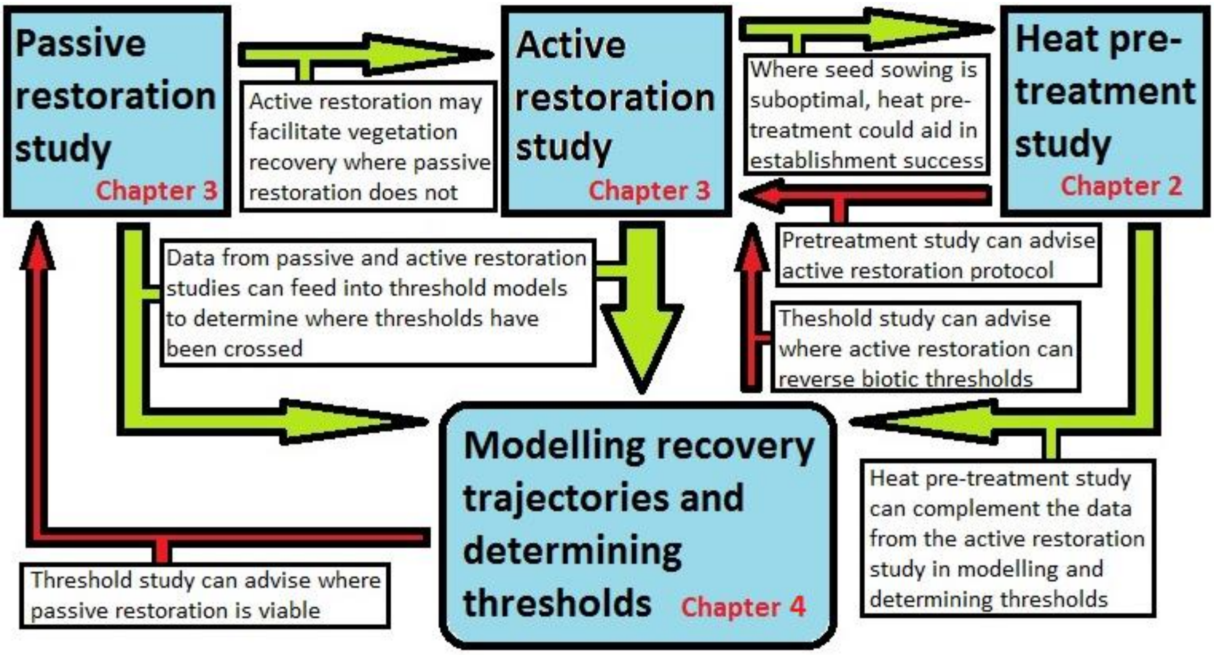


Figure 5. Outline of dissertation chapters showing how each section motivates further actions (green arrows) and advises future management (red arrows) in order to inform management guidelines.

1.5 References

Aronson, J., Floret, C., Floc'h, E., Ovalle, C., Pontanier, R. (1993) Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. I. A View from the South. *Restor. Ecol.*. **1**, 8–17.

Beisner, B., Haydon, D., Cuddington, K. (2003) Alternative stable states in ecology. *Front. Ecol. Environ*.. **1**, 376–382.

Bond, W. J. (1980) Fire and senescent fynbos in the Swartberg, Southern Cape. *South African For. J.*. **114**, 68–74.

Bond, W. J., Honig, M., Maze, K. E. (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia*. **120**, 132–136.

Briske, D. D., Fuhlendorf, S. D., Smeins, F. E. (2006) A Unified Framework for Assessment and Application of Ecological Thresholds. *Rangel. Ecol. Manag.*. **59**, 225–236.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C. (2002) Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conserv. Biol.*. **16**, 909–923.

Brown, N. A. C. (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytol.*. **123**, 575–83.

Cione, N. K., Padgett, P. E., Allen, E. B. (2002) Restoration of a Native Shrubland Impacted by Exotic Grasses, Frequent Fire, and Nitrogen Deposition in Southern California. *Restor. Ecol.*. **10**, 376–384.

Cocks, M. P., Stock, W. D. (1997) Heat stimulated germination in relation to seed characteristics in fynbos legumes of the Western Cape Province, South Africa. *South African J. Bot.*. **63**, 129–132.

Cowell, C. (2014) Sowing seeds for the future-restoring Cape Flats Sand Fynbos on an old field at Blaauwberg Nature Reserve. *Veld Flora*. **100**, 26–29.

Cowling, R. M., Rundel, P. W., Lamont, B. B., Arroyo, M. K., Arianoutsou, M. (1996) Plant diversity in mediterranean-climate regions. *Trends Ecol. Evol.*. **11**, 362–366.

Dorner, J. (2002) *An introduction to using native plants in restoration projects.* Plant Conservation Alliance Bureau of Land Management, US Department of Interior U.S. Environmental Protection Agency, Center for Urban Horticulture, University of Washington.

Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J., Richardson, D. M. (2014) Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships. *Divers. Distrib.*. **20**, 733–744.

Gaertner, M., Holmes, P. M., Richardson, D. M. (2012) Biological invasions, resilience and restoration. In: *Restoration Ecology: The new frontier* (eds J. Andel & J. Aronson) pp. 265–280 Oxford: Wiley-Blackwell.

Gaertner, M., Nottebrock, H., Fourie, H., Privett, S. D. J., Richardson, D. M. (2012) Plant invasions, restoration, and economics: Perspectives from South African fynbos. *Perspect. Plant Ecol. , Evol. Syst.*. **14**, 341–353.

Gaertner, M., Richardson, D. M., Privett, S. D. J. (2011) Effects of alien plants on ecosystem structure and functioning and implications for restoration: Insights from three degraded sites in South African fynbos. *Environ. Manage.*. **48**, 57–69.

Galloway, A. D., Holmes, P. M., Gaertner, M., Esler, K. J. (2017) The impact of pine plantations on fynbos above-ground vegetation and soil seed bank composition. *South African J. Bot.*. **113**, 300–307.

Goldblatt, P., Manning, J. (2000) *Cape Plants: a conspectus of the Cape Flora of South Africa.* Strelitzia 9, National Botanical Institute and Missouri Botanical Garden, Cape Town.

Groffman, P. M., Baron, J. S., Blett, T., Gold, A. J., Goodman, I., Gunderson, L. H., Levinson, B. M., Palmer, M. A., Paerl, H. W., Peterson, G. D., Poff, N. L., Rejeski, D. W., Reynolds, J. F., Turner, M. G., Weathers, K. C., Wiens, J. (2006) Ecological Thresholds: The Key to Successful Environmental Management or an Important Concept with No Practical Application? *Ecosystems*. **9**, 1–13.

Heijnis, C. E., Lombard, a. T., Cowling, R. M., Desmet, P. G. (1999) Picking up the pieces: A biosphere reserve framework for a fragmented landscape - The coastal lowlands of the Western Cape, South Africa. *Biodivers. Conserv.*. **8**, 471–496.

Herron, C. M., Jonas, J. L., Meiman, P. J., Paschke, M. W. (2013) Using native annual plants to restore post-fire habitats in western North America. *Int. J. Wildl. Fire*. **22**, 815–821.

Hitchcock, A., Cowell, C., Rebelo, T. (2012) The lost fynbos of Tokai Park. *Veld Flora*. **98**, 30–33.

Hobbs, R. J. (2007) Setting Effective and Realistic Restoration Goals: Key Directions for Research. *Restor. Ecol.*. **15**, 354–357.

Holmes, P. M. (2002) Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecol.*. **27**, 110–120.

Holmes, P. M. (2008) Optimal ground preparation treatments for restoring lowland Sand Fynbos vegetation on old fields. *South African J. Bot.*. **74**, 33–40.

Holmes, P. M., Cowling, R. M. (1997a) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrubland. *J. Appl. Ecol.*. **34**, 317–332.

Holmes, P. M., Cowling, R. M. (1997b) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecol.*. **133**, 107–122.

Holmes, P. M., Pugnalin, A. (2016) *The Biodiversity Network for Cape Town. C-plan and Marxan Analysis: 2016 Methods & Results.*

Holmes, P. M., Richardson, D. M., Van Wilgen, B. W., Gelderblom, C. (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecol.*. **25**, 631–639.

Horn, A., Krug, C. B., Newton, I. P., Esler, K. J. (2011) Specific edge effects in highly endangered Swartland Shale Renosterveld in the Cape Region. *Ecol. Mediterr.*. **37**, 63–74.

Jeffery, D. J., Holmes, P. M., Rebelo, A. G. (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. *South African J. Bot.*. **54**, 28–34.

Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., Rundel, P. W. (2012) *Fire in Mediterranean Ecosystems*. Cambridge University Press, Cambridge.

Keeley, J. E., Morton, B. A., Pedrosa, A., Trotter, P. (1985) Role of Allelopathy, Heat and Charred Wood in the Germination of Chaparral Herbs and Suffrutescents. *J. Ecol.*. **73**, 445–458.

Kruger, F. J. (1983) Plant community diversity and dynamics in relation to fire. In: *Mediterranean-type ecosystems: the role of nutrients* (eds F. J. Kruger, D. T. Mitchell, & J. U. M. Jarvis) pp. 466–472 Springer-Verlag, Berlin.

Le Maitre, D. C., Gaertner, M., Marchante, E., Ens, E. J., Holmes, P. M., Pauchard, A., O'Farrell, P. J., Rogers, A. M., Blanchard, R., Blignaut, J., Richardson, D. M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Divers. Distrib.*. **17**, 1015–1029.

Le Maitre, D. C., Midgley, J. J. (1992) Plant reproductive ecology. In: *The ecology of Fynbos: nutrients, fire and diversity* (ed R. M. Cowling) pp. 135–174 Oxford University Press, Cape Town.

Morgan, J. (1999) Have tubestock plantings successfully established populations of rare grassland species into reintroduction sites in western Victoria? *Biol. Conserv.*. **89**, 235–243.

Mostert, E., Gaertner, M., Holmes, P. M., Rebelo, A. G., Richardson, D. M. (2017) Impacts of invasive alien trees on threatened lowland vegetation types in the Cape Floristic Region, South Africa. *South African J. Bot.*. **108**, 209–222.

Mukundamago, M. (2016) *Restoration of Cape Flats Sand Fynbos : The significance of pre-germination treatments and moisture regime.* Stellenbosch University.

Petersen, N., Husted, L., Rebelo, T., Holmes, P. M. (2007) Turning back the clock. *Veld Flora*. **93**, 102–103.

Padilla, F. M., Pugnaire, F. I. (2006) The role of nurse plants in the restoration of degraded environments. *Front. Ecol. Environ.*. **4**, 196–202.

Raimondo, D., von Staden, L., Foden, W., Victor, J. E., Helme, N. A., Turner, R. C., Kamundi, D. A., Manyama, P. A. (2009) *Red list of South African plants 2009.* South African National Biodiversity Institute, Pretoria.

Rebelo, A. G., Boucher, C., Helme, N., Mucina, L., Rutherford, M. C. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland.* (eds L. Mucina & M. C. Rutherford) pp. 52–219 South African National Biodiversity Institute, Pretoria.

Reyes, O., Trabaud, L. (2009) Germination behaviour of 14 Mediterranean species in relation to fire factors : smoke and heat. *Plant Ecol.*. **202**, 113–121.

Richardson, D. M., Carruthers, J., Hui, C., Impson, F. a. C., Miller, J. T., Robertson, M. P., Rouget, M., Le Roux, J. J., Wilson, J. R. U. (2011) Human-mediated introductions of Australian acacias - a global experiment in biogeography. *Divers. Distrib.*. **17**, 771–787.

Richardson, D. M., Van Wilgen, B. W. (1986) The effects of fire in felled *Hakea sericea* and natural fynbos and implications for weed control in mountain catchments. *South African For. J.*. **139**, 4–14.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B., Cowling, R. M. (2004) *South African National Spatial Biodiversity Assessment 2004: Technical report. Volume 1: terrestrial component.* Pretoria.

Rouget, M., Richardson, D. M., Cowling, R. M., Lloyd, J. W., Lombard, A. T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biol. Conserv.*. **112**, 63–85.

Rourke, J. P., Fairall, P., Snijman, D. A. (1981) William Frederick Purcell and the flora of Bergvliet. *South African J. Bot.*. **47**, 547–566.

SER, (Society for Ecological Restoration Science and Policy Working Group) (2002) *The SER primer on ecological restoration*.

Sharma, G. P., Muhl, S. A., Esler, K. J., Milton, S. J. (2010) Competitive interactions between the alien invasive annual grass *Avena fatua* and indigenous herbaceous plants in South African Renosterveld: the role of nitrogen enrichment. *Biol. Invasions*. **12**, 3371–3378.

Strydom, M., Veldtman, R., Ngwenya, M. Z., Esler, K. J. (2017) Invasive Australian Acacia seed banks: Size and relationship with stem diameter in the presence of gall-forming biological control agents. *PLoS One*. **12**, 1–16.

Suding, K. N., Hobbs, R. J. (2009) Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.*. **24**, 271–9.

Tieu, A., Dixon, K. W., Meney, K. A., Sivasithamparam, K. (2001) The Interaction of Heat and Smoke in the Release of Seed Dormancy in Seven Species from Southwestern Western Australia. *Ann. Bot.*. **88**, 259–265.

Vranjic, J. A., Morin, L., Reid, A. M., Groves, R. H. (2012) Integrating revegetation with management methods to rehabilitate coastal vegetation invaded by Bitou bush (*Chrysanthemoides monilifera ssp. rotundata*) in Australia. *Austral Ecol.*. **37**, 78–89.

Waller, P. A., Anderson, P. M. L., Holmes, P. M., Allsopp, N. (2016) Seedling recruitment responses to interventions in seed-based ecological restoration of Peninsula Shale Renosterveld, Cape Town. *South African J. Bot.*. **103**, 193–209.

Whisenant, S. G. (2002) Terrestrial Ecosystems. In: *Handbook of ecological restoration. Volume 1. Principles of restoration.* (eds M. R. Perrow & A. J. Davy) pp. 83–105 Cambridge University Press, New York.

Van Wilgen, B. W. (1982) Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. *J. Ecol.*. **70**, 217–225.

Van Wilgen, B. W. (2009) The evolution of fire and invasive alien plant management practices in fynbos. *S. Afr. J. Sci.*. **105**, 335–342.

Van Wilgen, B. W., Bond, W. J., Richardson, D. M. (1992) Ecosystem management. In: *The ecology of fynbos. Nutrients, fire and diversity* (ed R. M. Cowling) pp. 345–371 Oxford University Press, Cape Town.

Van Wilgen, B. W., Forsyth, G. G. (1992) Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In: *Fire in South African mountain fynbos.* (eds B. W. Van Wilgen, D. M. Richardson, F. J. Kruger, & J. J. Van Hensbergen) pp. 54–80 Springer-Verlag, Berlin.

Wotsitsa, M., Mgese, S. (2012) *Blaauwberg Nature Reserve land use history and current habitat condition assessment.* City of Cape Town Report.

Yelenik, S. G., Stock, W. D., Richardson, D. M. (2004) Ecosystem Level Impacts of Invasive *Acacia saligna* in the South African Fynbos. *Restor. Ecol.*. **12**, 44–51.

Chapter 2: Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type.

Hall, S. A., Newton, R. J., Holmes, P. M., Gaertner, M., Esler, K. J. (2016) Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type. *Austral Ecology*. **42**, 354–366.

2.1 Abstract

Invasive alien plants impact ecosystems, which often necessitates their removal. Where indigenous species recovery fails following removal alone, an active intervention involving reintroduction of seed of native species may be needed. This study investigated the potential for a combination of the fire cues of smoke and heat as a pre-treatment of seeds in breaking dormancy and facilitating increased germination. Species were selected to represent different functional types within Cape Flats Sand Fynbos; a fire-prone, critically endangered vegetation type in South Africa. Seeds were exposed to either a heat pulse (temperatures between 60°C and 300°C for durations of between 30 seconds and 20 minutes) or dry after-ripening (1 or 2 months at milder temperatures of 45°C or less). Thereafter, seeds were soaked in smoke solution for 18 hours and subsequently placed on agar at 10/20°C for germination. Most species fell into one of two main groups: Seed germination in the first group was greatest following a lower temperature (60°C) heat pulse, an extended period of mild temperature (20/40°C or 45°C) exposure, or no pre-treatment with heat. Seed germination in the second group was promoted after brief exposure to higher (100°C) temperatures. No germination occurred in any species following heat treatments of 150°C or higher. Species which responded better to higher temperatures were mainly those possessing physical dormancy, but seed morphology did not correlate with germination success. This study showed that heat-stimulation of seeds is more widespread in fynbos plant families than previously known and will enable the development of better seed pre-treatment protocols before large-scale sowing as an active restoration treatment after alien plant clearing.

Keywords

active restoration, Cape Flats Sand Fynbos, dry after-ripening, germination facilitation, heat pulse, seed dormancy.

2.2 Introduction

Invasive alien plants impact ecosystems (Richardson *et al*. 2000) by decreasing diversity and altering ecosystem functionality (Levine *et al*. 2003). Management interventions include preventing introductions, eradicating or controlling invasive species and mitigating their impacts (Wilson *et al.* 2011). Maintenance control following removal will likely be necessary for decades to prevent reinvasion (Pretorius *et al.* 2008). Alien species removal alone often fails to achieve a functional native ecosystem due to the lack of active intervention (Reid *et al*. 2009). In areas which have a long history of invasion, this may be due to native seed bank depletion (Holmes 2002). In such cases, the vegetation may recover if missing species are re-introduced (Pretorius *et al*. 2008). However, propagation of seedlings is costly, and an active restoration intervention using reseeding after alien clearing may fail to achieve successful re-establishment if seeds possessing dormancy do not receive appropriate dormancy-breaking cues. This becomes more important, but also more complicated to achieve, in highly biodiverse ecosystems such as the Cape Floristic Region.

The fynbos vegetation of the Cape Floristic Region, South Africa, is mainly characterised by a Mediterranean climate with winter rainfall and summer drought. This vegetation is dependent on periodic fire for regeneration (Kruger 1984), as most species produce seeds that lie dormant in the soil or are stored in the canopy until a fire. Many species are killed by fire and rely entirely on seed to re-establish while other species survive fire by resprouting (Van Wilgen and Forsyth 1992). Determining pre-sowing treatments that improve percentage germination can increase the establishment of mature plants, thus improving restoration success.

While germination success of many fynbos species increases greatly following exposure to smoke (Brown 1993), heat pulse is another fire-related cue that is important in stimulating certain species to germinate (Cocks and Stock 1997; Jeffery *et al*. 1988; Keeley and Bond 1997; Van de Venter and Esterhuizen 1988). Heat pulse stimulated seed germination has been studied in the Mediterranean region (Reyes and Trabaud 2009) as well as Californian chaparral (Keeley *et al*. 1985) and Australian Kwongan (Tieu 2001), but aside from the afore-mentioned studies, heat pulse stimulation has thus far received limited attention in the fynbos.

The majority of species in fire-prone ecosystems accumulate seeds in the soil, for which the most common mechanism for preventing germination is physical dormancy (Ooi *et al*. 2014). During the inter-fire period, vegetation insulates the seeds from temperature fluctuations, but after fire, exposed soil will experience higher fluctuations in temperature between day and night (Auld and Bradstock 1996). Some fynbos species respond better to widely alternating diurnal temperatures than a single heat pulse (Pierce and Moll 1994). Ooi et al. (2014) identified two groups of species with physical dormancy based on seeds stimulated by fire-induced high temperatures or by milder peak summer temperatures.

Increased biomass close to the soil surface following alien tree felling would result in an altered fire regime if a fire were to take place (Levine *et al.* 2003), resulting in increased fire temperature and duration. Fynbos seeds are potentially sensitive to hotter fires (Holmes *et al.* 2000; Blanchard and Holmes 2008), and in such cases increased seed mortality and an already depleted seed bank due to invasion (Holmes 2002) would negatively impact fynbos recovery. In the Cape, few studies have examined maximum temperature tolerance before seeds are killed (Cocks and Stock 1997; Jeffery *et al.* 1988). These studies focused on Fabaceae, where most species respond best to temperatures up to 100°C, or higher for a short duration. Fabaceae typically have a hard seed coat, and species with a soft coat may be less resilient to severe fires. Conversely, since many species are dependent on fire for regeneration it is important to understand their threshold temperatures for germination and mortality to determine if burning after alien tree felling is appropriate for existing soil-stored seed.

A restoration initiative at Blaauwberg Nature Reserve, Western Cape, South Africa aims to facilitate recovery of critically endangered Cape Flats Sand Fynbos following clearing of dense stands of invasive woody Australian acacias. The standard clearing practice involves clearing acacias followed by stacking and burning biomass, which does not appear to facilitate successful recovery in lowland fynbos. The restoration study investigated different clearing methods, one of which involved burning of felled acacia biomass to stimulate any fynbos seeds requiring fire to break dormancy and to reduce the acacia seed bank (Blanchard and Holmes 2008). However, the fuel load was denser and in closer proximity to the soil surface than in non-invaded fynbos and therefore would have burnt hotter and longer as a result (Holmes *et al.* 2000). This motivated the need for data on upper thermal tolerance limits for germination of fynbos species. Although slash and burn is specific to clearing of acacias, understanding seed dormancy is important for restoration in all habitats.

Owing to the *Acacia saligna* (Fabaceae) invasion, the fynbos seed bank appears to be depleted at the site (Holmes 2002). To mitigate this impact, seeds were sown *in situ* as an active restoration experiment immediately after a controlled burn. Many species showed poor germination success (Hall, unpublished data, 2015), which could be due to a lack of dormancy-breaking cues being applied before sowing. Some species only germinated in the second year after sowing, giving invasive plant species a competitive advantage as they can establish quickly after fire. Increasing germination rates and success of native species can increase competitive ability of sown seed, facilitating better resilience to secondary invasions.

This study focused on heat treatment as well as dry after-ripening of seeds, in combination with smoke, as a means of facilitating restoration of critically endangered Cape Flats Sand Fynbos following clearing of invasive alien acacia stands. We determined whether seeds of species within this vegetation type germinate better in response to exposure to selected temperatures and time durations before sowing. We included the invasive species *Acacia saligna* to provide a comparison in terms of invasive species response to heat pulse. We also investigated the maximum thermal tolerance before exposure becomes lethal to seeds. It is likely that response of seeds to heat treatment is affected by permeability to water (Stone and Juhren 1951) or seed morphology, such as seed coat thickness (Wright 1931) or overall seed size (Bond *et al*. 1999). These variables were therefore analysed to determine whether seed morphology or imbibing ability can predict likely response of seeds to heat treatment. The outcomes of this research will improve restoration protocols in fynbos and other fire-prone Mediterranean shrubland vegetation where active interventions are necessary following alien clearing.

2.3 Materials and Methods

2.3.1 Study site, species selection, seed collection and seed processing

Seeds were collected from Blaauwberg Nature Reserve, close to Melkbosstrand in South Africa (33.75°S, 18.48°E). Fourteen species were selected to represent a range of vegetation structural components, growth-forms and seed morphologies (Table 1). This was a similar selection to that sown *in situ*. Seeds were collected within Cape Flats Sand Fynbos vegetation between late 2013 and early 2014 while each species was producing seed. All seeds were collected fresh from the field, except alien *Acacia saligna* for which the seed was collected by sieving leaf litter under trees. Seeds were then stored under conditions of 15% RH and 15°C until germination experiments were conducted in June 2014.

In this study, the term "seed" refers both to true seeds and diaspores without easily detachable structures. The majority of species produce true seeds, while *Anthospermum aethiopicum* (Rubiaceae), *Pelargonium elongatum* (Geraniaceae), *Thamnochortus punctatus* (Restionaceae) and *Watsonia meriana* (Iridaceae) fall into the latter category.

Thamnochortus punctatus, Serruria fasciflora (Proteaceae), *Anthospermum aethiopicum* and *Passerina corymbosa* (Thymelaeaceae) seed collections were cleaned using a zig-zag seed aspirator (Zig-Zag type 1, Selecta Machinefabriek BV, Enkhuizen, The Netherlands) to eliminate lighter, partially filled or empty seeds. All other seed collections were visually inspected and cleaned manually.

Table 1. Species used in the study testing the effect of different temperatures and durations of exposure on seed germination. Estimated seed quality was determined by the percentage of filled seed from x-ray. Number of seeds sown was increased to compensate for empty seeds present in samples. Where too few seeds were available to sow an average of 25 viable seeds per replicate of each treatment, the number of seed per tray was scaled down to the amount available.

Family	**Genus**	**Species**	**Species code**	**Survival strategy**	**Growth form**	**Previous research on fire-cued germination**	**Date of seed collection**	**Seed quality estimate (% filled seeds)**	**Number of seeds per replicate**
Fabacaeae	*Acacia*	*saligna*	AS	seeder / resprouter	tree	Heat (Jeffery *et al.* 1988)	Mar-14	96	26
Rutaceae	*Agathosma*	*imbricata*	AI	resprouter	ericoid shrub		Dec-13	82	24
Rubiaceae	*Anthospermum*	*aethiopicum*	AA	seeder	ericoid shrub		Mar-14	42	50
Rutaceae	*Diosma*	*oppositifolia*	DO	resprouter	ericoid shrub		Dec-13	74	27
Ericaceae	*Erica*	*mammosa*	EM	resprouter	ericoid shrub		Mar-14	88	28
Aizoaceae	*Lampranthus*	*reptans*	LR	seeder	herbaceous perennial		Jan-14	70	25
Asteraceae	*Metalasia*	*densa*	MD	seeder	ericoid shrub	Smoke (Brown 1993)	Jul-13	90	28
Thymelaeaceae	*Passerina*	*corymbosa*	PCO	seeder	ericoid shrub	Multiple cues (Pierce and Moll 1994)	Dec-13	60	42
Geraniaceae	*Pelargonium*	*elongatum*	PE	seeder	herbaceous annual	Scarification (Kakihara and Hondo 2013)	Nov-13	96	26
Rhamnaceae	*Phylica*	*cephalantha*	PCE	resprouter	ericoid shrub	Acid scarification (Allsopp and Stock 1995)	Dec-13	60	42
Proteaceae	*Serruria*	*fasciflora*	SF	seeder	ericoid shrub		Dec-13	56	25
Restionaceae	*Thamnochortus*	*punctatus*	TP	seeder	graminoid shrub	Smoke (Brown 1993)	Jun-13	22	75
Rhamnaceae	*Trichocephalus*	*stipularis*	TS	resprouter	ericoid shrub		Dec-13	84	30
Iridaceae	*Watsonia*	*meriana*	WM	resprouter	geophyte		Dec-13	96	26

In order to ascertain seed fill of cleaned seeds as an initial method of estimating potential viability, one subsample of 50 seeds from each species was X-rayed using a Faxitron digital X-ray machine (Qados, Sandhurst, U.K.). During commissioning the X-ray machine was internally validated and the settings of 22 kV and 0.3 mA for 20 s identified as optimal for the wide range of seed types that are encountered during routine processing at the Millennium Seed Bank. As *Erica mammosa* (Ericaceae) seeds were too small to accurately interpret seed fill from X-ray, 50 seeds were dissected longitudinally to determine whether the embryo was visually healthy, apparent from a seed being plump and white on the inside, as opposed to a shrivelled or empty seed.

For each species, the percentage of full seeds from X-ray results was used to calculate the number of seeds to sow to obtain an estimated 25 full seeds per replicate, with the exception of some species for which this number was lower due to insufficient seed availability. Each treatment consisted of four replicates of between 24 and 75 seeds (Table 1).

2.3.2 Comparison of seed morphology and testing for seed coat dormancy

Six seeds from each species were bisected longitudinally under a Leica M125 microscope (Leica, Heerbrugg, Switzerland) and photographed using a DFC 320 Leica camera and Leica application suite 4.4.0 software to measure seed length and mean seed (or diaspore) coat thickness. Remaining seed quantities were limited; therefore the six seeds were randomly selected, representative of the population.

The permeability of the seed or fruit coat (hereafter for simplicity referred to as “seed coat”) was checked by imbibing two subsamples of between 6 and 20 seeds per species in water and weighing seeds daily until water uptake levelled off (Baskin and Baskin 2003). Prior to imbibition, the seed coat of the first subsample of seeds was pierced with a scalpel while that of the second subsample was left intact (Cook *et al.* 2008). This allowed for seed coat imposed dormancy to be tested within the selected species.

2.3.3 Experimental design for heat treatment study

Treatments were selected to simulate conditions under which seeds would be exposed during a range of potential fire intensities that have been recorded in fynbos (Kruger 1984), and incorporating temperatures and durations that stimulate fynbos species of Fabaceae (Cocks and Stock 1997; Jeffery *et al.* 1988). Two control treatments without heat were included, one with and one without smoke treatment. Heat treatment temperatures included 60°C (10 and 20 minutes), 100°C (2.5, 5 and 10 minutes), 150°C (1 and 5 minutes), 200°C (0.5 and 1 minute) and 300°C (0.5 minutes). Heat treatments were applied independently for each replicate, to avoid pseudoreplication (Morrison and Morris 2000). In addition to heat, seeds were also treated with smoke, as this more closely mimics natural conditions associated with a fire, and most species experience increased germination success, or at least no negative effect, from exposure to smoke (Brown *et al.* 2003). For ease of communication, the presence of a smoke pre-treatment is assumed to be part of all heat treatments hereafter.

Seed samples for each treatment were wrapped in aluminium foil. Heat pulse treatments involved preheating silver sand (Sporting Surface Supplies Ltd., Smallfield, UK) to the necessary temperature in an oven for at least two hours and then checking sand temperature using a 250mm Type K insulated stainless steel probe thermocouple attached to a Grant squirrel logger (Series 1200, Type 1203, Grant Instruments (Cambridge) Ltd, Shepreth, U.K.). Ovens were operated at a set temperature, with a maximum deviation of ± 2°C. The exception was the 300°C treatment, for which sand was instead heated over a Bunsen burner and a temperature probe was used to determine when the sand had reached the correct temperature. In this case there was higher variability in the temperature, but it was kept within a maximum deviation of 20°C. Samples were placed into the sand along with a temperature probe to record temperature for the given duration (Cocks and Stock 1997). After heat treatment exposure, seed samples were immediately removed from the sand and allowed to cool to ambient temperature, then removed from the foil package and placed into a plastic vial within a chamber of 100% humidity for 24 hours to allow seeds to imbibe. Thereafter, seeds were soaked in smoke solution (1:10 dilution of aqueous smoke extract with distilled water) for a further 18 hours, a modification of the method used by Brown (1993). Aqueous smoke extract was obtained using the method of De Lange and Boucher (1990), in which smoke from burnt fynbos plant biomass was bubbled through water to dissolve the active chemicals. For control treatments, samples were wrapped in foil but not placed in an oven before being removed from foil and imbibed. The smoke-treated control samples were placed in smoke solution as was done for heat experiments while the control without smoke samples were placed in the same volume of distilled water.

After soaking, seeds were removed and placed onto Petri dishes containing 1% agar gel, and kept in an incubator (LMS Ltd., Sevenoaks, UK) with lateral illumination by 30W cool white light. This was set at alternating temperature of 10/20°C and a 12 hour light and dark cycle, as alternating temperature is known to promote germination in fynbos species (Pierce and Moll 1994).

Petri dishes were monitored once every week after sowing. Seeds with a radicle of more than 2 mm in length were removed and recorded as germinated. When Petri dishes contained visible fungal contamination, seeds were removed, cleaned gently with tissue paper, and placed on fresh agar. Any seeds that had deteriorated when changing agar were discarded and recorded as dead.

Germination tests were terminated after 14 weeks if no germination occurred, once all seeds had germinated or if no further germination occurred for 4 weeks following a peak in germination. Remaining seeds were dissected with a scalpel to assess whether they were still fresh (and so assumed viable) or had deteriorated. This could indicate whether seeds did not germinate because of losing viability due to excessive heat exposure, or because dormancy had not been effectively broken. Viability of seeds following different experimental treatments was calculated by adding the number of seeds that germinated to those that were fresh on dissection for each replicate. Percent germination and viability were calculated in relation to total number of seeds sown per replicate.

3.2.4 Experimental design for the dry after-ripening experiment

A dry after-ripening (DAR) experiment exposed seeds to a temperature regime that would be expected in surface soil during summer and autumn conditions following removal of vegetation by fire (Auld and Bradstock 1996). A constant temperature of 45°C as well as an alternating temperature regime of 20/40°C was selected, both for four and eight weeks' duration in an incubator. Apart from the temperature and duration of exposure, all other conditions and treatments were the same as those described for the heat treatment experiment. For ease of communication, the presence of a smoke pre-treatment is assumed to be part of all DAR treatments hereafter.

2.3.5 Data analysis

After plotting raw residuals and confirming that data were normally distributed, a one-way ANOVA was used to determine which treatment and duration worked best for stimulating germination in each species and also how heat treatments impacted seed viability. Independence of observations was satisfied as all replicates were separate heat treatments (Morrison and Morris 2000). Levene's test showed that most species did not have homogenous variances, with the exception of *Diosma oppositifolia* (Rutaceae), *Erica mammosa* and *Serruria fasciflora*. A Fisher LSD post-hoc test was used for these three species, but for all other species a Games-Howell post-hoc test was more appropriate. Seed morphology data were analysed using an ANOVA to determine whether larger, heavier or thicker-coated seeds responded better to higher temperatures and longer durations of exposure than smaller, lighter and thinner-coated seeds. In all cases variance was not homogeneous, so a Games-Howell post-hoc test was used. The seed imbibition data were analysed between the two treatments using a t-test for independent variables.

Furthermore, a principal component analysis was performed to determine the relationship between temperature and duration of exposure in terms of the four replicates of germination success in each species.

2.4 Results

2.4.1 Potential seed quality

Percentage of filled seeds ranged from 96% to only 22% (Table 1). Only three species had less than 60% of seeds filled.

2.4.2 Comparison of heat treatments

Species showed a range of responses to treatments which could be explained by two main groups (Figure 1). One cluster of treatments included the four species *Agathosma imbricata* (Rutaceae)*, Anthospermum aethiopicum, Metalasia densa* (Asteraceae) and *Watsonia meriana*, which responded to the lower temperature (60°C), DAR, and control treatments. The second cluster of treatments included the six species that responded to higher temperature treatment (100°C). The species not represented in Figure 1 were not well explained by either of the principal components of temperature or duration of exposure.

2.4.3 Species not requiring germination cues

The control treatment (without smoke or heat) was statistically similar to all other treatments except 100°C for any duration for *Watsonia meriana* and 100°C for 10 minutes for *Agathosma imbricata* , while it resulted in intermediate germination success for *Serruria fasciflora.* All other species had lowest germination success in the control (Table 2).

2.4.4 Species responding to smoke without heat

Four species showed greatest germination response to smoke-treatment alone (Table 2). *Passerina corymbosa* appeared to respond best to the smoke without heat treatment, but this was not significantly different from other treatments based on the Games-Howell post-hoc test.

2.4.5 Species responding to smoke and heat pulse treatments

No germination was recorded for any species at temperatures of 150°C and above. Eight species showed greater germination success following one or more heat pulse treatments relative to the control (i.e. without heat or smoke); four of which also showed significantly greater germination compared with the smoke control (Table 2).

Phylica cephalantha (Rhamnaceae) had optimal germination under all heat pulse treatments up to 100°C, and also responded to three DAR treatments. *Acacia saligna, Pelargonium elongatum* and *Trichocephalus stipularis* (Rhamnaceae) performed better at 100°C than at 60°C, of which only *Trichocephalus stipularis* germinated equally well at all 100°C and the two month DAR treatments. *Lampranthus reptans* (Aizoaceae) appeared to respond best to 100°C for 10 minutes, but this was not significantly different to the other treatments due to high variability of results. No species were primarily stimulated by exposure to 60°C.

Six species experienced a negative effect on germination at one or more of the 100°C treatments, including three species which responded optimally to smoke without heat treatment. In *Diosma oppositifolia,* germination was reduced by all heat pulse treatments.

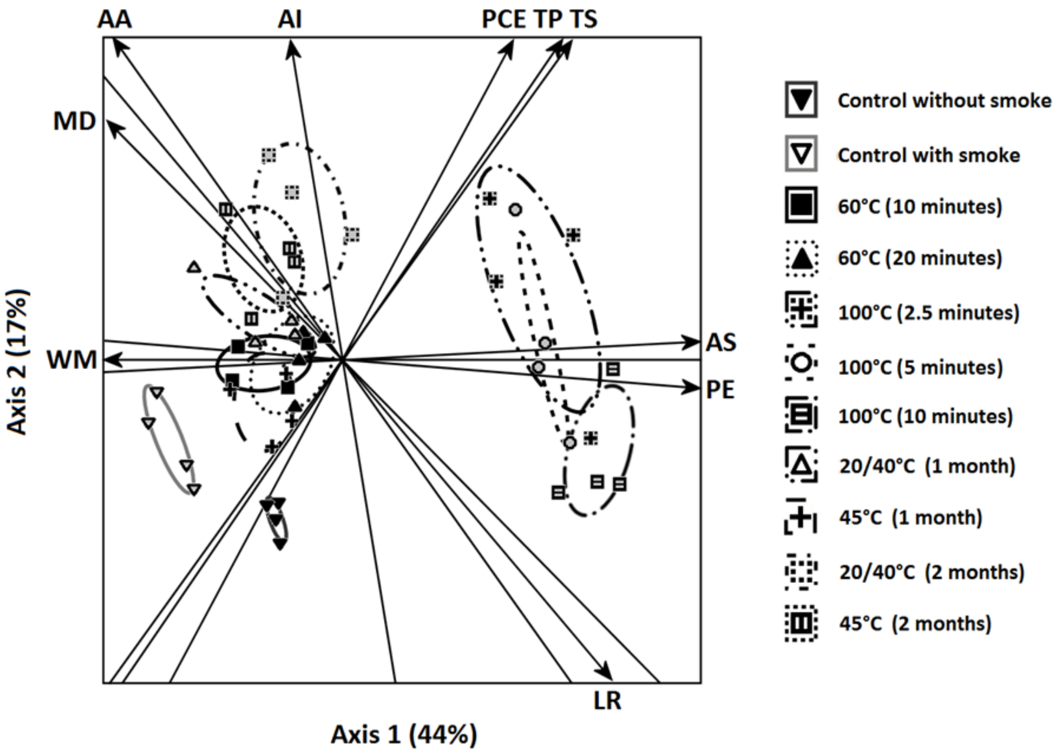


Figure 1. Species responses to treatments testing the effect of different temperatures and durations of exposure on seed germination, in terms of both heat pulse and long-term dry after-ripening treatment of seeds, as determined by principal component analysis of temperature on axis 1 and duration of exposure on axis 2. Only species with $R^2 > 0.5$ were represented on the graph. *Passerina corymbosa*, *Diosma oppositifolia* and *Erica mammosa* ($R^2 < 0.5$) were not well explained by either of the principal components, and did not show a strong response to any treatment combinations. AA – *Anthospermum aethiopicum*; AI – *Agathosma imbricata*; AS – *Acacia saligna*; LR – *Lampranthus reptans*; MD – *Metalasia densa*; PCE – *Phylica cephalantha*; PE – *Pelargonium elongatum*; TP – *Thamnochortus punctatus*; TS – *Trichocephalus stipularis*; WM – *Watsonia meriana*.

Table 2. Mean percentage germination and standard error values for each treatment testing the effect of different temperatures and durations of exposure on seed germination, using a one-way ANOVA. Statistical comparisons are between treatments and not between species. Values that are significantly different are indicated by different letters. Treatments not performed on *Serruria fasciflora* denoted by "NA". AA – *Anthospermum aethiopicum*; AI – *Agathosma imbricata*; AS – *Acacia saligna*; DO – *Diosma oppositifolia*; EM – *Erica mammosa*; LR – *Lampranthus reptans*; MD – *Metalasia densa*; PCE – *Phylica cephalantha*; PCO – *Passerina corymbosa*; PE – *Pelargonium elongatum*; SF – *Serruria fasciflora*; TP – *Thamnochortus punctatus*; TS – *Trichocephalus stipularis*; WM – *Watsonia meriana*.

Treatment temperature	**Treatment duration**	**Smoke treated**	**AA**	**AI**	**AS**	**DO**	**EM**	**LR**	**MD**	**PCE**	**PCO**	**PE**	**SF**	**TP**	**TS**	**WM**
Control	NA	no	21 ± 3.9^{bc}	21 ± 4.6^{abc}	1 ± 1.0^{c}	4 ± 1.5^{cb}	16 ± 2.5^{c}	1 ± 1.0	0 ± 0.0^{b}	2 ± 1.1^{c}	4 ± 1.2	16 ± 4.9^{bc}	16 ± 2.8^{b}	0 ± 0.0^{b}	0 ± 0.0^{c}	97 ± 1.7^{a}
Control	NA	yes	55 ± 5.9^{ab}	27 ± 3.2^{b}	2 ± 1.1^{c}	11 ± 2.3^{a}	24 ± 4.3^{cb}	1 ± 1.0	15 ± 4.0^{ab}	4 ± 1.6^{c}	19 ± 3.8	7 ± 2.0^{c}	28 ± 2.8^{a}	2 ± 1.3^{b}	4 ± 3.1^{bc}	100 ± 0.0^{a}
60^{0}C	10 minutes	yes	50 ± 4.1^{a}	26 ± 5.3^{abc}	32 ± 2.9^{b}	5 ± 1.8^{cb}	33 ± 7.1^{ab}	0 ± 0.0	14 ± 1.8^{a}	31 ± 2.9^{ab}	8 ± 2.1	23 ± 5.9^{bc}	27 ± 4.3^{a}	3 ± 1.3^{ab}	5 ± 2.7^{bc}	99 ± 0.9^{a}
60^{0}C	20 minutes	yes	50 ± 7.8^{abc}	27 ± 9.4^{abc}	36 ± 8.2^{bc}	2 ± 1.1^{c}	22 ± 8.2^{cb}	1 ± 1.0	19 ± 5.6^{ab}	33 ± 2.3^{a}	7 ± 1.7	27 ± 1.9^{b}	NA	3 ± 1.5^{ab}	10 ± 3.0^{bc}	96 ± 1.5^{a}
100^{0}C	2.5 minutes	yes	34 ± 13.5^{abc}	38 ± 10.6^{abc}	100 ± 0.0^{a}	4 ± 1.5^{cb}	24 ± 5.2^{cb}	4 ± 4.0	0 ± 0.0^{b}	36 ± 8.4^{abc}	0 ± 0.0	82 ± 3.4^{a}	NA	15 ± 3.2^{ab}	37 ± 8.1^{abc}	0 ± 0.0^{b}
100^{0}C	5 minutes	yes	17 ± 9.7^{abc}	32 ± 17.5^{abc}	100 ± 0.0^{a}	1 ± 1.1^{c}	16 ± 5.5^{c}	4 ± 2.8	0 ± 0.0^{b}	53 ± 6.6^{ab}	1 ± 0.6	62 ± 11.9^{abc}	4 ± 2.8^{c}	8 ± 2.0^{ab}	34 ± 2.1^{a}	0 ± 0.0^{b}
100^{0}C	10 minutes	yes	1 ± 0.9^{c}	0 ± 0.0^{c}	100 ± 0.0^{a}	0 ± 0.0^{c}	21 ± 3.6^{cb}	18 ± 6.0	0 ± 0.0^{b}	44 ± 7.0^{abc}	0 ± 0.0	72 ± 5.1^{a}	NA	12 ± 2.1^{ab}	26 ± 3.4^{a}	0 ± 0.0^{b}
$20/40^{0}$C	1 month	yes	47 ± 3.3^{a}	32 ± 3.1^{ab}	10 ± 3.3^{c}	11 ± 3.9^{a}	31 ± 5.4^{ab}	1 ± 1.0	11 ± 3.5^{ab}	33 ± 2.5^{a}	4 ± 1.1	3 ± 2.7^{c}	19 ± 3.0^{ab}	6 ± 2.0^{ab}	17 ± 1.5^{b}	97 ± 1.7^{a}
45^{0}C	1 month	yes	38 ± 6.1^{abc}	20 ± 6.0^{abc}	3 ± 1.8^{c}	9 ± 1.7^{ab}	26 ± 1.4^{ac}	4 ± 1.7	13 ± 4.3^{ab}	18 ± 1.5^{b}	4 ± 2.8	3 ± 2.0^{c}	27 ± 3.8^{a}	5 ± 1.3^{ab}	11 ± 2.1^{bc}	93 ± 2.5^{a}
$20/40^{0}$C	2 months	yes	47 ± 13.4^{abc}	45 ± 4.4^{ab}	13 ± 3.3^{bc}	4 ± 1.6^{cb}	39 ± 3.3^{a}	0 ± 0.0	24 ± 3.4^{a}	46 ± 5.7^{ab}	6 ± 2.9	2 ± 1.1^{c}	NA	13 ± 2.5^{ab}	32 ± 6.8^{abc}	97 ± 1.7^{a}
45^{0}C	2 months	yes	65 ± 8.7^{ab}	47 ± 2.9^{a}	1 ± 1.0^{c}	5 ± 1.8^{cb}	29 ± 3.3^{ac}	1 ± 1.0	23 ± 5.0^{ab}	33 ± 3.5^{ab}	9 ± 3.4	5 ± 2.2^{c}	NA	9 ± 0.8^{a}	20 ± 4.8^{abc}	99 ± 0.9^{a}

2.4.6 Species responding to smoke and dry after-ripening treatments

Erica mammosa experienced optimal germination under alternating temperature after 2 months exposure relative to control and higher temperature treatments while *Thamnochortus punctatus* experienced optimal germination under constant temperature after 2 months exposure relative to control treatments (Table 2). A further six species showed significantly greater germination for one or more of the DAR treatments compared with the control (without heat or smoke). Of these, *Phylica cephalantha* also showed significantly greater germination than the smoke control. Only two species showed a significant difference between treatments within the DAR experiment. *Diosma oppositifolia* had greatest germination in both one month DAR treatments (i.e. constant 45°C and alternating 20°C/40°C), while in *Phylica cephalantha* the only difference was within the one month treatment, with the alternating DAR temperature resulting in greater germination than constant DAR temperature. Only *Diosma oppositifolia* performed better in the DAR treatments than in any heat pulse treatments. However, only *Acacia saligna* and *Pelargonium elongatum* responded better to heat pulse treatments than the DAR experiment (both had highest germination at 100°C).

2.4.7 Estimated viable seed at the end of germination

Species generally exhibited high variability in seed viability in response to different treatments (Table 3). Four species had low overall viability (< 25%). Three species either germinated or died, as no fresh seeds remained in any treatment [i.e. viability (Table 3) was equal to germination (Table 2)], with the exception of 1% fresh *Erica mammosa* seeds in the 20 minute 60°C heat treatment. Of the remaining species, only two did not show a reduction in viability in any treatments compared with control (Table 3). No fresh seed remained in 100°C heat treatments in *Phylica cephalantha* (Table 2 *cf.* Table 3), and viability in these treatments was significantly reduced compared with all other treatments (Table 3). Similarly no fresh seeds remained in the 10 minute 100°C treatment for *Trichocephalus stipularis*, and fresh seeds were much reduced in the 2.5 and 5 minute 100°C treatments compared with all other treatments in this species (Table 2 *cf.* Table 3). No fresh seed remained in DAR or 100°C treatments in both *Agathosma imbricata* and *Serruria fasciflora* (Table 2 *cf.* Table 3), and almost all of these treatments showed significantly reduced viability (Table 3). *Passerina corymbosa* showed reduced viability in all treatments compared with the controls, except for the 2 month DAR treatments (Table 3), which exhibited greater, albeit not significant, germination than the 100°C treatments (Table 2).

Table 3. Mean percentage of viable seed remaining and standard error values at the end of the germination test for each treatment testing the effect of different temperatures and durations of exposure on seed germination, using a one-way ANOVA. Statistical comparisons are between treatments and not between species. Values that are significantly different are indicated by different letters. Treatments not performed on *Serruria fasciflora* denoted by "NA". AA – *Anthospermum aethiopicum*; AI – *Agathosma imbricata*; AS – *Acacia saligna*; DO – *Diosma oppositifolia*; EM – *Erica mammosa*; LR – *Lampranthus reptans*; MD – *Metalasia densa*; PCE – *Phylica cephalantha*; PCO – *Passerina corymbosa*; PE – *Pelargonium elongatum*; SF – *Serruria fasciflora*; TP – *Thamnochortus punctatus*; TS – *Trichocephalus stipularis*; WM – *Watsonia meriana*.

Treatment temperature	Treatment duration	Smoke treated	AA	AI	AS	DO	EM	LR	MD	PCE	PCO	PE	SF	TP	TS	WM
Control	NA	no	21 ± 3.9^{bc}	72 ± 2.6^{a}	88 ± 4.5	4 ± 1.5^{cd}	16 ± 2.5^{c}	1 ± 1.0	12 ± 2.1^{ab}	77 ± 3.7^{bc}	24 ± 1.7^{a}	88 ± 1.6^{b}	71 ± 3.5^{a}	0 ± 0.0^{b}	76 ± 3.5^{cd}	97 ± 1.7^{a}
Control	NA	yes	55 ± 5.9^{ab}	27 ± 3.4^{d}	92 ± 2.7	24 ± 2.5^{a}	24 ± 4.3^{ac}	1 ± 1.0	15 ± 4.0^{ab}	80 ± 2.7^{ac}	56 ± 7.9^{ab}	92 ± 2.7^{ab}	49 ± 10.0^{b}	2 ± 1.3^{b}	91 ± 2.5^{ab}	100 ± 0.0^{a}
60°C	10 minutes	yes	50 ± 4.1^{a}	88 ± 7.5^{ab}	94 ± 2.5	5 ± 1.8^{cd}	33 ± 7.1^{ab}	0 ± 0.0	14 ± 1.8^{a}	87 ± 2.1^{ab}	8 ± 2.1^{bc}	81 ± 8.5^{ab}	35 ± 6.8^{bc}	3 ± 1.3^{b}	83 ± 4.0^{bc}	99 ± 0.9^{a}
60°C	20 minutes	yes	50 ± 7.8^{abc}	72 ± 5.5^{ab}	93 ± 3.3	2 ± 1.1^{d}	23 ± 9.0^{bc}	1 ± 1.0	19 ± 5.6^{ab}	88 ± 1.1^{ab}	7 ± 1.7^{bc}	83 ± 10.9^{ab}	NA	3 ± 1.5^{b}	86 ± 3.0^{bc}	96 ± 1.5^{a}
100°C	2.5 minutes	yes	34 ± 13.5^{abc}	38 ± 10.6^{abde}	100 ± 0.0	4 ± 1.5^{cd}	24 ± 5.2^{ac}	4 ± 4.0	0 ± 0.0^{b}	36 ± 8.4^{e}	0 ± 0.0^{c}	82 ± 3.4^{ab}	NA	15 ± 3.2^{ab}	58 ± 4.4^{e}	0 ± 0.0^{b}
100°C	5 minutes	yes	17 ± 9.7^{abc}	32 ± 17.5^{abde}	100 ± 0.0	1 ± 1.1^{d}	16 ± 5.5^{c}	4 ± 2.8	0 ± 0.0^{b}	53 ± 6.6^{d}	1 ± 0.6^{c}	62 ± 11.9^{ab}	4 ± 2.8^{d}	8 ± 2.0^{ab}	46 ± 6.0^{f}	0 ± 0.0^{b}
100°C	10 minutes	yes	1 ± 0.9^{c}	0 ± 0.0^{e}	100 ± 0.0	0 ± 0.0^{d}	21 ± 3.6^{bc}	18 ± 6.0	0 ± 0.0^{b}	44 ± 7.0^{de}	0 ± 0.0^{c}	72 ± 5.1^{ab}	NA	12 ± 2.1^{ab}	26 ± 3.4^{g}	0 ± 0.0^{b}
20/40°C	1 month	yes	47 ± 3.3^{a}	32 ± 3.1^{cd}	98 ± 1.1	11 ± 3.9^{b}	31 ± 5.4^{ab}	1 ± 1.0	11 ± 3.5^{ab}	84 ± 3.8^{ac}	4 ± 1.1^{bc}	97 ± 2.7^{ab}	19 ± 3.0^{cd}	6 ± 2.0^{ab}	99 ± 0.8^{a}	97 ± 1.7^{a}
45°C	1 month	yes	38 ± 6.1^{abc}	20 ± 6.0^{cde}	96 ± 2.7	9 ± 1.7^{bc}	26 ± 1.4^{ac}	4 ± 1.7	13 ± 4.3^{ab}	91 ± 2.5^{a}	4 ± 2.8^{c}	100 ± 0.0^{a}	27 ± 3.8^{c}	5 ± 1.3^{b}	99 ± 0.8^{a}	93 ± 2.5^{a}
20/40°C	2 months	yes	47 ± 13.4^{abc}	45 ± 4.4^{bd}	97 ± 1.0	4 ± 1.6^{cd}	39 ± 3.3^{a}	17 ± 3.4	24 ± 3.4^{a}	71 ± 4.1^{c}	10 ± 4.3^{abc}	92 ± 4.3^{ab}	NA	22 ± 2.7^{a}	67 ± 4.5^{de}	97 ± 1.7^{a}
45°C	2 months	yes	65 ± 8.7^{ab}	47 ± 2.9^{bc}	100 ± 0,0	5 ± 1.8^{cd}	29 ± 3.3^{ac}	5 ± 1.0	23 ± 5.0^{ab}	90 ± 3.8^{ab}	10 ± 4.1^{abc}	88 ± 5.9^{ab}	NA	15 ± 1.2^{a}	80 ± 5.3^{bc}	99 ± 0.9^{a}

2.4.8 Seed morphology and dormancy

Five species had large seeds, as determined by seed length (Table 4). *Diosma oppositifolia* and *Trichocephalus stipularis* had very thick seed coats, the latter also having the heaviest seeds. While no species had highest values for all three seed morphology measurements, *Acacia saligna, Diosma oppositifolia, Phylica cephalantha* and *Trichocephalus stipularis* were close to the highest values for each category. *Erica mammosa* and *Lampranthus reptans* had the smallest seeds, five species had equally thin seed coats, while *Erica mammosa* and *Metalasia densa* had the lightest seeds. Although no species fell into the lowest of all three measures, *Erica mammosa*, *Lampranthus reptans, Metalasia densa* and *Thamnochortus punctatus* were close to the lowest values in each category. The remaining six species were mostly intermediate in each category.

Five species were found to possess physical dormancy as determined by seeds imbibing significantly more water when pierced than when not (Table 4). These species also benefited from 100°C temperature treatments. Species with dormant seeds also had far greater viable seed than germinated seed in the control treatment, except for *Lampranthus reptans*. In *Watsonia meriana* and *Anthospermum aethiopicum* germination occurred in pierced and unpierced seed while in *Lampranthus reptans,* as with *Acacia saligna* and *Pelargonium elongatum*, germination occurred only in pierced seed after imbibition.

2.5 Discussion

The germination behaviour of the species in this study comprised two main categories, as determined by Ooi et al. (2014) – those which germinated best following 100°C temperature treatment and those which did not. Within the latter category, species could be further divided into those benefiting from smoke and those either having an intermediate response or else equally poor response to all treatments. However, while patterns were found within these categories, species exhibited a broad range of responses, with no two species having the same response across all treatments.

2.5.1 Species with heat and smoke-stimulated seed germination

Many species in fire-prone ecosystems accumulate seeds in the soil which have impermeable seed coats that are disrupted by the heat of a fire, thus triggering germination (Keeley and Fotheringham 2000). The four most strongly heat-stimulated species in this study all exhibited physical dormancy. *Acacia saligna* and *Pelargonium elongatum* seeds did not respond to DAR treatments, showing that they are dependent on a relatively high (100°C) temperature heat pulse for germination. *Acacia*

Table 4. Three seed morphology measurements (seed length, seed coat thickness and seed weight) analyzed using a one-way ANOVA, and seed mass increase following imbibition to test for physical dormancy with standard error values for all study species, analyzed using a t-test for independent variables. Statistical comparisons are between species and not between measurement variables for morphology variables, whereas seed mass increase is compared between cut and uncut seed coat. Species that are significantly different are indicated by different letters. AA – *Anthospermum aethiopicum*; AI – *Agathosma imbricata*; AS – *Acacia saligna*; DO – *Diosma oppositifolia*; EM – *Erica mammosa*; LR – *Lampranthus reptans*; MD – *Metalasia densa*; PCE – *Phylica cephalantha*; PCO – *Passerina corymbosa*; PE – *Pelargonium elongatum*; SF – *Serruria fasciflora*; TP – *Thamnochortus punctatus*; TS – *Trichocephalus stipularis*; WM – *Watsonia meriana*.

Measurements	AA	AI	AS	DO	EM	LR	MD	PCE	PCO	PE	SF	TP	TS	WM
Seed length (mm)	3.4 ±0.07^{c}	2.7 ±0.05^{d}	5.0 ±0.08^{b}	5.8 ±0.07^{a}	1.0 ±0.06^{f}	12 ±0.05^{f}	1.7 ±0.08^{e}	5.3 ±0.08^{a}	2.8 ±0.07^{d}	5.2 ±0.13^{ab}	5.8 ±0.25^{ab}	2.1± 0.05^{e}	4.2 ±0.19^{bc}	110 ± 106^{abc}
Seed coat thickness (μm)	42.3 ±3.68^{ghf}	68.7 ±0.71^{e}	142.2 ±3.64^{b}	191.2 ± 130^{a}	39.5 ±2.32^{g}	27.0 ±1.34^{h}	33.8 ±0.60^{gh}	148.2 ±4.09^{b}	103.8 ±3.13^{cd}	73.3 ±10.85^{cegh}	113.3 ±4.15^{c}	44.5 ±3.85^{ghf}	211.0 ±7.58^{a}	75.2 ±6.64^{edf}
Seed weight (mg)	12 ±0.09^{g}	2.9 ±0.12^{f}	14.9 ±0.40^{b}	14.1±0.35^{b}	0.2 ±0.04^{j}	0.4 ±0.01	0.5 ±0.07^{ijh}	11.7 ±0.75^{bc}	3.4 ±0.26^{ef}	4.2 ±0.11^{e}	6.2 ±0.29^{d}	0.8 ±0.04^{gh}	19.6 ±0.29^{a}	9.0 ±0.13^{c}
Maximum increase in seed mass after imbibition (%)	78.3 ±70.4^{b}	20.2 ±2.3^{b}	0.4 ±0.6^{a}	50.5 ±16.4^{b}	40.9^{b}	11.1^{a}	26.9 ±2.3^{b}	43.2 ±47.4^{a}	21.5 ±10.9^{b}	25.7 ±2.8^{b}	53.2 ±13.5^{b}	40 ±2.2^{b}	1.3 ±1.1^{a}	97.8 ±11.2^{b}
Maximum increase in seed mass after seed coat cut and imbibition (%)	82.2 ±21.8^{b}	26.3 ±5.9^{b}	142.4 ±7.0^{b}	32.0 ±8.9^{a}	36.0^{b}	41.9^{b}	28.6 ±2.6^{b}	83.9 ±57.8^{b}	18.3 ±23.1^{b}	99.4 ±0.1^{a}	48.9 ±8.1^{b}	46 ±4.6^{b}	109.8±24.1^{b}	126.8±22.3^{b}

saligna seeds are known to germinate *en masse* after fire (Richardson and Kluge 2008). *Pelargonium elongatum* seeds also germinated in large quantities after the Blaauwberg Nature Reserve burn (personal observation; Hall, 2013). The latter is a fire ephemeral species: it germinates, matures and flowers within seven months after fire (Marais 2012).

Species within the family Rhamnaceae are known to produce seeds in which germination is stimulated by heat in both South Africa and California (Keeley and Bond 1997). Seeds of *Phylica cephalantha* and *Trichocephalus stipularis* germinated after a heat pulse, and also responded well following longer duration DAR treatments. As has been found for *Phylica pubescens* (Witt and Giliomee 2004), these species possess an elaiosome (a fleshy structure attached to the seeds that often attracts ants) and so are presumably buried by ants at a depth at which seeds are stimulated to germinate (Cowling *et al.* 1994), rather than being killed by the heat of a passing fire. Since these species resprout and can set seed shortly after a fire, similar to *Phylica spicata* (Marais 2012), exposure of seed in bare soil to increased summer temperatures could also facilitate germination before substantial vegetation regrowth.

Germination in *Thamnochortus punctatus* seeds was marginally greater following heat and DAR treatments. Seed germination shortly after fire would allow for rapid growth to maturity (Van Wilgen and Forsyth 1992) where seed is present in the soil. Alternatively, seed dispersed by wind (Brown *et al.* 1994) from adjacent unburnt vegetation into recently burnt areas, followed by extended periods of increased soil temperatures, could stimulate germination before the site is colonised by other plants.

Seeds of *Erica mammosa* were not negatively affected by exposure to higher temperatures (100°C) relative to the control, but were stimulated by the DAR treatments. This is partly supported by observations of *E. sessiliflora* seeds, which were not negatively affected by exposure to 96.5°C (Van de Venter and Esterhuizen 1988).

2.5.2 Species with smoke-stimulated seed germination

As expected, seeds of none of the species stimulated by smoke alone possessed physical dormancy. Since *Serruria fasciflora* and *Diosma oppositifolia* both possess an elaiosome (personal observation; Hall, 2014) and thus appear to exhibit myrmecochory (Cowling *et al*. 1994), seed of these species would likely be buried deep enough to escape a high heat pulse during a fire, yet would still be exposed to smoke residue in the soil as well as alternating temperatures of the exposed post-burn soil, resembling the DAR treatment (Auld and Bradstock 1996). *Anthospermum aethiopicum* and

Metalasia densa were primarily stimulated by smoke, and therefore would probably rely on patches of less intense fire or areas near the edge of a burn in order for populations to re-establish.

2.5.3 Species requiring neither heat nor smoke for seed germination

Seeds of some fynbos species are opportunistic and germinate during a long inter-fire interval when some plants may become senescent, thereby opening up the shrub canopy (Van Wilgen and Forsyth 1992). Opportunistic species such as *Passerina corymbosa* can become dominant in such cases (Rebelo *et al*. 2011). Seeds of *Watsonia meriana*, as with geophytes in general, did not require heat or smoke for germination. Instead, this species flowers and seeds during the first few years after fire (Le Maitre and Brown 1992). Smoke may stimulate flowering in this species, rather than seed germination, as has been found for *Watsonia borbonica* (Light *et al.* 2007), and is common in other Mediterranean-climate geophytes (Lamont and Downes 2011). *Agathosma imbricata* is a resprouting species, which can flower shortly after fire and is able to germinate and establish in the absence of fire (personal observation; Hall, 2015).

Although the succulent *Lampranthus reptans* showed low germination in all treatments, seeds were of reasonably high quality, as 70% were filled. However, this species does possess physical dormancy, as most of the pierced seeds were found to germinate within a few days while unpierced seeds did not. As high and alternating temperatures did not promote germination, but physical disruption of the seed coat did, it is possible that scarification by sand or a slow degradation of the fruit coat will break physical dormancy in this species, resulting in seed germination being spread out over time.

2.5.4 Dormancy and seed bank persistence

Seed morphology has been found to influence potential for seeds to exhibit dormancy (Keeley and Fotheringham 2000). However, physical dormancy was found not only for seeds with a thick seed coat or larger seeds (e.g. *Lampranthus reptans* has small seeds with thin coats, while *Diosma oppositifolia* does not possess physical dormancy in spite of a thick seed coat). Apart from these exceptions, the general trend followed that larger or thicker-coated seeds possessed physical dormancy and responded better to heat treatment.

Almost complete germination in the control (without smoke) occurred in *Watsonia meriana*, suggesting that this species is unlikely to form a persistent soil seed bank (Le Maitre and Brown 1992). In addition, a further five species showed limited germination (i.e. >15%), suggesting that sporadic recruitment may occur in these species during favourable conditions for germination. Seeds of species such as *Acacia saligna* possess physical dormancy which requires a heat pulse to break the seed coat. Seeds of this species should persist in the soil seed bank until the next fire event (Richardson and Kluge 2008), with important implications for management of this invasive species.

2.5.5 Maximum temperature threshold

Cocks and Stock (1997) found optimal germination of fynbos legume species to be between 80°C and 100°C, while highest mortality occurred at longer durations of 100°C exposure and 120°C. Similar trends were found by Auld and O'Connell (1991), while Reyes and Trabaud (2009) determined that exposure to 150°C is lethal to seeds.

In our study a number of species' seeds were negatively affected by exposure to 100°C. These species however possess adaptations to survive high temperatures. Resprouting species are not entirely dependent on seed surviving fire (Van Wilgen and Forsyth 1992), while non-sprouting species are more vulnerable in terms of regeneration ability. *Passerina* produces large amounts of seed (Pierce and Cowling 1991), which could counteract high seed mortality. *Metalasia* has a high dispersal ability (Pierce and Moll 1994), which combined with high seed production could facilitate recolonization after a hot fire. Seeds of the myrmecochorous species *Serruria, Phylica, Trichocephalus,* and *Diosma* would be buried in the soil by ants (Slingsby and Bond 1983). This would prevent exposure to a more intense heat pulse during a fire, and being larger seeds they could still germinate from greater depths (Bond *et al.* 1999).

Germination success would be negatively affected by increased fuel load due to alien biomass, as this can lead to an increased severity of the heat pulse during a fire (Holmes 1989), resulting in increased temperature to a greater depth and for a longer duration.

The fact that even 150°C for 1 minute killed all the seed in our study suggests that even the most heat tolerant seeds close to the soil surface would likely have been destroyed by burning acacia slash (Holmes 1989). *Acacia saligna*, one of the most heat-tolerant species in the study, mostly germinated from deeper in the soil following a prescribed burn at Blaauwberg Nature Reserve in April 2013, with a mean minimum depth of 10.5 mm (K. Merrett, pers. com.). Seeds above this depth must have been exposed to temperatures greater than 100°C since this species was killed by higher temperatures tested in our study. This agrees with the finding by Auld (1986) that some seeds of the Australian species *Acacia sauveolens* were killed within 10 mm of the soil surface in a simulated hot fire. Less heat-tolerant species were likely destroyed to greater depths in the soil. Since larger seeds can germinate from greater depths than small seeds, the latter may have been too deep to germinate (Bond *et al.* 1999).

2.5.6 Explanations for lower than expected germination

Even the best performing treatment still gave lower germination success than estimated viability for the majority of species tested. This could be due to seeds not receiving the right pre-treatment or combination of treatments to break dormancy, such as moisture combined with heat (Martin *et al*. 1975), desiccation (Brits *et al*. 1993), or acid scarification (Baker *et al*. 2005). Soil storage may also be important prior to heat and smoke treatment (Newton *et al*. 2006), or a longer period of drying before trying to germinate seeds (Bewley and Black 1994) since germination tests were set up within a year of seed collection and DAR experiments were a maximum of only two months in duration.

Alternatively, lower than expected germination success could indicate a bet-hedging strategy – not all seeds germinate in response to a single stimulus (Keeley 1991; Letnic *et al*. 2000). This would increase chances of population persistence, as a dry winter in the first season after fire decreases chances of seedling establishment (Mustart *et al*. 2012). If part of the seed bank is not stimulated by the heat pulse of the fire, but rather the extended period of alternating temperatures of the following summer before a more favourable winter, this would help to spread the risk involved in seedling establishment. For *Watsonia meriana* and *Acacia saligna*, where all seeds germinated under certain tested treatments (Table 2), corms and vigorous resprouting ability, respectively, mean that these species are less reliant on seeds to persist (Van Wilgen and Forsyth 1992) if seedlings fail to establish in any given year.

2.5.7 Conclusions and implications for practice

Seeds which respond well to heat and smoke treatment or that maintain viability at higher temperatures and longer durations of exposure are not necessarily seeds with a thicker seed coat, or larger in size. Dormancy appears to be linked to seed coat thickness, but not in all cases.

The species for which heat treatment is detrimental (i.e. seeds are killed) would likely lose seeds from their seed bank when a fire goes through the area; non-sprouting species compensate for this loss by producing large numbers of seeds. Resprouting species are less reliant on seeds surviving fire as they can flower and set seed shortly after fire.

Previous fynbos heat studies involved species mostly within the Fabaceae (Cocks and Stock 1997; Jeffery *et al.* 1988). This study showed that species from genera in other families (*Trichocephalus* within Rhamnaceae and *Pelargonium* within Geraniaceae) also respond to heat and smoke treatment, which was not previously proven within the fynbos. This provides further evidence to support heat-stimulated seeds being specific to certain plant families i.e. Fabaceae, Geraniaceae, Rhamnaceae, across different regions of the world (Keeley and Bond 1997). Other species, whose seeds contribute to the soil seed bank for which a heat pulse with smoke does not stimulate germination, respond to other dormancy-breaking cues associated directly (smoke) or indirectly (high alternating temperatures) with fire.

Vigorous germination of *Acacia saligna* after a higher heat-pulse highlights the importance of considering the effect of fire and invasive species on native plant species. An altered fire regime, due to additional alien biomass, will also affect which species germinate post-fire; thus alien clearing and biomass removal prior to fire could be beneficial to restoration. Acacias are invasive in different regions of the world where they impact on fire regimes and therefore native vegetation (Le Maitre *et al.* 2011). The effect on indigenous seed banks and establishment success of alien species invading natural habitats is likely an underappreciated impact in many parts of the world.

Heat and smoke treatment can be a useful means of increasing germination success, thereby improving restoration effectiveness for relatively little extra effort involved. Heat and/or smoke treatments would need to be optimised for individual species before sowing trials in the field.

2.6 Acknowledgements

This research was undertaken with financial support from the Arcadia Fund and the Bentham Moxon Trust, as well as the DST-NRF Centre of Excellence for Invasion Biology and Working for Water Programme through their collaborative research project on “Integrated Management of invasive alien species in South Africa”. Seed collection and sorting was assisted by volunteers and staff of City of Cape Town Biodiversity Management Branch. Thanks to Beatrice Dewenter and Pablo Gómez for assistance with setting up heat-treatment experiments, Pablo Gómez for monitoring germination and John Adams for laboratory support. The two anonymous reviewers are thanked for their constructive comments which substantially improved the manuscript.

2.7 References

Allsopp, N., Stock, W. D. (1995) Relationships between Seed Reserves, Seedling Growth and Mycorrhizal Responses in 14 Related Shrubs (Rosidae) from a Low-Nutrient Environment. *Br. Ecol. Soc.*. **9**, 248–254.

Auld, T. D. (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Fire and the transition to seedlings. *Austral Ecol.*. **11**, 373–385.

Auld, T. D., Bradstock, R. A. (1996) Soil temperatures after the passage of a fire: Do they influence the germination of buried seeds? *Aust. J. Ecol.*. **21**, 106–109.

Auld, T. D., O’Connell, M. A. (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Austral Ecol.*. **16**, 53–70.

Baker, K. S., Steadman, K. J., Plummer, J. A., Dixon, K. W. (2005) Seed dormancy and germination responses of nine Australian fire ephemerals. *Plant Soil*. **277**, 345–358.

Baskin, C. C., Baskin, J. M. (2003) When Breaking Seed Dormancy is a Problem. *Nativ. Plants*, 17–21.

Bewley, J. D., Black, M. (1994) *Seeds: Physiology of Development and Germination, Second edition.* Plenum Press, New York.

Blanchard, R., Holmes, P. M. (2008) Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. *South African J. Bot.*. **74**, 421–431.

Bond, W. J., Honig, M., Maze, K. E. (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia*. **120**, 132–136.

Brits, G. J., Calitz, F. J., Brown, N. A. C., Manning, J. C. (1993) Desiccation as the active principle in heat-stimulated seed germination of *Leucospermum* R. Br. (Proteaceae) in fynbos*. *New Phytol.*. **125**, 397–403.

Brown, N. A. C. (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytol.*. **123**, 575–83.

Brown, N. A. C., Jamieson, H., Botha, P. A. (1994) Stimulation of seed germination in South African species of Restionaceae by plant-derived smoke. *Plant Growth Regul.*. **15**, 93–100.

Brown, N. A. C., Van Staden, J., Daws, M. I., Johnson, T. (2003) Patterns in the seed germination response to smoke in plants from the Cape Floristic Region , South Africa. . **69**, 514–525.

Cocks, M. P., Stock, W. D. (1997) Heat stimulated germination in relation to seed characteristics in fynbos legumes of the Western Cape Province, South Africa. *South African J. Bot.*. **63**, 129–132.

Cook, A., Turner, S. R., Baskin, J. M., Baskin, C. C., Steadman, K. J., Dixon, K. W. (2008) Occurrence of physical dormancy in seeds of Australian Sapindaceae: a survey of 14 species in nine genera. *Ann. Bot.*. **101**, 1349–1362.

Cowling, R. M., Pierce, S. M., Stock, W. D., Cocks, M. (1994) Why are there so many myrmecochorous species in the Cape fynbos? In: *Plant-animal interactions in Mediterranean-type ecosystems* pp. 159–168 Springer Netherlands.

Holmes, P. M. (1989) Effects of different clearing treatments on the seed-bank dynamics of an invasive Australian shrub, *Acacia cyclops*, in the Southwestern Cape, South Africa. *For. Ecol. Manage.*. **28**, 33–46.

Holmes, P. M. (2002) Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecol.*. **27**, 110–120.

Holmes, P. M., Richardson, D. M., Van Wilgen, B. W., Gelderblom, C. (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecol.*. **25**, 631–639.

Jeffery, D. J., Holmes, P. M., Rebelo, A. G. (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. *South African J. Bot.*. **54**, 28–34.

Kakihara, F., Hondo, K. (2013) Effect of Treatment with Concentrated Sulfuric Acid and a Homogenizer, and Temperature at Germination and Storage on Seed Germination in Eight Pelargonium Species. *Environ. Control Biol.*. **51**, 71–77.

Keeley, J. E. (1991) Seed Germination and Life History Syndromes in the California Chaparral. *Bot. Rev.*. **57**, 81–116.

Keeley, J. E., Bond, W. J. (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecol.*. **133**, 153–167.

Keeley, J. E., Fotheringham, C. J. (2000) Role of Fire in Regeneration from Seed. In: *Seeds: The Ecology of Regeneration of Plant Communities* (ed M. Fenner) pp. 311–330

Keeley, J. E., Morton, B. A., Pedrosa, A., Trotter, P. (1985) Role of Allelopathy, Heat and Charred Wood in the Germination of Chaparral Herbs and Suffrutescents. *J. Ecol.*. **73**, 445–458.

Kruger, F. J. (1984) Fire in fynbos. In: *Ecological Effects of Fire in South African Ecosystems, Ecological Studies* (eds P. de V. Booysen & N. M. Tainton) pp. 68–114 Springer-Verlag, Berlin.

Lamont, B. B., Downes, K. S. (2011) Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecol.*. **212**, 2111–2125.

De Lange, J. H., Boucher, C. (1990) Autecological studies on *Audouinia capitata* (Bruniaceae). I. Plant-derived smoke as a seed germination cue. *South African J. Bot.*. **56**, 700–703.

Letnic, M., Dickman, C. R., McNaught, G. (2000) Bet-hedging and germination in the Australian arid zone shrub *Acacia ligulata*. *Austral Ecol.*. **25**, 368–374.

Levine, J. M., Vilà, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. Biol. Sci.*. **270**, 775–781.

Light, M. E., Kulkarni, M. G., Ascough, G. D., Van Staden, J. (2007) Improved flowering of a South African *Watsonia* with smoke treatments. *South African J. Bot.*. **73**, 298.

Le Maitre, D. C., Brown, P. J. (1992) Life cycles and fire-stimulated flowering in geophytes. In: *Fire in South African mountain fynbos* (eds B. W. van Wilgen, D. M. Richardson, F. J. Kruger, & H. J. van Hensbergen) pp. 145–160 Springer-Verlag, Berlin.

Le Maitre, D. C., Gaertner, M., Marchante, E., Ens, E. J., Holmes, P. M., Pauchard, A., O'Farrell, P. J., Rogers, A. M., Blanchard, R., Blignaut, J., Richardson, D. M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Divers. Distrib.*. **17**, 1015–1029.

Marais, K. E. (2012) Postfire regeneration of mountain fynbos by resprouting : a comparison of species with different life history types (Masters dissertation, Stellenbosch: Stellenbosch University).

Martin, R. E., Miller, R. L., Cushwa, C. T. (1975) Germination Response of Legume Seeds Subjected to Moist and Dry Heat. *Ecology*. **56**, 1441–1445.

Morrison, D. A., Morris, E. C. (2000) Pseudoreplication in experimental designs for the manipulation of seed germination treatments. *Austral Ecol.*. **25**, 292–296.

Mustart, P. J., Rebelo, A. G., Juritz, J., Cowling, R. M. (2012) Wide variation in post-emergence desiccation tolerance of seedlings of fynbos proteoid shrubs. *South African J. Bot.*. **80**, 110–117.

Newton, R. J., Bond, W. J., Farrant, J. M. (2006) Effects of seed storage and fire on germination in the nut-fruited Restionaceae species, *Cannomois virgata*. *South African J. Bot.*. **72**, 177–180.

Ooi, M. K. J., Denham, A. J., Santana, V. M., Auld, T. D. (2014) Temperature thresholds of physically dormant seeds and plant functional response to fire: variation among species and relative impact of climate change. *Ecol. Evol.*. **4**, 656–671.

Pierce, S. M., Cowling, R. M. (1991) Dynamics of soil-stored seed banks of six shrubs in fire-prone Dune Fynbos. *J. Ecol.*. **79**, 731–747.

Pierce, S. M., Moll, E. J. (1994) Germination Ecology of Six Shrubs in Fire-Prone Cape Fynbos. *Vegetatio*. **110**, 25–41.

Pretorius, M. R., Esler, K. J., Holmes, P. M., Prins, N. (2008) The effectiveness of active restoration following alien clearance in fynbos riparian zones and resilience of treatments to fire. *South African J. Bot.*. **74**, 517–525.

Rebelo, A. G., Holmes, P. M., Dorse, C., Wood, J. (2011) Impacts of urbanization in a biodiversity hotspot: Conservation challenges in Metropolitan Cape Town. *South African J. Bot.*. **77**, 20–35.

Reid, A. M., Morin, L., Downey, P. O., French, K., Virtue, J. G. (2009) Does invasive plant management aid the restoration of natural ecosystems? *Biol. Conserv.*. **142**, 2342–2349.

Reyes, O., Trabaud, L. (2009) Germination behaviour of 14 Mediterranean species in relation to fire factors : smoke and heat. *Plant Ecol.*. **202**, 113–121.

Richardson, D. M., Kluge, R. L. (2008) Seed banks of invasive Australian Acacia species in South Africa: Role in invasiveness and options for management. *Perspect. Plant Ecol. Evol. Syst.*. **10**, 161–177.

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., West, C. J. (2000) Naturalization and invasion of alien plants : concepts and definitions. *Divers. Distrib.*. **6**, 93–107.

Slingsby, P., Bond, W. J. (1983) Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. Afr. J. Sci.*. **79**, 231–233.

Stone, E. C., Juhren, G. (1951) The Effect of Fire on the Germination of the Seed of *Rhus ovata* Wats. *Am. J. Bot.*. **38**, 368–372.

Tieu, A., Dixon, K. W., Meney, K. A., Sivasithamparam, K. (2001) The Interaction of Heat and Smoke in the Release of Seed Dormancy in Seven Species from Southwestern Western Australia. *Ann. Bot.*. **88**, 259–265.

Van de Venter, H. A., Esterhuizen, A. D. (1988) The effect of factors associated with fire on seed germination of *Erica sessiliflora* and *E. hebecalyx* (Ericaceae). *South African J. Bot.*. **54**, 301–304.

Van Wilgen, B. W., Forsyth, G. G. (1992) Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In: *Fire in South African mountain fynbos.* (eds B. W. Van Wilgen, D. M. Richardson, F. J. Kruger, & J. J. Van Hensbergen) pp. 54–80 Springer-Verlag, Berlin.

Wilson, J. R. U., Gairifo, C., Gibson, M. R. *et al.* (2011) Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions. *Divers. Distrib.*. **17**, 1030–1046.

Witt, A. B. R., Giliomee, J. H. (2004) The impact of an invasive ant, *Linepithema humile* (Mayr), on the dispersal of *Phylica pubescens* Aiton seeds in South Africa. *African Entomol.*. **12**, 179–185.

Wright, E. (1931) The effect of high temperature on seed germination. *J. For.*. **29**, 679–687.

Chapter 3: Assessing the effectiveness of passive and active restoration techniques in overcoming constraints to restoration of a critically endangered vegetation type

3.1 Abstract

Invasive alien plants negatively impact ecosystems, but recovery of native vegetation may fail following standard methods of alien species removal alone. Alternative management actions may thus be required. Cape Flats Sand Fynbos is a critically endangered vegetation type in the Cape Floristic Region of South Africa which is threatened by *Acacia saligna* invasion, but standard clearing methods have failed to restore native vegetation structure. A restoration study was performed comparing passive treatments i.e. clearing without burning (stack-block) versus clearing and burning (burn-block), as well as active intervention by sowing seeds of native species, either initially after burning or a year later, in which seeds were either not pre-treated or pre-treated with smoke and heat exposure before sowing. After two years all treatments resulted in different recovery trajectories, although none resembled the reference condition. Clearing without burning was the cheapest method and facilitated recovery in less degraded areas with higher initial native shrub cover, but otherwise resulted in limited vegetation recovery. Limited recovery facilitated secondary invasion by herbaceous weeds. Active seed sowing was the most expensive treatment but resulted in the highest recovery of native shrub cover and diversity. These findings suggest that passive restoration is constrained due seed limitation, due to the lack of recovery of vegetation components under passive clearing treatment. Active sowing was able to partially overcome this constraint through improved recovery of total shrub cover. However, non-sprouting shrub cover was over-represented while resprouting shrubs and species of Restionaceae were under-represented relative to the reference condition. Pre-treatment of seeds before sowing improved establishment of some species. Active treatment involving sowing pre-treated seeds after clearing and burning therefore resulted in best fynbos recovery compared to either of the passive treatments tested.

3.2 Introduction

Invasive alien plants are currently a major environmental problem on a global scale (Richardson and Rejmanek 2011) through negative impacts on diversity and ecosystem function (Levine *et al.* 2003). Counteracting these effects, including preventing introductions, eradicating or controlling invasive species (Wilson *et al.* 2011), and follow-up control, will likely be necessary for decades (Pretorius *et al.* 2008), while impacts of invasive species are predicted to further increase around the world (Walther *et al.* 2009). Plant invasions are particularly problematic in Mediterranean-type vegetation global biodiversity hotspots, where effects have been studied in regions including Portugal (Marchante *et al.* 2003), California (D'Antonio *et al.* 2007) and Western Australia (Fisher *et al.* 2009), as well as South Africa (Van Wilgen *et al.* 1998) where the Working for Water Programme was initiated to deal with invasive species.

Fynbos vegetation is a highly diverse sclerophyllous shrubland confined to the Mediterranean climate region in the south-west of South Africa, where many areas are invaded by invasive alien tree species, particularly Australian acacias (Le Maitre *et al.* 2011). Fire is necessary to stimulate germination of most fynbos species due to fire-related germination cues such as smoke (Brown 1993) and heat (Hall *et al.* 2016; Chapter 2), as has been found for other Mediterranean regions such as Californian chaparral (Keeley 1987) and Australian kwongan (Tieu *et al.* 2001). Invasive alien species including *Acacia saligna* (Jeffery *et al.* 1988) are also stimulated to germinate by burning, but fire also facilitates rapid reduction of acacia seed banks which would otherwise persist for decades (Holmes *et al.* 1987). However, increased rate of biomass accumulation of alien vegetation relative to fynbos results in fires of higher severity and increased frequency, which can negatively impact on fynbos recovery (Holmes *et al.* 2000).

Invaded mountain fynbos may have a persistent native soil seed bank (Holmes and Cowling 1997*b*) while in lowland fynbos this appears not to be the case (Holmes 2002); here, native seed banks become depleted over time after invasion. Serotinous Proteaceae, which includes the majority of overstorey fynbos species, do not have a soil seed bank, so once they disappear from invaded fynbos sites (Holmes and Cowling 1997*b*; Mostert *et al.* 2017) they will not reappear after alien clearing alone. Obligate resprouting species persist for a limited time and then disappear from the system, after which they may be hard to reintroduce since they have small seed banks (Holmes and Richardson 1999) and do not readily produce seedlings (Marais *et al.* 2014). Resprouting shrubs are an important vegetation component since they can provide cover more rapidly after fire than seedlings (Rutherford *et al.* 2011), and the loss of this component will have important implications for the ecosystem. Seed dispersal distance is limited in fynbos since most species are dispersed by ants, ballistically or passively (Holmes and Cowling 1997*a*). Limited dispersal distance has been found to present a restoration barrier in Australian kwongan (Standish *et al.* 2007) and Californian grasslands (Seabloom *et al.* 2003). Species diversity does not recover in these vegetation communities following disturbance, suggesting that a biotic threshold may have been crossed (Suding *et al.* 2004). Limited dispersal ability of many fynbos species (Slingsby and Bond 1983) therefore suggests that fynbos vegetation degraded by invasion is constrained by seed-limitation and may also have crossed a biotic threshold where ecologically important species have disappeared from the ecosystem.

Active restoration could achieve two objectives. Sowing fast-establishing native annual seeds could provide resilience against reinvasion by invasive alien plant species (Falk *et al.* 2013; Herron *et al.* 2013) in the absence of native resprouting shrubs that would otherwise be able to establish rapid cover after a fire. Native annual plants could also provide protection for enhanced establishment of native perennial species germinating from the seed bank (Padilla and Pugnaire 2006). Sowing seeds of species representing a mix of different fynbos guilds could facilitate restoration of vegetation structure and diversity where certain of these components have been lost (Holmes 2002). Sowing shortly after a fire while smoke residue is still present on the soil surface will stimulate germination of smoke-stimulated seeds (Brown *et al.* 2003), but not those requiring a heat pulse as experienced during a fire (Jeffery *et al.* 1988; Hall *et al.* 2016). Pre-treatment of seeds by mimicking fire conditions can improve efficiency of seed sowing in both fynbos (Hall *et al.* 2016; Chapter 2), chaparral (Wilkin *et al.* 2013) and kwongan (Roche *et al.* 1997).

In addition to a depleted native seed bank, invasive plants can also alter soil chemistry (Yelenik *et al.* 2004; Fisher *et al.* 2006; Marchante *et al.* 2008). This may result in native vegetation failing to establish either due to competition from secondary invasive species (Pearson *et al.* 2016) which take advantage of these conditions, or due to native species' sensitivity to toxicity effects resulting from altered soil chemistry (Witkowski 1991).

Lowland vegetation types in the Cape region of South Africa are highly threatened, in part by degradation due to invasive alien plants including *Acacia saligna* (Rebelo *et al.* 2006). If cleared and restored, invaded habitats possess high conservation value. Following less severe invasion, indigenous vegetation will recover after clearing alone (Mostert *et al.* 2017). However, recovery will be dependent on fire where vegetation cover is depleted, but the duration of invasion may have depleted the native soil seed bank (Le Maitre *et al.* 2011), thus requiring active seed sowing to reintroduce lost vegetation components.

Studies concerning the use of fire in invasive plant management are mostly limited to mountain catchments within the Cape fynbos (Holmes *et al.* 2000; Holmes and Marais 2000; Holmes and Cowling 1997*b*; Blanchard and Holmes 2008), and Californian chaparral (Moyes *et al.* 2005; Alexander and D'Antonio 2003). Furthermore, limited work has been done to assess the effectiveness of active restoration in fynbos (Gaertner *et al.* 2012; Waller *et al.* 2016; Pretorius *et* *al.* 2008), while pre-sowing seed treatment has been poorly studied. Effectiveness of active restoration has been studied in chaparral (Cione *et al.* 2002), while the incorporation of pre-sowing seed treatments has been tested in field trials in kwongan (Rokich and Dixon 2007).

Restoration studies do not often evaluate costs of different treatments being compared (Kettenring and Adams 2011), which complicates management decisions when budgets are limited. However, where this has been evaluated, the cheapest option may be the least effective (Musil *et al.* 2005) while the most effective option may not be feasible due to high costs (Hewitt *et al.* 2005), and therefore it must be determined whether the most successful tested methods are economically viable.

The aims of this study were: (1) to determine whether biotic constraints exist to fynbos restoration following passive acacia clearing i.e. if restoration is seed limited; (2) to determine whether abiotic constraints exist to fynbos restoration that hinder recovery in spite of active seed sowing of species representing vegetation structural components; (3) to assess which treatment is most successful ecologically and in terms of cost. We examined the following hypotheses: (i) Native seed banks have been depleted due to acacia invasion, resulting in poor fynbos recovery following passive clearing treatment, but burning after clearing will be more effective in stimulating fynbos germination where seed banks still exist. (ii) Fynbos will re-establish following seed sowing thus showing that restoration is not limited by abiotic constraints and biotic constraints can be overcome through active intervention. (iii) Passive clearing without burning will be cheapest, while active sowing with pre-treated seeds will be most successful ecologically.

In order to investigate our aims, biotic constraints were determined by comparing vegetation recovery between passive and active restoration treatments, while abiotic constraints were determined by comparing vegetation recovery as well as soil chemistry between active restoration treatments and reference sites. Restoration success was determined by comparing vegetation recovery under all treatments with reference site vegetation.

3.3 Methods

3.3.1 Field site description

The field site at Blaauwberg Nature Reserve is located within the largest remaining area of critically endangered Cape Flats Sand Fynbos, just north of the city of Cape Town, South Africa (33.75°S, 18.48°E) (Figure 1). This vegetation type is confined to deep sandy soil of low pH at low altitudes, within a strongly Mediterranean climate region of hot, dry summers and cool, wet winters. Most of the vegetation was invaded by *Acacia saligna*, although a small area of high fynbos cover and diversity was cleared about six years prior to initiating this restoration study. A survey of the site in May 2012 prior to alien clearance found that standing cover of native species (mapped as restoration potential) varied greatly across the site (figure 2) as did duration of invasion (P.M. Holmes pers. com.). A 64 hectare area was included in the study, incorporating mostly areas of very low (<1%) and low (1-10%) remaining fynbos vegetation cover, but also including a few plots classified as having medium (11-50%) fynbos cover.

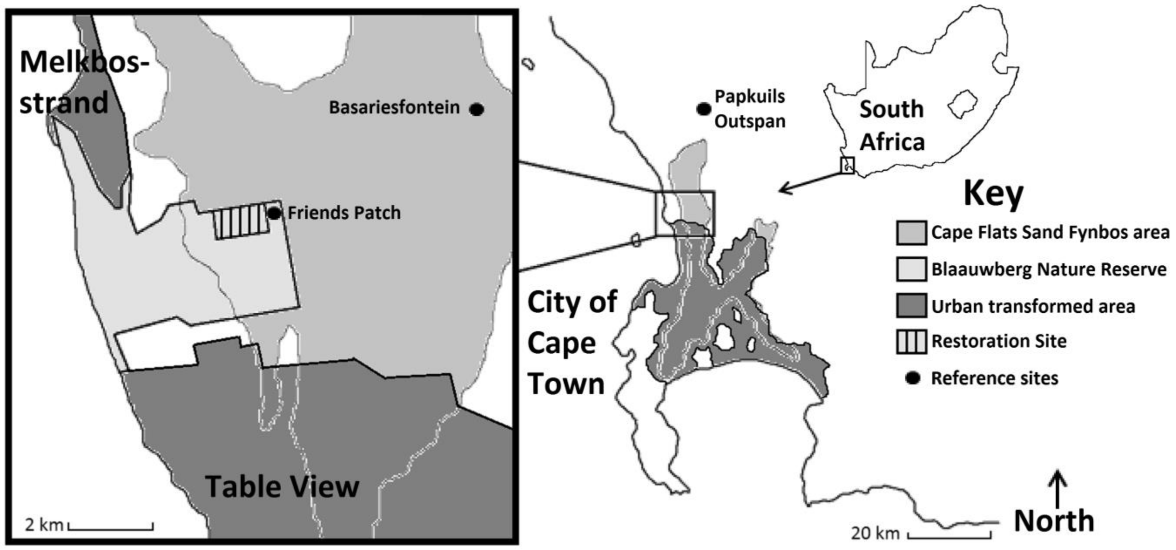


Figure 1. Location of the study area at Blaauwberg Nature Reserve and reference vegetation sites north of the city of Cape Town, within the Western Cape province of South Africa.

3.3.2 Reference sites

One patch of good quality fynbos vegetation adjacent to the restoration site within Blaauwberg Nature Reserve (Friends Patch) 33°45’09”S 18°29’35”E, as well as two other reference sites of vegetation with representative structure and plant species diversity, Basariesfontein 33°43’11”S 18°32’41”E and Papkuils Outspan 33°32’00”S 18°30’00”E were used as reference sites to compare with restoration treatments as a measure of success, and monitoring plots were established at these sites. While the Friends Patch and Basariesfontein contain Cape Flats Sand Fynbos, Papkuils Outspan contains Atlantis Sand Fynbos; the latter site was deemed appropriate since the vegetation structure and dominant species are mostly the same as in Cape Flats Sand Fynbos (Rebelo *et al.* 2006). All sites contained mature fynbos vegetation although at Papkuils Outspan there was also an area that burnt at the same time as the burn-block treatment at Blaauwberg Nature Reserve, and therefore additional plots were established and monitored after the fire to determine rates of vegetation recovery post-fire in pristine vegetation. Soil chemistry data were sampled by collecting six replicate soil cores per plot in both passive treatment and reference sites and combining into one sample per plot. Soil samples were then analysed at Bemlab (Pty) Ltd. (Somerset West, South Africa) for available phosphorus (P, mg/kg, PBray II), mineral nitrogen (ammonium, NH4-N, mg/kg, and nitrate; NO3-N, mg/kg), Electrical conductivity (EC, mS), percentage carbon (%C) and nitrogen (%N). pH was analysed at Stellenbosch University, using a 0.01M $CaCl_2{\cdot}2H_2O$ solution (25 mL) and the pH of the supernatant was measured with a pH meter. Soil chemistry was sampled at the time of initiating treatments in March 2013 and again after one year in March 2014. Vegetation surveys of plots involved recording vegetation richness, cover and plant density of fynbos plant guilds, as well as soil chemistry analysis. Vegetation surveys of mature fynbos plots were done once while burnt reference plots were monitored at six month intervals for two years after burning, with the exception of September 2014 when reference site data were not recorded.

3.3.3 Passive restoration experiment

The restoration site was divided into two main passive treatment blocks. The stack-block treatment involved stacking cleared acacia biomass into brush piles, while the burn-block treatment involved spreading biomass evenly and burning it. Each treatment covered 32 hectares, and these were further divided into single hectare blocks with one monitoring plot of 5 x 10 metres marked out in each, making a total of 64 passive restoration monitoring plots. Plots were monitored for vegetation richness, cover and plant density of native and alien plant guilds at six month intervals (autumn and spring) for two years after initiating treatments in March 2013.

The prescribed fire in the burn-block treatment was conducted on a warm, windless day in early April 2013, which is the latest possible time still within the optimal season to burn for fynbos recruitment (Van Wilgen and Viviers 1985). Soil chemistry was surveyed as described in section 3.3.2.

The sizes of native and acacia seed banks were determined by collecting six replicate soil cores per plot which were combined and sieved to collect and count acacia seeds, then divided between two seed trays of 240 x 170 x 60mm for each plot. Each plot's sample therefore represented $0.012m^2$ of surface area, or $0.75m^2$ including all plots. Trays were treated by exposing soil samples to smoke residue to stimulate germination of seeds in the soil (Brown 1993), after which they were placed into a greenhouse with open sides to maintain ambient temperature but with a constant irrigation regime of three times per week. Trays were then monitored for seedling germination at weekly intervals for five months from June until October. Samples were collected at the time of initiating treatments for native and acacia seed bank as well as one and two years after initial clearing to determine acacia seed bank reduction rate.

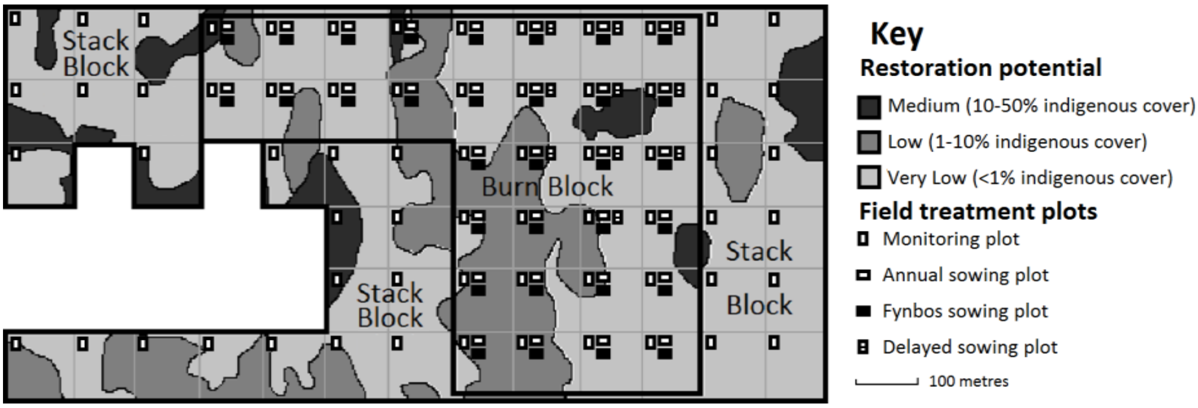


Figure 2. Treatment setup at Blaauwberg Nature Reserve. The 64ha site was divided into 2 passive clearing treatments: the 32ha burn-block treatment was nested within the surrounding stack-block treatment. Active sowing treatments were set up within burn-block plots.

3.3.4 Active restoration experiment

Two plots of 9 x 4 m were laid out perpendicular to each of the 5 x 10 m monitoring plots in the 32 hectares under the burn-block treatment. The two 9 x 4 m plots were sown with seed mixes, one being made up of annual and short-lived perennial forb species, and the other being a mix of species representing fynbos structural components including serotinous overstorey proteas, ericoid shrubs, Restionaceae (hereafter restios) and geophytes, and within these were a number of both resprouting and non-sprouting taxa. Annual forb seeds were sourced from Vula Environmental Services who collected seeds from within 10 km of the restoration site. Fynbos seeds were collected between late 2012 and early 2013 from within Blaauwberg Nature Reserve, or from comparable Cape Flats Sand Fynbos habitat within a 6 km radius. Twenty four species were selected to represent a range of vegetation structural components, growth-forms and seed morphologies (Appendix 1a). This experiment was set up at the end of April 2013 to allow for high temperature fluctuation between day and night, since widely alternating diurnal temperatures stimulate germination in some species (Pierce and Moll 1994). It was hoped that the combination of post-fire residues remaining in the soil, as well as the high temperature fluctuations would be sufficient to stimulate germination of sown seeds once winter rainfall began. Plots were monitored for vegetation richness, cover and plant density of native and alien plant guilds at six month intervals (autumn and spring) for two years after sowing.

Since only a few species germinated from the initial fynbos seed mix, a follow-up sowing experiment was done a year after the initial active restoration treatment. This involved a similar fynbos seed mix but with two plots of 5 x 5 metres sown in each hectare block, one plot with untreated seeds as before and one plot with seeds pre-treated with a combination of smoke solution and heat treatment. Species were treated based on seed germination requirement data (Brown 1993; Hall *et al*. 2016; Mukundamago 2016). Plots were surveyed using the same method as the other treatments but for two years after initiation of this treatment - three years after initial clearing.

3.3.5 Costs associated with each treatment

The financial costs of labour, materials and equipment involved in the different restoration methods, including alien clearance, seed collection and sowing, as well as prescribed burning were recorded. Costs were added over the duration of the experiment and the total amount compared in order to assess which is the cheapest restoration treatment. Costs in South African Rands were also expressed in US Dollars (using the conversion rate of R12.99 to a US$ in September 2017).

3.3.6 Data analysis

The combined *Acacia* seed bank data were shown to be normally distributed and therefore were analysed over the three time periods to compare between stack-block and burn-block treatments. This was done using a repeat measures ANOVA as well as by performing a Fisher LSD post-hoc test in STATISTICA (version 13).

Soil chemistry data were shown to be normally distributed and were therefore analysed to provide a comparison between stack-block and burn-block treatments as well as with the reference sites, using an ANOVA, followed by a Fisher LSD test. Block-burn treatments were compared with the burnt reference site at the same times following the fire, while the stack-block treatment was compared with the initial unburnt reference site immediately after initial clearing as well as one year post-clearance .

All passive and active clearing treatments were compared by performing a repeat measures ANOVA for all treatments at all survey times for percentage cover, plant density and species richness of each vegetation component. Burn-block and stack-block treatments were compared with reference site data using the same analyses. Stack-block treatment was compared with mature unburnt fynbos vegetation while burn-block treatment was compared with vegetation of the same age post-fire at each survey time. Data that were not normally distributed were transformed using a BoxCox transformation. Significance values were determined by performing a Fisher LSD post-hoc test in STATISTICA (version 13). In all analyses, differences were reported as significant where $p < 0.05$.

3.4 Results

3.4.1 Biotic constraints to fynbos restoration

3.4.1.1 Indigenous seed bank study

Indigenous soil seed banks across the restoration site were extremely species poor with only 21 species recorded, of which only two were perennials represented by one individual seedling each. Therefore the density of the total indigenous perennial seed bank was estimated to be 0.44/m^2, versus 1.76/m^2 and six species for geophytes (emerged from soil stored corms), 11.22/m^2 and nine species for annual forbs and 4.62/m^2 and four species for graminoids, the latter two groups dominated by invasive alien species. Soil seed banks from reference sites were not determined, but Holmes et al (2002) found good representation of fynbos shrub diversity in seed bank studies within uninvaded fynbos sites.

3.4.1.2 Acacia seed bank study

There was a significant difference in the initial acacia seed bank size between treatments (Figure 3). In the burn-block treatment there was a large decrease in the acacia seed bank following burning, but the seed bank did not decrease further after the first year. The acacia seed bank size under the stack-block treatment also decreased following clearing but by a smaller amount initially. In the second year after clearing there was a further decrease, after which the seed bank size was not significantly different between passive treatments.

3.4.2 Abiotic constraints to fynbos restoration

3.4.2.1 Soil chemistry comparisons between passive treatments

Changes in NH_4^+, total N, and Electrical Conductivity (EC) (Figure 4) (as well as soil pH and total C (Appendix 1b)) did not differ between treatments and between initial clearing and one year post-clearing. NO_3^- remained stable over time in the stack-block treatment but decreased during the first year post-fire in the burn-block treatment. P remained stable in the burn-block treatment while there was a decrease over time in the stack-block treatment (Figure 4). Soil moisture was initially lower in the stack-block treatment than the burn-block, but in both treatments this dropped to a similar value after a year (Appendix 1b).

In the burnt reference site, P, NO_3^-, NH_4^+, Soil C and soil moisture remained constant over time, while total N and EC decreased. In the burn-block treatment, P and N remained higher than the reference site a year after burning. In the stack-block treatment, soil moisture and soil carbon showed the same response as with burning, but NO_3^- as well as total N increased within a year after initial clearing to higher levels than in the reference site. P remained higher than the reference site since clearing (Figure 4), while NH_4^+ and EC did not differ over time.

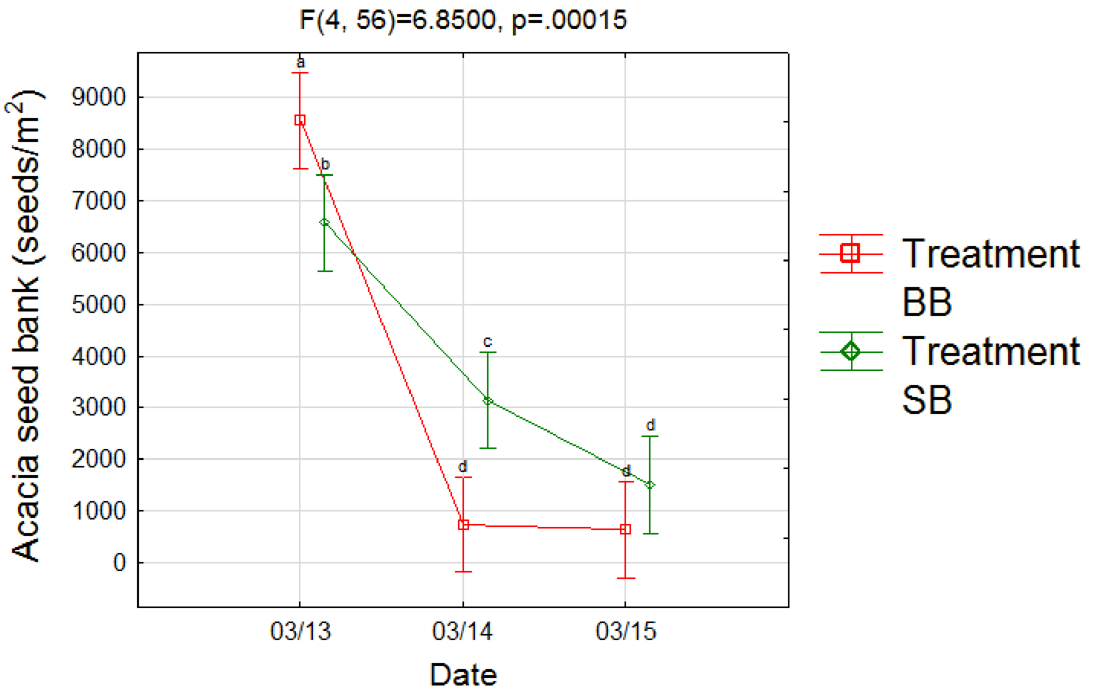


Figure 3. Change in acacia seed bank with time after initial clearing up to two years post-clearing for passive treatments burn-block (BB) and stack-block (SB) analysed using ANOVA. Seed bank size refers to number of seeds collected per soil sample within plots. Vertical bars denote 0.95 confidence intervals.

3.4.3 Restoration treatment effectiveness

3.4.3.1 Recovery of vegetation components under passive restoration treatments

The stack-block treatment resulted in higher cover of alien annual graminoids (Figure 5a) than the burn-block in both spring (September) surveys. Invasive alien *Acacia saligna* cover (Figure 5d) was lower under the stack-block treatment than all other treatments at all times other than immediately after initial and follow-up clearing. Perennial graminoid cover (Figure 5g) was lower in the burn-block initially but after a year had increased to the level of the stack-block. The stack-block treatment had higher cover of non-sprouting shrubs (Figure 5i) and lower cover of resprouting shrubs (Appendix 1c) than burn-block treatment from the second spring. Overall native species richness (Figure 5l) was higher after two years in the burn-block than in the stack-block treatment, although much of the richness in both treatments consisted of annual species.

In comparison with the mature reference vegetation site, native perennial forb richness was higher in the stack-block treatment while forb cover was higher only two years after clearing

(Figure 6a, b). Non-sprouting shrub densities were comparable to the reference site (Figure 6c), but cover (Figure 6d) (along with all other native vegetation components) was significantly lower in the stack-block treatment at all times compared to the reference.

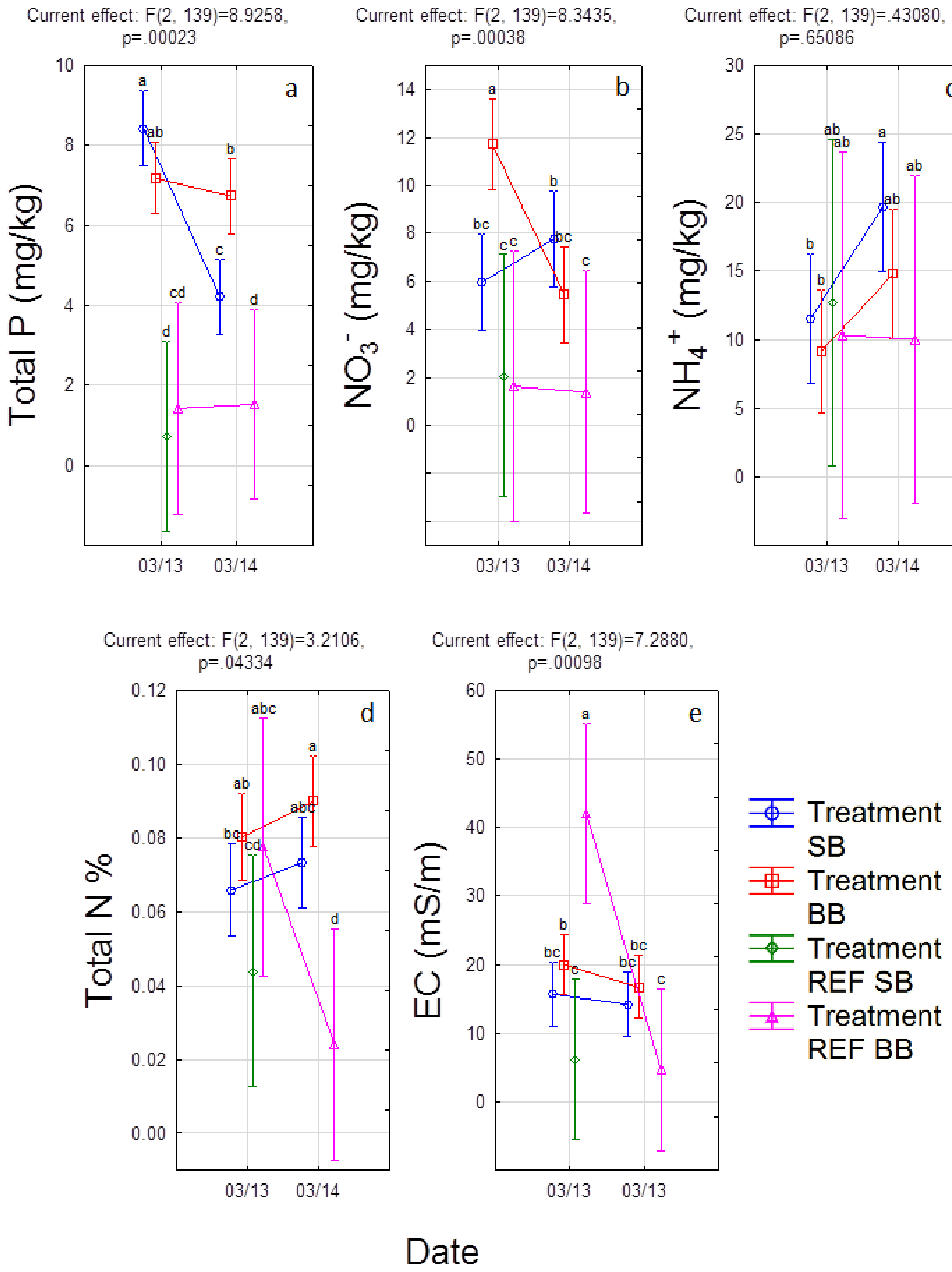


Figure 4. Soil chemistry variables analysed using ANOVA for passive treatments burn-block (BB) and stack-block (SB) at time of initial clearing (03/13) and a year after clearing (03/14) as well as burnt reference (REF BB) and mature reference vegetation (REF SB). Vertical bars denote 0.95 confidence intervals.

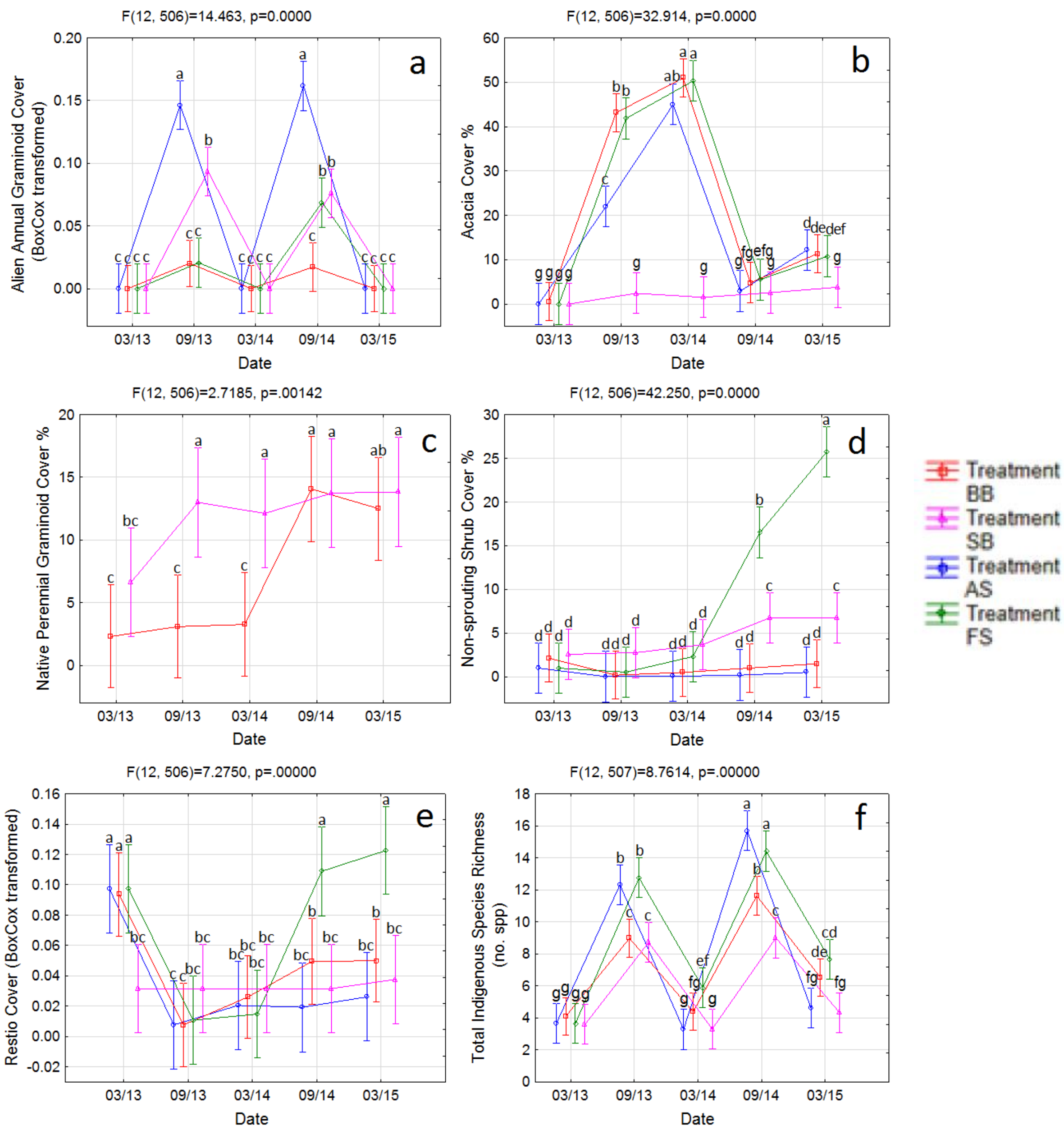


Figure 5. Comparison of vegetation components over five survey times between passive clearing treatments burn-block (BB) and stack-block (SB), and initial sowing treatments Annual sowing (AS) and Fynbos sowing (FS): a) Alien annual graminoid cover; b) Acacia cover; c) Native perennial graminoid cover; d) Non-sprouting shrub cover; e) Restionaceae cover; f) Total indigenous species richness. Cover represented as percent cover where not BoxCox transformed, and richness is in number of species present. Same letters show which samples do not differ significantly based on repeat measures ANOVA. Vertical bars denote 0.95 confidence intervals.

The burn-block treatment did not differ from the burnt reference site in terms of cover of graminoids (Figure7a) and annual forbs (not shown). All other vegetation components were significantly lower in the burn-block, as shown by lower total indigenous cover (Figure 7c). Only annual graminoid species richness was the same in the burn-block treatment and reference site (Figure 7b); all other vegetation components had lower species richness in the burn-block treatment (Figure 7d).

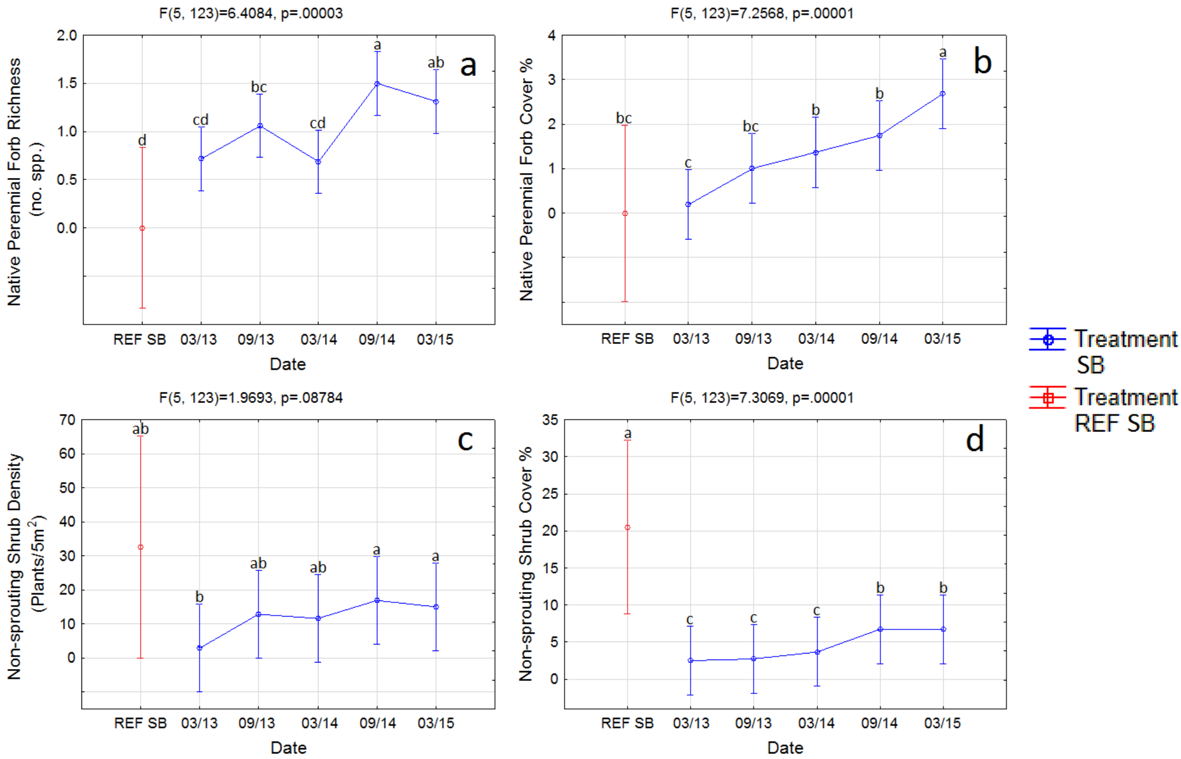


Figure 6. Comparison of vegetation cover and species richness of selected vegetation components between stack-block treatment (SB) and unburnt reference site (REF SB): a) Perennial forb cover; b) Perennial forb richness; c) Non-sprouting shrub density; d) Non-sprouting shrub cover. Same letters show which samples do not differ significantly based on repeat measures ANOVA. Vertical bars denote 0.95 confidence intervals.

3.4.3.2 Recovery of vegetation components under initial active restoration treatments

Sowing of annuals resulted in higher alien annual graminoid cover (Figure 5a) during spring surveys compared to other initially burnt treatments. Acacia cover (Figure 5b) was lower until the first follow-up clearing treatment, although compared to burn-block, there was less difference in acacia cover after one year than after 6 months. Compared to all other treatments, plots sown with annuals had higher native annual forb cover and species richness during both spring surveys, although there was a decline in cover in the second year.

Non-sprouting shrub cover (Figure 5d) was higher in fynbos-sown plots than annual sown or unsown treatments from the second spring but richness and density was higher at all times after burning and sowing. The fynbos sown treatment had higher Restionaceae cover (Figure 5e), density and richness than annual sown or unsown treatments from the second spring.

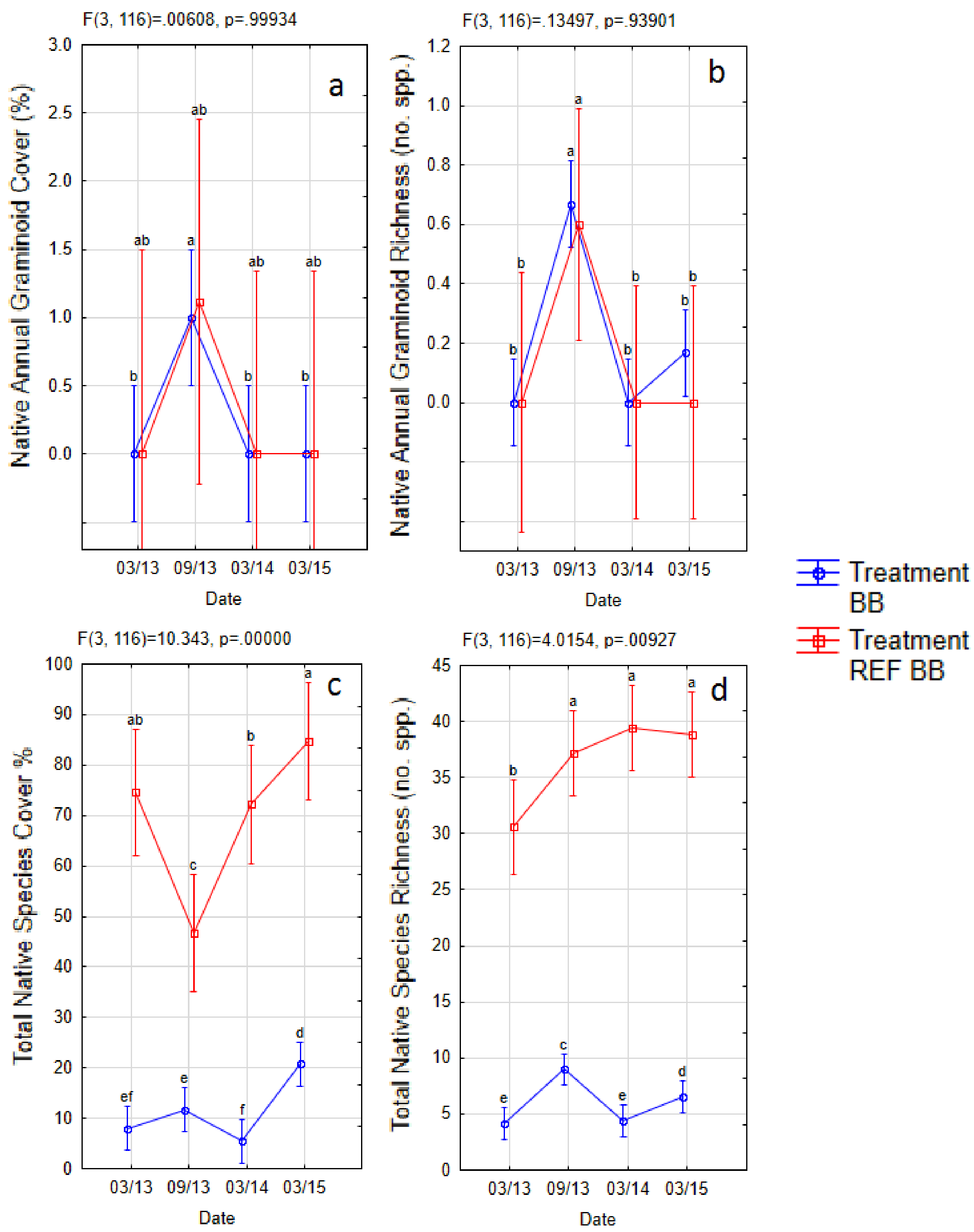


Figure 7. Comparison of vegetation cover and species richness of selected vegetation components between burn-block treatment (BB) and burnt reference site (REF BB): a) Native annual graminoid cover; b) Native annual graminoid richness; c) Total native species cover; d) Total native species richness. Same letters show which samples do not differ significantly based on repeat measures ANOVA. Vertical bars denote 0.95 confidence intervals.

3.4.3.3 Follow-up sowing treatments with untreated and pre-treated seed

Plots where follow-up sowing treatments occurred showed no change in acacia cover over the duration of surveying, and did not differ at the end of the experiment from the burn-block or initial fynbos sowing treatments. Restio cover was higher in the pre-treated sown plots from the second autumn compared to untreated follow-up sowing and unsown plots (Figure 8a). Restio density was highest for pre-treated seeding plots after the first winter, but then decreased and after the second winter did not differ from the untreated follow-up sowing or the initial sowing treatment (Figure 8b). Resprouting shrub cover was higher in the pre-treated sowing plots than un-treated follow-up sowing or initial sowing plots during the first spring survey, but was higher than the initial sowing treatment at all times after the initial survey (Figure 8c). Resprouting shrub richness of both follow-up sowing treatments was higher than the initial sowing treatment, but species richness of the pre-treated sowing treatment was only higher than unsown plots in the first spring and final survey (Figure 8d). Non-sprouting shrub cover increased equally in both pre-treated and untreated sowing treatments, and was higher than initial sowing treatment in the final survey (Figure 8e). Nonsprouting shrub density was higher in pre-treated than initial sowing treatment in the first spring survey, after which densities in all sowing treatments were the same, but higher than unsown burn-block treatment (Figure 8f).

3.4.4 Costs associated with each treatment

In terms of costs per treatment, including initial treatment and follow-up clearing after one year, stack-block was the cheapest method at R17,505 ($1,347) per ha, followed by burn-block at R44,536 ($3,426) per ha (burning was done in house, while calculated costs include equipment and personnel involved), and active fynbos sowing treatments being most expensive at R52,520 ($4,040) per ha. However, by the end of the monitoring period, herbaceous secondary invader species were becoming problematic particularly in plots not sown with fynbos seeds and would likely require clearing in future, but this unfortunately could not be incorporated into these costs.

3.5 Discussion

The main aims of this study were to determine the most effective passive and active restoration technique in overcoming constraints to restoration of Cape Flats Sand Fynbos. The hypothesis that native seed banks are depleted due to acacia invasion was supported, and burning after clearing did not facilitate better fynbos recruitment; thus passive restoration is seed-limited and a biotic threshold may have been crossed. The study supported the hypothesis that sowing seeds facilitates better fynbos establishment, thereby overcoming the constraint of seed-limitation.

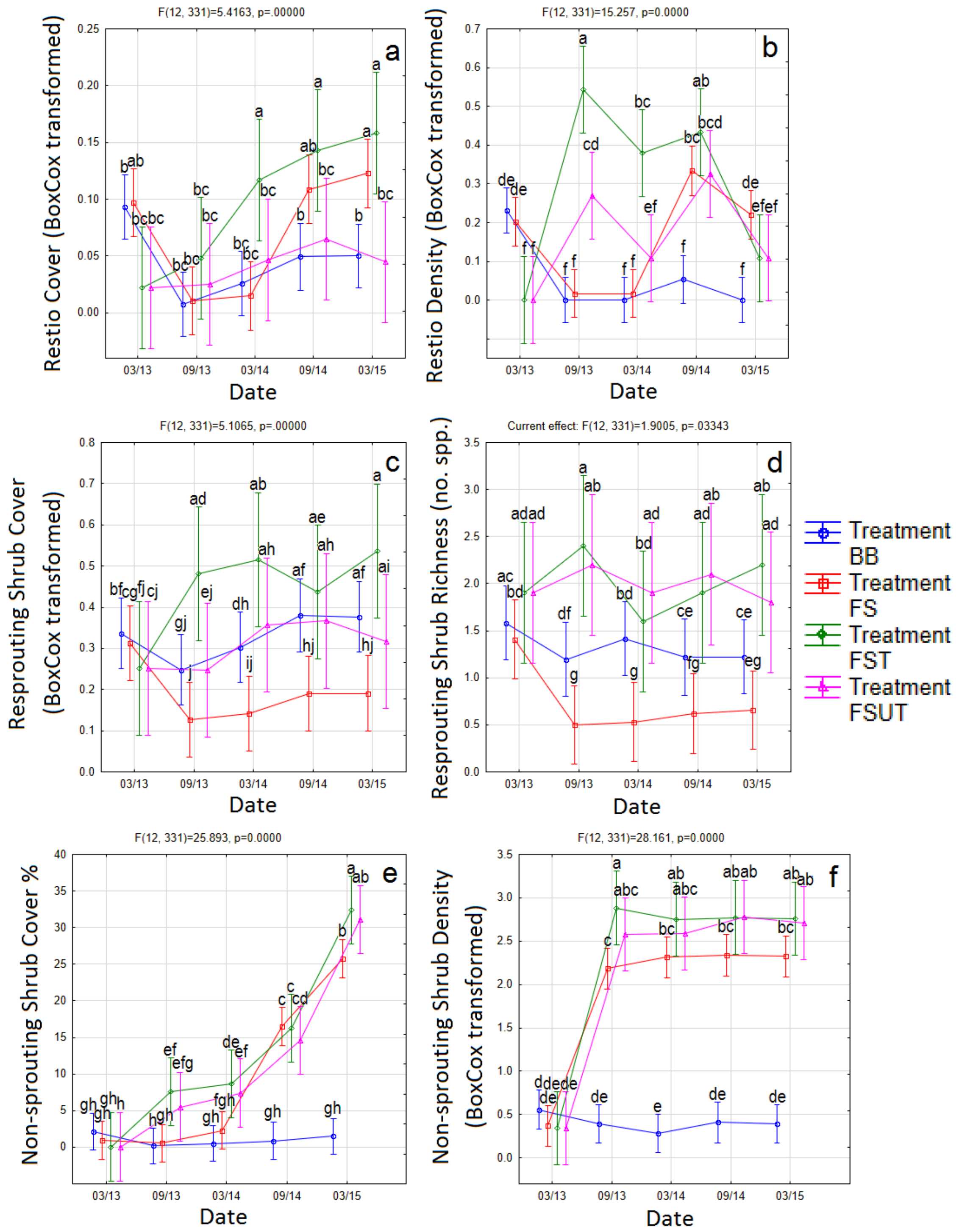


Figure 8. Comparison of vegetation components over five survey times between burn-block (BB), Initial Fynbos sowing (FS), Follow-up pre-treated Fynbos Sowing (FST) and Follow-up untreated Fynbos Sowing (FSUT) treatments: a) Restio cover (BoxCox transformed data); b) Restio density (BoxCox transformed data); c) Resprouting shrub cover (BoxCox transformed data); d) Resprouting shrub richness; e) Non-sprouting shrub cover; f) Non-sprouting shrub density (BoxCox transformed data). Cover represented as percent cover where not BoxCox transformed, and richness is in number of species present. Same letters show which samples do not differ significantly based on repeat measures ANOVA. Vertical bars denote 0.95 confidence intervals.

Furthermore, although being the most expensive treatment, active restoration through sowing seeds resulted in the most successful restoration in terms of native shrub cover.

While all treatments differed from each other after two years and from the state immediately prior to clearing, no treatment had approached vegetation structure comparable to a reference site. Two years is perhaps not long enough to easily assess treatment success in restoring vegetation structure, since different vegetation components dominate at different points in time following disturbance (Hoffman *et al*. 1987). However, within two years following fire all species in a fynbos community should be present since most fynbos species have seeds that germinate in response to fire-related cues (Le Maitre and Midgley 1992).

3.5.1 Biotic constraints to fynbos restoration following passive acacia clearing

The seed bank study showed that native seed banks lacked the expected density and diversity of shrub species at the time of clearing, which supports the finding by Holmes (2002) that fynbos seed banks become depleted over time during invasion. Native seed bank depletion has also been found in acacia-invaded Portuguese dune ecosystems (Marchante *et al.* 2011*a*) as well as in grass-invaded Californian coastal shrubland (Cione *et al.* 2002), in both cases suggesting that biotic thresholds may have been crossed.

In our study, non-sprouting shrub cover increased within the stack-block treatment after two years due to recruitment of seedlings of a few species not requiring fire-related cues for germination (Hall *et al.* 2016; Chapter 2). In time this could facilitate recovery of shrub cover, but since most fynbos species are only capable of short-distance dispersal (Holmes and Cowling 1997*a*) it is unlikely that there would be an increase in shrub species richness with time, even after subsequent fires.

Burning after clearing resulted in minimal recovery of non-sprouting native shrub species, due to a combination of the depleted native seed bank, harbouring only one species *Passerina corymbosa*, and competition from mass post-fire acacia recruitment (Holmes 2002; Musil 1993). A similar phenomenon has been found in ecosystems with different invasive species (Yurkonis *et al.* 2005). Furthermore, the fire temperature through acacia slash may have been too hot as *P. corymbosa* possess less heat tolerant seeds (Hall *et al.* 2016, Chapter 2). Restio and resprouter recovery was limited to established plants persisting at the time of initial clearing in passive treatments.

Acacia densities were found by Holmes and Cowling (1997*b*) to have a significant negative impact on establishment success of shrub seedlings in sowing experiments. In follow-up sowing treatments acacia cover and growth rate was much lower since follow-up clearing operations took place shortly before sowing. The motivation of burning before sowing was to clear litter from the soil surface which otherwise inhibits native seedling germination (Marchante *et al.* 2011*b*), and provide smoke residue to stimulate germination (Brown 1993), but the competitive effect of the high invasive seedling density (Adams and Galatowitsch 2008) outweighed potential benefits.

3.5.2 Abiotic constraints to fynbos restoration and the impact of associated soil chemistry legacy effects

Comparison of soil chemistry variables between each passive clearing treatment and the corresponding reference sites showed that after a year there is a legacy effect of certain soil chemistry variables, as indicated by higher levels of P and N in cleared sites compared to reference sites. These findings correspond with those of Nsikani *et al.* (2017) who found that altered soil chemistry effects persisted for an extended time after alien clearing. The elevated nutrient availability could negatively affect growth of some fynbos species (Witkowski 1991; Lamb and Klaussner 1988). However, where *Protea repens* established in plots or was planted as seedlings adjacent to plots, there was no evidence of toxicity effects, and therefore it does not appear that an abiotic threshold has been crossed.

Lack of fire after clearing or lack of rapid native shrub establishment after burning left gaps for secondary invasive species to establish and dominate; in this case resulting in a persistent herbaceous-dominated vegetation state before native shrub species could establish. Combined with increased nutrient availability, bare ground promotes invasion by alien annual grasses (Maron and Jefferies 1999), as well as opportunistic weedy indigenous species including *Ehrharta calycina* (Yelenik *et al.* 2004; Fisher *et al.* 2006), that compete against native shrubs unable to benefit from increased nutrients (Musil 1993). Grass-dominated vegetation is more prone to burning than native shrub cover (Cione *et al.* 2002), and these combined effects prevent reversal of this biotic threshold, resulting in a persistent alternative ecosystem state (i.e. novel ecosystem (Hobbs *et al.* 2009)).

In both passive treatments, soil carbon decreased by the same amount to within levels found in reference sites, and therefore this may be a limiting factor in facilitating excess N immobilization. Soil remediation through input of carbon-rich mulch may be a means to deplete excess nutrients in order to decrease competition from secondary invasive annuals and therefore facilitate better establishment of less competitive native shrub species (Zink and Allen 1998).

3.5.3 Assessment of ecologically successful and cost effective restoration treatments

The stack-block treatment was the least expensive and also arguably the most effective passive restoration method in terms of restoring a balance of different native vegetation components, although this depended on shrubs persisting before initial clearing. Bare ground was subsequently invaded by herbaceous species. Lack of fire hindered the recovery of many fynbos species requiring fire-related cues for germination (Holmes and Cowling 1997*b*). *Acacia saligna* recruitment would however also be hindered by lack of fire (Richardson and Kluge 2008), resulting in much lower costs for acacia follow-up clearing than the burn-block treatment. The acacia seed bank of the stack-block treatment was reduced by almost as much as the burn-block within three years of initial clearing, perhaps due to removal by rodents (Holmes 1990), showing that fire is not necessarily the most effective method of reducing acacia seed banks in this ecosystem.

Burning effectively controlled alien annual graminoids, suggesting that the heat of the fire killed annual seeds rather than competition from acacia recruitment, since annual grasses were already apparent in the stack-block treatment but not in the burn-block, before acacia seedlings germinated. Alien forbs were initially controlled in the burn-block treatment, but this was not sustained for more than one year after burning, likely due to initial suppression by acacia reestablishment and lack of competition after follow-up acacia clearing in the second winter. The decreased alien annual grass cover may also have facilitated establishment of alien forbs, as has been found following attempts to control alien grasses (Cox and Allen 2008). Sowing of native annual forbs can unintentionally spread secondary invasives, since higher overall alien herbaceous cover was found in the annual sowing treatment over the longer term. Along with higher native perennial forb cover, this resulted in establishment of herbaceous dominated vegetation rather than facilitating native shrub establishment and is therefore an undesirable treatment.

Pre-treating restio seeds resulted in an initially higher number of plants, which subsequently decreased after the following summer, suggesting that drought stress hampers optimal restio establishment from seed. Resprouting species are not entirely dependent on seeds for maintaining populations (Van Wilgen and Forsyth 1992) and exhibit very low recruitment rates (Marais *et al.* 2014). However, pre-treated seeds of *Phylica cephalantha* and *Trichocephalus stipularis* showed high germination success under laboratory conditions (Hall *et al.* 2016, Chapter 2), suggesting that there are post-germination barriers to establishment in the field.

Drought sensitivity has been found to hamper shrub establishment from seeding treatments (Cione *et al.* 2002; Moreno *et al.* 2011). Higher establishment success could be achieved through supplemental watering after sowing seeds (although only practical on a small scale). Watering may benefit secondary invader establishment, but could facilitate more rapid native cover establishment (Daehler and Goergen 2005). Resprouting and restio species may also establish more successfully by planting out nursery grown plants which have more resources to put down roots before the following summer. Nursery propagated planting has achieved limited success in Australia, although the plants which survived showed very poor reproductive success (Morgan 1999). Reintroductions of threatened species by planting seedlings have been successful in Tokai Park within Cape Flats Sand Fynbos (Hitchcock *et al.* 2012), although reproductive success has not been established.

In conclusion, based on the treatments tested, where some fynbos vegetation structure remains at the time of acacia clearing, stack-block passive treatment alone can be considered since native seed banks have likely not been depleted. Where vegetation structure has been lost by the time of clearing, native seedbanks appear also to have been depleted, suggesting that biotic thresholds may have been crossed. In such cases active intervention will be necessary. If plots are burned after clearing, delayed sowing with pre-treated seeds may be a better option than initial sowing as this allows acacia seedlings to be removed, and autogenic recovery can be better assessed. Alternatively, sowing pre-treated seeds without burning could be considered, if sufficient cleared alien biomass can be removed. However, in this case secondary invasives may compete with seedling establishment, but appropriate means of control can help decrease the competitive advantage until shrubs establish sufficient cover. Native vegetation can be restored following invasive alien removal, so long as consideration is given to the habitat state at the time of clearing.

3.6 References

Adams, C. R., Galatowitsch, S. M. (2008) The transition from invasive species control to native species promotion and its dependence on seed density thresholds. *Appl. Veg. Sci.*. **11**, 131–138.

Alexander, J. M., D'Antonio, C. M. (2003) Seed bank dynamic of French broom in coastal California grasslands: Effects of stand age and prescribed burning on control and restoration. *Restor. Ecol.*. **11**, 185–197.

Blanchard, R., Holmes, P. M. (2008) Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. *South African J. Bot.*. **74**, 421–431.

Brown, N. A. C. (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytol.*. **123**, 575–83.

Brown, N. A. C., Van Staden, J., Daws, M. I., Johnson, T. (2003) Patterns in the seed germination response to smoke in plants from the Cape Floristic Region , South Africa. *South African J. Bot.*. **69**, 514–525.

Cione, N. K., Padgett, P. E., Allen, E. B. (2002) Restoration of a Native Shrubland Impacted by Exotic Grasses, Frequent Fire, and Nitrogen Deposition in Southern California. *Restor. Ecol.*. **10**, 376–384.

Cox, R. D., Allen, E. B. (2008) Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *J. Appl. Ecol.*. **45**, 495–504.

D'Antonio, C. M., Malmstrom, C., Reynolds, S. A., Gerlach, J. (2007) Ecology of invasive non-native species in California grassland. In: *California Grasslands: Ecology and Management* (eds M. R. Stromberg, J. D. Corbin, & C. M. D'Antonio) pp. 67–83 University of California Press, California.

Daehler, C. C., Goergen, E. M. (2005) Experimental Restoration of an Indigenous Hawaiian Grassland after Invasion by Buffel Grass (*Cenchrus ciliaris*). *Restor. Ecol.*. **13**, 380–389.

Falk, A. D., Fulbright, T. E., Smith, F. S., Brennan, L. A., Ortega-Santos, A. J., Benn, S. (2013) Does Seeding a Locally Adapted Native Mixture Inhibit Ingress by Exotic Plants? *Restor. Ecol.*. **21**, 474–480.

Fisher, J. L., Loneragan, W. A., Dixon, K., Veneklaas, E. J. (2009) Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biol. Conserv.*. **142**, 256–269.

Fisher, J. L., Veneklaas, E. J., Lambers, H., Loneragan, W. A. (2006) Enhanced soil and leaf nutrient status of a Western Australian Banksia woodland community invaded by *Ehrharta calycina* and *Pelargonium capitatum*. *Plant Soil*. **284**, 253–264.

Gaertner, M., Nottebrock, H., Fourie, H., Privett, S. D. J., Richardson, D. M. (2012) Plant invasions, restoration, and economics: Perspectives from South African fynbos. *Perspect. Plant Ecol. , Evol. Syst.*. **14**, 341–353.

Hall, S. A., Newton, R. J., Holmes, P. M., Gaertner, M., Esler, K. J. (2016) Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type. *Austral Ecol.*. **42**, 354–366.

Herron, C. M., Jonas, J. L., Meiman, P. J., Paschke, M. W. (2013) Using native annual plants to restore post-fire habitats in western North America. *Int. J. Wildl. Fire*. **22**, 815–821.

Hewitt, C. L., Campbell, M. L., McEnnulty, F., Moore, K. M., Murfet, N. B., Robertson, B., Schaffelke, B. (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. *Biol. Invasions*. **7**, 251–263.

Hitchcock, A., Cowell, C., Rebelo, T. (2012) The lost fynbos of Tokai Park. *Veld Flora*. **98**, 30–33.

Hobbs, R. J., Higgs, E., Harris, J. a (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.*. **24**, 599–605.

Hoffman, M. T., Moll, E. J., Boucher, C. (1987) Post-fire succession at Pella, a South African lowland fynbos site. *South African J. Bot.*. **53**, 370–374.

Holmes, P. M. (1990) Dispersal and predation of alien Acacia seeds: effects of season and invading stand density. *South African J. Bot.*. **56**, 428–434.

Holmes, P. M. (2002) Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecol.*. **27**, 110–120.

Holmes, P. M., Cowling, R. M. (1997a) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecol.*. **133**, 107–122.

Holmes, P. M., Cowling, R. M. (1997b) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrubland. *J. Appl. Ecol.*. **34**, 317–332.

Holmes, P. M., Macdonald, I. A. W., Juritz, J. (1987) Effects of Clearing Treatment on Seed Banks of the Alien Invasive Shrubs *Acacia saligna* and *Acacia cyclops* in the Southern and South-Western Cape, South Africa. *J. Appl. Ecol.*. **24**, 1045–1051.

Holmes, P. M., Marais, C. (2000) Impacts of alien plant clearance on vegetation in the mountain catchments of the Western Cape. *South. African For. J.*. **189**, 113–117.

Holmes, P. M., Richardson, D. M. (1999) Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: Perspectives from South African fynbos. *Restor. Ecol.*. **7**, 215–230.

Holmes, P. M., Richardson, D. M., Van Wilgen, B. W., Gelderblom, C. (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecol.*. **25**, 631–639.

Jeffery, D. J., Holmes, P. M., Rebelo, A. G. (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. *South African J. Bot.*. **54**, 28–34.

Keeley, J. E. (1987) Role of Fire in Seed Germination of Woody Taxa in California Chaparral. *Ecology*. **68**, 434–443.

Kettenring, K. M., Adams, C. R. (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *J. Appl. Ecol.*. **48**, 970–979.

Lamb, A. J., Klaussner, E. (1988) Response of the fynbos shrubs *Protea repens* and *Erica plukenetii* to low levels of nitrogen and phosphorus applications. *South African J. Bot.*. **54**, 558–564.

Levine, J. M., Vilà, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. Biol. Sci.*. **270**, 775–781.

Le Maitre, D. C., Gaertner, M., Marchante, E., Ens, E. J., Holmes, P. M., Pauchard, A., O'Farrell, P. J., Rogers, A. M., Blanchard, R., Blignaut, J., Richardson, D. M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Divers. Distrib.*. **17**, 1015–1029.

Le Maitre, D. C., Midgley, J. J. (1992) Plant reproductive ecology. In: *The ecology of Fynbos: nutrients, fire and diversity* (ed R. M. Cowling) pp. 135–174 Oxford University Press, Cape Town.

Marais, K. E., Pratt, R. B., Jacobs, S. M., Jacobsen, A. L., Esler, K. J. (2014) Postfire regeneration of resprouting mountain fynbos shrubs: differentiating obligate resprouters and facultative seeders. *Plant Ecol.*. **215**, 195–208.

Marchante, H., Freitas, H., Hoffmann, J. H. (2011*a*) The potential role of seed banks in the recovery of dune ecosystems after removal of invasive plant species. *Appl. Veg. Sci.*. **14**, 107–119.

Marchante, H., Freitas, H., Hoffmann, J. H. (2011*b*) Post-clearing recovery of coastal dunes invaded by *Acacia longifolia*: is duration of invasion relevant for management success? *J. Appl. Ecol.*. **48**, 1295–1304.

Marchante, E., Kjøller, A., Struwe, S., Freitas, H. (2008) Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Appl. Soil Ecol.*. **40**, 210–217.

Marchante, H., Marchante, E., Freitas, H. (2003) Invasion of the Portuguese dune ecosystems by the exotic species *Acacia longifolia* (Andrews) Willd .: effects at the community level . In: *Plant Invasions: Ecological Threats and Management Solutions* pp. 75–85 Backhuys, Leiden, The Netherlands.

Maron, J. L., Jefferies, R. L. (1999) Bush Lupine Mortality, Altered Resource Availability, and Alternative Vegetation States. *Ecology*. **80**, 443.

Moreno, J. M., Zuazua, E., Pérez, B., Luna, B., Velasco, a., Resco de Dios, V. (2011) Rainfall patterns after fire differentially affect the recruitment of three Mediterranean shrubs. *Biogeosciences*. **8**, 3721–3732.

Morgan, J. (1999) Have tubestock plantings successfully established populations of rare grassland species into reintroduction sites in western Victoria? *Biol. Conserv.*. **89**, 235–243.

Mostert, E., Gaertner, M., Holmes, P. M., Rebelo, A. G., Richardson, D. M. (2017) Impacts of invasive alien trees on threatened lowland vegetation types in the Cape Floristic Region, South Africa. *South African J. Bot.*. **108**, 209–222.

Moyes, A. B., Witter, M. S., Gamon, J. A. (2005) Restoration of Native Perennials in a California Annual Grassland after Prescribed Spring Burning and Solarization. *Restor. Ecol.*. **13**, 659–666.

Mukundamago, M. (2016) *Restoration of Cape Flats Sand Fynbos : The significance of pre-germination treatments and moisture regime.* Stellenbosch University.

Musil, C. F. (1993) Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. *J. Appl. Ecol.*. **30**, 361–372.

Musil, C. F., Milton, S. J., Davis, G. W. (2005) The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. *S. Afr. J. Sci.*. **101**, 337–344.

Nsikani, M. M., Novoa, A., Van Wilgen, B., Keet, J., Gaertner, M. (2017) *Acacia saligna's* soil legacy effects persist up to 10 years after clearing: Implications for ecological restoration. *South African J. Bot.* **42**, 880-889.

Padilla, F. M., Pugnaire, F. I. (2006) The role of nurse plants in the restoration of degraded environments. *Front. Ecol. Environ*.. **4**, 196–202.

Pearson, D. E., Ortega, Y. K., Runyon, J. B., Butler, J. L. (2016) Secondary invasion: The bane of weed management. *Biol. Conserv.*. **197**, 8–17.

Pierce, S. M., Moll, E. J. (1994) Germination Ecology of Six Shrubs in Fire-Prone Cape Fynbos. *Vegetatio*. **110**, 25–41.

Pretorius, M. R., Esler, K. J., Holmes, P. M., Prins, N. (2008) The effectiveness of active restoration following alien clearance in fynbos riparian zones and resilience of treatments to fire. *South African J. Bot.*. **74**, 517–525.

Rebelo, A. G., Boucher, C., Helme, N., Mucina, L., Rutherford, M. C. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland.* (eds L. Mucina & M. C. Rutherford) pp. 52–219 South African National Biodiversity Institute, Pretoria.

Richardson, D. M., Kluge, R. L. (2008) Seed banks of invasive Australian Acacia species in South Africa: Role in invasiveness and options for management. *Perspect. Plant Ecol. Evol. Syst.*. **10**, 161–177.

Richardson, D. M., Rejmánek, M. (2011) Trees and shrubs as invasive alien species - a global review. *Divers. Distrib.*. **17**, 788–809.

Roche, S., Koch, J. M., Dixon, K. W. (1997) Smoke Enhanced Seed Germination for Mine Rehabilitation in the Southwest of Western Australia. *Restor. Ecol.*. **5**, 191–203.

Rokich, D. P., Dixon, K. W. (2007) Recent advances in restoration ecology, with a focus on the Banksia woodland and the smoke germination tool. *Aust. J. Bot.*. **55**, 375–389.

Rutherford, M. C., Powrie, L. W., Husted, L. B., Turner, R. C. (2011) Early post-fire plant succession in Peninsula Sandstone Fynbos: The first three years after disturbance. *South African J. Bot.*. **77**, 665–674.

Seabloom, E. W., Harpole, W. S., Reichman, O. J., Tilman, D. (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci. U. S. A.*. **100**, 13384–13389.

Slingsby, P., Bond, W. J. (1983) Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. Afr. J. Sci*.. **79**, 231–233.

Standish, R. J., Cramer, V. A., Wild, S. L., Hobbs, R. J. (2007) Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. *J. Appl. Ecol.*. **44**, 435–445.

Suding, K. N., Gross, K. L., Houseman, G. R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.*. **19**, 46–53.

Tieu, A., Dixon, K. W., Meney, K. A., Sivasithamparam, K. (2001) The Interaction of Heat and Smoke in the Release of Seed Dormancy in Seven Species from Southwestern Western Australia. *Ann. Bot.*. **88**, 259–265.

Waller, P. A., Anderson, P. M. L., Holmes, P. M., Allsopp, N. (2016) Seedling recruitment responses to interventions in seed-based ecological restoration of Peninsula Shale Renosterveld, Cape Town. *South African J. Bot.*. **103**, 193–209.

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H. (2009) Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.*. **24**, 686–693.

Van Wilgen, B. W., Forsyth, G. G. (1992) Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In: *Fire in South African mountain fynbos.* (eds B. W. Van Wilgen, D. M. Richardson, F. J. Kruger, & J. J. Van Hensbergen) pp. 54–80 Springer-Verlag, Berlin.

Van Wilgen, B. W., Le Maitre, D. C., Cowling, R. M. (1998) Ecosystem services, efficiency, sustainability and equity: South Africa's Working for Water Programme. *Trends Ecol. Evol.*. **13**, 378.

Van Wilgen, B. W., Viviers, M. (1985) The Effect of Season of Fire on Serotinous Proteaceae in the Western Cape and the Implications for Fynbos Management. *South African For. J.*. **133**, 49–53.

Wilkin, K. M., Holland, V. L., Keil, D., Schaffner, A. (2013) Mimicking Fire for Successful Chaparral Restoration. *Madroño*. **60**, 165–172.

Wilson, J. R. U., Gairifo, C., Gibson, M. R., Arianoutsou, M., Bakar, B. B., Baret, S., Celesti-Grapow, L., DiTomaso, J. M., Dufour-Dror, J.-M., Kueffer, C., Kull, C. A., Hoffmann, J. H., Impson, F. A. C., Loope, L. L., Marchante, E., Marchante, H., Moore, J. L., Murphy, D. J., Tassin, J., Witt, A., *et al.* (2011) Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions. *Divers. Distrib.*. **17**, 1030–1046.

Witkowski, E. T. F. (1991) Growth and Competition Between Seedlings of *Protea repens* (L.) L. and the Alien Invasive, *Acacia saligna* (Labill.) Wendle. in Relation to Nutrient Availability. *Funct. Ecol.*

Yelenik, S. G., Stock, W. D., Richardson, D. M. (2004) Ecosystem Level Impacts of Invasive *Acacia saligna* in the South African Fynbos. *Restor. Ecol.*. **12**, 44–51.

Yurkonis, K. A., Meiners, S. J., Wachholder, B. E. (2005) Invasion impacts diversity through altered community dynamics. *J. Ecol.*. **93**, 1053–1061.

Zink, T. A., Allen, M. F. (1998) The Effects of Organic Amendments on the Restoration of a Disturbed Coastal Sage Scrub Habitat. *Restor. Ecol.*. **6**, 52–58.

Chapter 4: Anticipating the effectiveness of invasive plant control and native vegetation recovery: An innovative dynamic tool to optimise South African Fynbos management decision-making

4.1 Abstract

Since invasive alien plants may negatively impact ecosystems, including where recovery of native vegetation fails following their removal alone, further management actions and preventive strategies may be required. Cape Flats Sand Fynbos is a critically endangered vegetation type in the Cape Floristic Region of South Africa and threatened by *Acacia saligna* invasion. In this vegetation type, a restoration study was performed comparing different clearing treatments and active intervention with seed sowing in terms of facilitating successful restoration. A dynamic model was designed and implemented to analyze the effectiveness of the different restoration methods, enabling the extrapolation of recovery trajectories over a long time span which could not be determined from short-term field surveys alone. Data for rates of vegetation recovery over the course of two years were fed into the model. Our model simulations showed that different treatments in similar degraded states at the time of clearing resulted in vastly different recovery trajectories. Active seed sowing was initially the most expensive treatment but resulted in highest indigenous shrub recovery which in turn decreased the costs of longer term follow-up alien clearing. Clearing without burning was the cheapest method but resulted in limited recovery of indigenous or acacia cover, leaving space to facilitate secondary invasion by herbaceous weeds. Therefore it is assumed that ecological thresholds have been crossed which prevented recovery of certain vegetation components. Active sowing was able to partially reverse these thresholds, but even this treatment did not resemble the reference condition after simulating over an extended period of 30 years. Overall, our model simulations can therefore support decision-making by providing management recommendations for more effective alien clearing protocols for future alien plant clearing projects. Moreover, the proposed dynamic modelling approach also provides a potential means by which to compare different ecosystems with varying levels of degradation and with different treatments to those used in this study.

4.2 Introduction

Invasive alien plants negatively impact natural ecosystems (Richardson *et al.* 2000; Ortega and Pearson 2005) through long-term decrease in biodiversity and altered ecosystem functioning, along with serious economic and social consequences (Didham *et al.* 2007; Levine *et al.* 2003; Vitousek *et al.* 1997). Invasive alien species removal attempts to mitigate these impacts, but this often fails to achieve a functional native ecosystem due to the lack of active intervention after the initial clearing (Blackwood *et al.* 2010; D'Antonio and Meyerson 2002; Hulme 2006; Reid *et al.* 2009). Most restoration initiatives have only been assessed in terms of short-term vegetation recovery and these have shown mixed results (Godefroid *et al.* 2011). It is therefore important to determine the likely long-term community trajectories, especially in ecosystems with high levels of species richness and local endemism such as the fynbos vegetation within the Cape Floristic Region of South Africa.

In a natural system, fynbos vegetation includes a variety of species which can be grouped into the key structural components: non-sprouting shrubs, resprouting shrubs, overstorey proteoids (large shrubs of the family Proteaceae) and restios (graminoid shrubs within the family Restionaceae). Herbaceous, geophytic and graminoid plants contribute to species richness but usually account for low vegetation cover in mature fynbos. Over time following invasion, some of these components are lost from the ecosystem (Holmes *et al.* 2000; Gaertner *et al.* 2012) leading to altered ecosystem components such as changes in soil chemistry (Yelenik *et al.* 2004).

The most common practice for invasive alien plant clearing in fynbos currently involves stacking of removed biomass into a small area which is then burnt, in order to limit disturbance across the majority of the area. This can facilitate recovery where standing fynbos cover is present, but may not stimulate germination of many native species which possess dormant seeds requiring fire-related cues for germination (Keeley and Bond 1997). Therefore, an alternative method could be to burn the site after clearing, to stimulate germination of dormant fynbos seeds (Holmes and Cowling 1997), as well as reduce the dormant acacia seed bank still present in the soil (Holmes *et al.* 1987).

Indigenous seed banks are likely to be depleted under dense acacia invasion (Holmes 2002). In such cases an active intervention involving sowing seeds of appropriate species would be necessary for reestablishment of native species no longer present. Sowing could therefore bypass this barrier to restoration by establishing a balance of species representing different structural components of fynbos vegetation. However, to date there has been limited work done to assess active restoration success in fynbos (Gaertner *et al.* 2012). This work, which examined soil restoration techniques and sowing of native species after alien clearing and burning, was only documented up to three years after initiating treatments. Where longer-term data exists, it has been shown that legacy effects such as altered soil chemistry can persist for an extended period of time (Nsikani 2017). It would be valuable to determine the relationship between long-term vegetation recovery and potentially related variables such as soil chemistry, or vegetation richness and plant density.

In a study conducted at Blaauwberg Nature Reserve, both passive and active restoration treatments were surveyed for two years after initial clearing to compare methods in terms of native vegetation recovery following alien clearing (Chapter 3). This may not determine the most effective treatment in the long term since different vegetation components dominate the community at different times during succession (Hoffman *et al.* 1987). Long-term management costs will also be dependent on rates of invasive alien plant re-establishment which would be hard to predict based only on short term data.

Ecological modelling is an important tool to better understand ecosystem properties and processes, by using simplified characteristics of a system (Jørgensen 1994). Models can be developed and adapted to applications ranging from ecosystem responses to invasion (Le Maitre *et al.* 2011), to informing management for habitat or species conservation (Arosa *et al.* 2017; Bastos *et al.* 2012) or in modelling vegetation dynamics (Scheffer *et al.* 1993). Data from short-term studies of ecological processes can be scaled up in order to better understand long-term ecosystem dynamics (Rastetter *et al.* 2003). Models are static when parameters are fixed, in which case they are unable to estimate structural changes when habitat conditions are substantially changed (Jørgensen and De Bernardi 1997). This can be overcome with dynamic models that capture both structural and composition patterns in systems experiencing long-term environmental disturbances (Santos *et al.* 2011). The ecological study of active and passive restoration described above can also be improved by the use of ecological dynamic models that can simulate conditions that are difficult or impossible to understand otherwise (e.g. environmental conditions not present in the study area, alternative management practices, stochastic disturbances) (Jørgensen and Bendoricchio 2001). Furthermore, dynamic modelling can also be useful in forecasting the outcome of alternative contrasting scenarios, therefore guiding management options based on predicted future targets.

The main objective of this study was to anticipate and evaluate the efficiency of several contrasting restoration techniques using a dynamic modelling tool to support decision-making. We achieved this goal by developing the following aims: (1) to determine whether dynamic models reproduce realistic fynbos vegetation recovery following invasive plant control; (2) to determine the impact of different restoration treatments on invasive and native vegetation recovery and cost in the long term; (3) to detect potential restoration thresholds and treatments which could facilitate their reversal.These aims were investigated through application of our innovative approach in order to predict long-term recovery following alien plant clearing. Data were collected at a restoration study site at Blaauwberg Nature Reserve, located in the Cape Floristic Region of South Africa. The lowlands of this region are at present highly modified, leaving little intact natural habitat (Newbold *et al.* 2016) confined to small fragments, most of which are degraded due to invasion by alien species (Rebelo *et al*. 2006). A number of entire lowland fynbos vegetation types are threatened with extinction as a result, including the critically endangered Cape Flats Sand Fynbos (Rebelo *et al.* 2006). The potential of the proposed modelling approach and respective simulation results are discussed in the context of future management of the Cape Flats Sand Fynbos and alien clearing protocol.

4.3 Methods

4.3.1 Study area

Blaauwberg Nature Reserve is located within the largest remaining area of critically endangered Cape Flats Sand Fynbos, just north of the city of Cape Town, South Africa (33.75°S, 18.48°E; Figure 1). This is a vegetation type confined to deep sandy soil of low pH at low altitudes, within a strongly Mediterranean climate region of hot dry summers and cool wet winters. Due to the extended duration of invasion by *Acacia saligna* the native vegetation has been much degraded, lacking cover and much of the diversity of structural component species that are typical of this vegetation type.

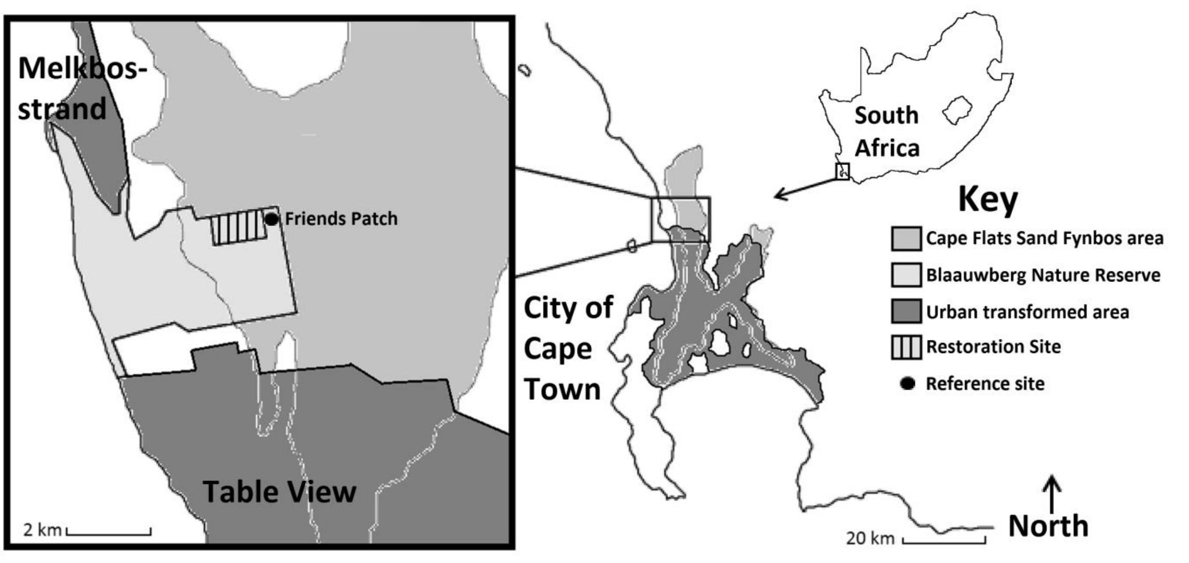


Figure 1. Location of the study area at Blaauwberg Nature Reserve north of the city of Cape Town, within the Western Cape province of South Africa.

4.3.2 Restoration treatments

Two different clearing treatments were applied at Blaauwberg to a block of 32ha each and compared as follows: (a) Stack-block (acacias were cut and stacked into brush piles), and (b) Burn-block (acacia slash spread evenly and the whole area burnt; Figure 2). Follow-up clearing took place at 12 months after initial clearing (Krupek *et al.* 2016) in order to control acacia recruitment. Since the duration of invasion appeared to have resulted in depletion of most of the native seed bank, clearing alone would not facilitate restoration of the native vegetation cover and diversity (Holmes 2002; Kettenring and Adams 2011). Within the Burn-block treatment, an active restoration intervention was further conducted involving sowing seeds of a mix of fynbos structural component species. This procedure was performed twice, initially a month after the managed burn, and again a year later. The later sowing treatment was divided into two sub-treatments, one with seeds sown without pre-treatment while the other had seeds treated with an appropriate combination of heat pulse and smoke to stimulate seed germination (Hall *et al.* 2016, Chapter 2). These treatments were compared with vegetation at two reference sites, one unburnt and one recovering following a wildfire at the same time as the managed burn took place at Blaauwberg.

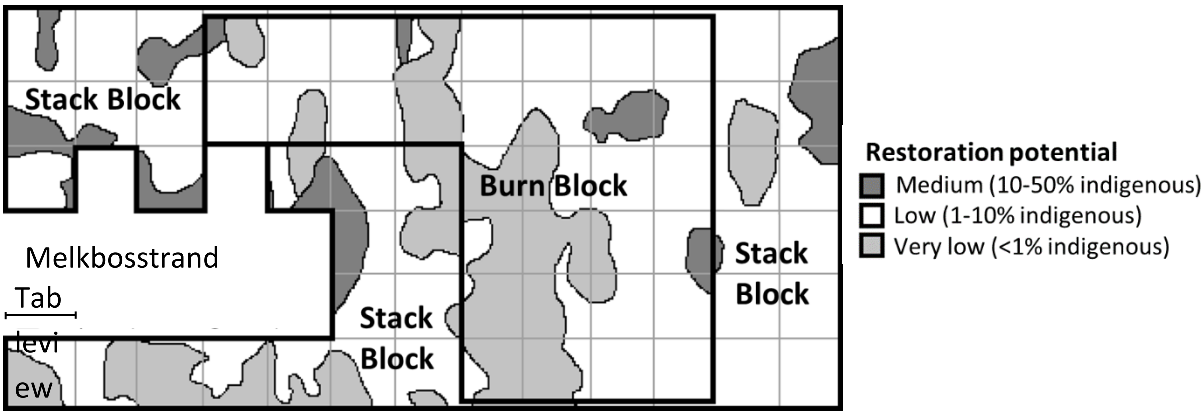


Figure 2. The treatment setup implemented at Blaauwberg Nature Reserve. Each small block is one hectare; 32ha Burn-block treatment was nested within the surrounding Stack-block treatment. Active sowing treatments were set up within Burn-block plots.

4.3.3 Sampling strategy

Thirty-two plots of 5x10 metres were marked in each of the two passive treatments (Figure 2, see Taylor (1984) for plot methodology), with a second plot adjacent to each Burn-block plot for the initial sowing treatment. In the second year a plot was marked out adjacent to 10 of the Burn-block plots for the follow-up sowing treatment. Five plots were marked in burnt and five in unburnt vegetation at the reference site. Data were collected for indigenous cover, species richness and plant density, as well as soil chemistry in each plot of each treatment. These data were collected immediately before clearing, and again at 6 month intervals up to two years after clearing. Plant species were grouped according to vegetation growth form (Non-sprouting Shrub, Resprouting Shrub, or Restio). The change in vegetation cover between each survey was used to determine rates of recovery of the different growth forms. The costs associated with each treatment were recorded, which included the initial clearing of the site and either stacking or spreading of slash, burning the stack piles versus Block-burn, follow-up clearing of acacia recruits under different treatments, and cost of acquiring and sowing seed.

4.3.4 Dynamic model conceptualization

Fynbos vegetation dynamics were modelled in order to anticipate the effects of different alien plant clearing treatments on expected long-term recovery of both acacia and fynbos vegetation cover. Other related parameters within the ecosystem - species richness, plant density, and soil chemistry – may be correlated with cover of different vegetation components, and where this was found to be the case these parameters could be estimated as well.

In this context, the developed dynamic modelling approach, based on the System Dynamics fundamentals (Sterman 2001), is composed of four main sub-models aiming to: a) recreate the vegetation dynamics based on different surface covers, b) estimate associated environmental parameters of community structure and soil composition correlating with vegetation cover, c) test different management scenario treatments and d) calculate the associated economic costs based on invasive alien vegetation clearing effort (Figure 3).

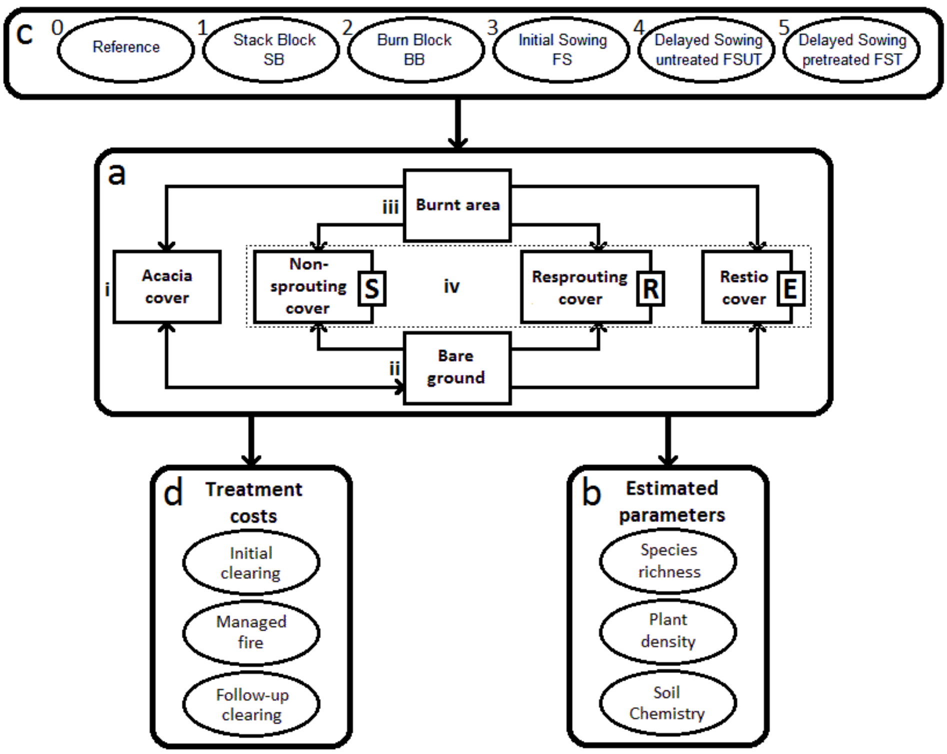


Figure 3. Conceptual diagram of the dynamic model used to simulate changes in vegetation cover under different alien clearing treatment scenarios. The sub-components of the model are grouped as follows: a) vegetation dynamics based on ground cover classes i-iv including vegetation components E, R and S, b) emergent indicators of community structure and soil composition, c) management scenario treatments 0-5 and d) associated management costs.

The month was chosen as time unit and the simulation period was established for 360 months (i.e. 30 years), a robust period to test multiple follow-up clearing interventions and incorporating a suitable period in which fynbos vegetation could reach a climax community following disturbance (Kruger 1984). All modelling procedures were performed using the software STELLA, version 10.0.5® (Isee Systems, Inc.). The original conceptual diagram of the overall sub-models and full explanation of processes, parameters and equations included into the model construction are available in Appendices 2 and 3.

4.3.5 Vegetation cover and Life-form components

The main vegetation covers included in the model (Figure 3b) were: i) acacia, characterized by areas dominated by *Acacia saligna*, the dominant cover before clearing that provides the greatest competition against fynbos reestablishment, ii) bare ground, characterized by areas lacking woody vegetation cover after acacia clearing in degraded sites, iii) burnt area, characterized by areas lacking woody vegetation cover as a result of fire, and iv) native perennial cover, characterized by areas of non-sprouting shrubs (S), resprouting shrubs (R) and restios (E), for which higher cover is a general goal of restoration. Perennial growth forms were chosen based on Hoffman et al. (1987), except for the exclusion of Proteaceae and herbaceous cover from the model since Proteaceae were generally absent from the site while herbaceous species account for insignificant cover in mature pristine vegetation. Ericoid shrubs were divided into non-sprouting and resprouting shrub cover since these groups have different yet important life-history strategies in this system (Le Maitre 1992), and along with restios should make up the majority of mature vegetation cover.

4.3.6 Vegetation regeneration dynamics

In order to recreate the succession between the main vegetation components considered (section 4.3.5), regeneration rates based on sampling data were included as parameters in the model. Monthly growth rates (MGR) were calculated by taking the average monthly fractional change in cover across all plots for each treatment separately, and incorporated into the following formula: $MGR = [(1 + ATGR)\exp(1/ITIY)] - 1$, where ATGR is the total growth rate, given by the vegetation component's current extent at the study area divided by their potential spread area, and ITIY is the invasion time interval, given by the number of months during which time the rates were calculated from the collected data.

Additionally, the rates of competition between different vegetation components were also included in the model. Where acacia is present, it competes with all native vegetation components by growing faster and taller which shades out fynbos underneath, while in a pristine ecosystem different fynbos vegetation components will compete with each other due to different growth rates and life-history strategies. Competition between vegetation components was calculated by dividing the annual change in cover of each growth form by 12 to get the monthly rates of change and then dividing this value for each growth form by each other to get a ratio of the monthly rate of change in cover between each growth form. Competition rates between native growth forms were solely considered in reference sites due to the very low cover of native vegetation growth forms in restoration sites.

4.3.7 Implementation of acacia control treatments

The interaction between the acacia control treatments (Figure 3c) and vegetation growth forms (Figure 3a) represents the main local influences for forecasting treatment effectiveness. Combinations of treatment options were therefore implemented in the dynamic model depending on the scenario chosen (Figure 3c), and this influenced vegetation cover through activation of different rates of increase in vegetation percentage cover as illustrated in Table 1. Specific settings of parameter activation within treatments are detailed in Table 2.

Pristine vegetation has higher diversity and larger seed banks of native vegetation components in comparison with degraded vegetation which has competition from acacias (Le Maitre *et al.* 2011). This was incorporated into the model as different growth rate potential of vegetation components depending on whether a site is invaded or not. When initial and follow-up clearing took place all acacia cover was converted to bare ground, while a managed fire resulted in all vegetation cover being converted to burnt area. This was colonized over time by vegetation components, with rates of increase in cover being dependent on the treatment activated. Furthermore, fire stimulated germination of acacias from the seed bank (Jeffery *et al.* 1988) thus accelerating the rate of increase in percentage cover after a burn took place. This was based on the rate recorded following Burn-block treatment in the field.

Wild fires are typical and recurrent events that markedly shape fynbos ecosystems (Kruger 1984), and its effects were simulated for reference fynbos vegetation scenarios but not in the restoration treatments since a restoration site would likely exclude wildfire due to limited native cover until intact cover is successfully restored. Therefore, wild fires were included in the dynamic model as stochastic phenomena, and average trends of wildfire impacts were measured by running 100 repeated independent simulations. Wildfires were mediated by parameters that reproduce the random fire occurrences at the study region during dry summer months between November and March (Esler *et al.* 2014). In the model, fire events were therefore restricted to the time before month 4 (April) or after month 10 (October) in the simulation, and within these times it was possible to change the chances of a fire taking place depending on local conditions or known fire frequency at a specific site. The post-fire succession was included in the vegetation cover dynamics by using temporal growth rates of each vegetation component based on rates recorded after fire in reference site fynbos in this study.

Seed sowing can counter the effect of lower rates of increase in cover of native vegetation where native seed banks have been depleted, resulting in increased shrub cover after sowing seeds in bare or burnt ground (Gaertner, Nottebrock, *et al.* 2012). Timing of sowing after clearing or burning, and whether or not seeds are pre-treated, will affect subsequent vegetation growth rates. Therefore after sowing treatment was activated in the model it influenced certain native vegetation growth rates as well as competitive effect on acacia cover, depending on what seed sowing scenario was used.

4.3.8 Management scenarios

In order to compare the effectiveness of the different combinations of restoration treatment options, five scenarios were implemented based on experiments tested in the field (for more information about the description of scenarios and selected treatment options see Table 1, for parameter settings for treatments see Table 2). The five scenarios considered for the study areas throughout the entire simulation period were: (0) Reference condition - Vegetation consisted of fynbos shrub components alone and the only impact was stochastic wildfire events after which fynbos components recovered and experienced competitive interactions; (1) Stack-block - Invaded vegetation was cleared of acacia without managed fire, so any fynbos cover present at each clearing event was left to recover based on the recovery rates recorded for this treatment; (2) Burn-block - Invaded vegetation was cleared of acacia followed by managed fire, after which the resulting burnt ground (occupying the entire site) was colonized by fynbos and acacia based on the recovery rates recorded for this treatment; (3) Initial Seed Sowing – This scenario followed the same initial path as the Burn-block treatment but the rates of acacia and fynbos recovery changed immediately after managed fire; (4) Delayed sowing with untreated seeds – This treatment followed the same initial path as the Burn-block treatment but the vegetation recovery rates changed a year after managed fire to rates recorded for sowing with un-treated seed; and (5) Delayed sowing with pre-treated seeds – This treatment followed the same path as for scenario 4 but the growth rates were those recorded for sowing with pre-treated seed.

4.3.9 Indicators of community structure and soil composition

To assess environmental factors responding as ecological indicators of community structure and soil composition being potentially affected by vegetation recovery (Figure 3b), several parameters associated with site characteristics were considered (Table 3). A principal components analysis (PCA) was performed using Canoco 4.5 (Ter Braak and Smilauer 2002) to determine which of these parameters were influencing the outcome of different treatments in particular directions. The selected parameters were tested for pairwise correlation using Spearman's rho correlation coefficient and only predictors with correlation lower than 0.7 were considered (Elith *et al.* 2006; Wisz and Guisan 2009). In the case of correlated pairs of predictors, we chose the one with the most direct ecological impact on plant species distributions (Guisan and Zimmermann 2000).

In order to assess the long-term influence of different alien clearing treatments on these indicators, Generalized Linear Models GzLMs were implemented to test for relationships between independent and dependant variables. The independent variables were bare ground, burnt area, acacia cover, restio cover, non-sprouting and resprouting cover (Figure 3a) while the dependant variables were plant species richness and density, as well as soil chemistry (Table 3). For plant species richness and density GzLMs, a Poisson variance distribution and a log link function were used, whereas for soil chemistry parameters, a Gaussian distribution and an identity link function were fitted to assess the best model supporting the data. All (valid) combinations of explanatory variables for the dependent variables were considered (Burnham and Anderson 2002) and the best model was selected among candidate models according to the lower value of the Akaike Information Criterion (AIC, Hurvich and Tsai 1989). This was incorporated into the dynamic model construction, following the principles of the Stochastic Dynamic Methodology (StDM) (Santos *et al*., 2011). The statistical analyses were carried out using R software (R Core Team 2015). Most parameters had higher than 20% correlation value and thus were considered to be explained by the model vegetation components; parameters with lower than 20% correlation value were considered to be insufficiently well explained by modelled vegetation components and were excluded from further analysis.

Table 1. Descriptions for the five modelled scenarios and reference state, showing which treatment options are activated in each scenario, as well as rational behind testing each scenario.

Name of Scenario	Symbol	Wildfire option	Invaded site	First clearing	Fire management	Followup clearing	Sowing management	Delayed Sowing	Pre-treated seed	Rational	Reference
Stack-Block	SB		1	1		1				Limit disturbance to standing vegetation	Holmes 1989
Burn-Block	BB		1	1	1	1				Stimulate native seed to germinate and deplete Acacia seed	Holmes 1989
Initial Fynbos sowing	FS		1	1	1	1	1			Reintroduce lost native vegetation structural components	Ruwanza et al 2013
Delayed sowing untreated seed	FSUT		1	1	1	1		1		Wait until after most intense follow-up clearing to decrease potential disturbance	Harwayne et al 2008
Delayed sowing pretreated seed	FST		1	1	1	1		1	1	Treat seed to increase germination success of species requiring heat/smoke cues.	Hall 2016
Reference state	REF	1								Comparison with pristine vegetation after burning	

Table 2. The description of all parameters and the respective settings considered within the model simulations. Parameters are set at the values indicated depending on whether or not the treatment involves an invaded or a reference vegetation state, and values are in the unit of measurement specified.

Parameters	Setting	Units of measurement	Set value in restoration treatments	Set value for reference state
Chances for fire to occur	Wildfire option	inverse probability	NA	10
Length of simulation without management	Invaded site	time duration (months)	NA	360
Initial Acacia cover	Invaded site	Percentage cover	70	0
Initial Bare cover	Invaded site	Percentage cover	0	0
Initial Burnt cover	Invaded site	Percentage cover	0	100
Initial E cover	Invaded site	Percentage cover	10	0
Initial R cover	Invaded site	Percentage cover	10	0
Initial S cover	Invaded site	Percentage cover	10	0
Clearing time after initial	First clearing	point in time (months)	2	NA
Clearing period	First clearing	time duration (months)	120	NA
Number of clearing cycles per simulation	First clearing	point in time (months)	3	NA
Management fire time after first clearing	Fire management	point in time (months)	2	NA
Followup clearing time after first clearing	Followup clearing	point in time (months)	12	NA

4.3.10 Economic assessment

Costs of initial clearing, burning and sowing (for scenarios where these treatments were activated) were constant values based on costs recorded for these treatments in the field. Costs of follow-up clearing treatments were simulated as a function of acacia cover at each clearing time. This utilized an equation based on the known cost of follow-up clearing for the acacia cover recorded in the field for each treatment, which increased or decreased follow-up costs in the model depending on whether acacia cover in the simulation was higher or lower than that in field experiments. Rates of change in costs were different for each of the scenarios in the field (Figure 3c), and this was therefore incorporated into the model.

4.4 Results

4.4.1 Effectiveness of management scenarios

Each management scenario resulted in different recovery trajectories (Figure 4). However, in terms of fynbos structural recovery neither the passive nor the active treatments resembled a reference state even after extended periods of time. In terms of acacia reinvasion potential and total native perennial cover the sowing treatments resembled an uninvaded state more closely with time.

Modelled vegetation cover is illustrated over the simulation period in Figure 4 and the percentage cover is shown in Table 4 and Figure 5. Over the course of the simulation the Burn-block treatment had the highest rate of increase in percentage acacia cover, although decreasing over time (13.72% total cover after 360 months). The delayed sowing treatments both had lowest rates of increase in percentage acacia cover (0.31% for untreated and 1.51% for pre-treated seed). Rate of increase in percentage non-sprouting shrub cover was highest in the initial sowing treatment (80.79%), and along with all other sowing treatments was much higher even than the reference site (16.49%), while there was almost no recovery in the Burn-block treatment (0.49%). Rate of increase in percentage resprouting shrub cover was lowest in the initial sowing treatment (1.44%), but higher in the delayed pre-treated sowing treatment (5.93%). Across all restoration treatments, Burn-block and Stack-block treatments had almost the same rates of increase in percentage resprouting shrub cover (13.12 and 13.2% respectively). Rate of increase in percentage restio cover was highest within the delayed pre-treated sowing treatment (3.97%), while in Stack-block the restio cover slowly decreased over time from 10% to 6.68%. Other scenarios showed almost no recovery of restio cover after burning (1.05% in Burn-block, 1.53% in initial sowing and 0.9% in delayed untreated sowing). Both resprouting shrub and restio cover was much higher in the reference site (21 and 31% after 360 months respectively) than across all invaded scenarios.

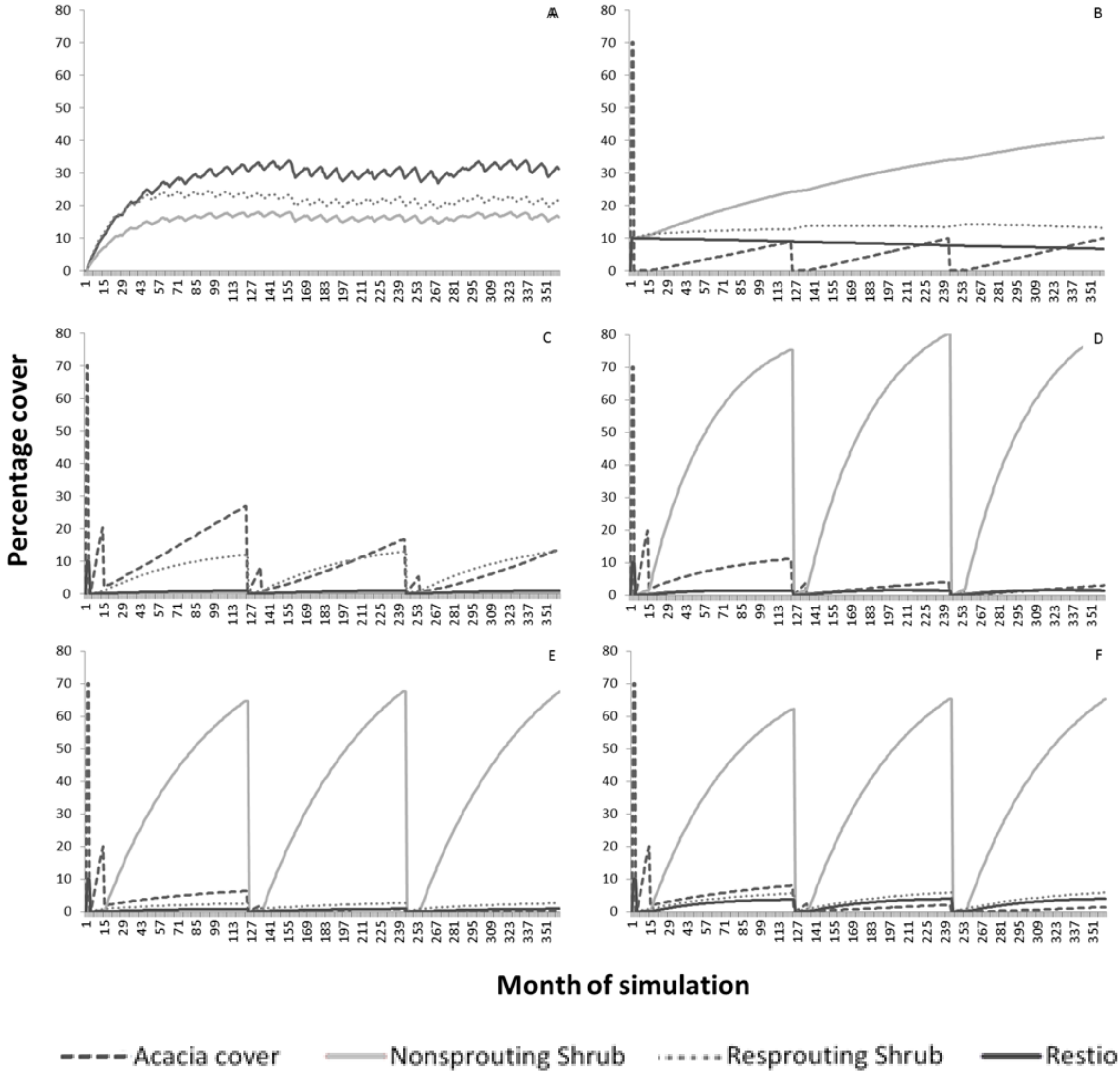


Figure 4. Model simulations of vegetation cover (acacia, non-sprouting shrub cover, resprout cover and restios) throughout 360 months of simulation, including the stochastic occurrence of fires in the reference scenario (simulation with 100 replications), as well as alien clearing and managed fire in relevant scenarios every 120 months. (A) Scenario 0: Reference. (B) Scenario 1: Stack-block. (C) Scenario 2: Burn-block. (D) Scenario 3: Initial Sowing. (E) Scenario 4: Delayed Sowing untreated seed. (F) Scenario 5: Delayed Sowing pre-treated seed.

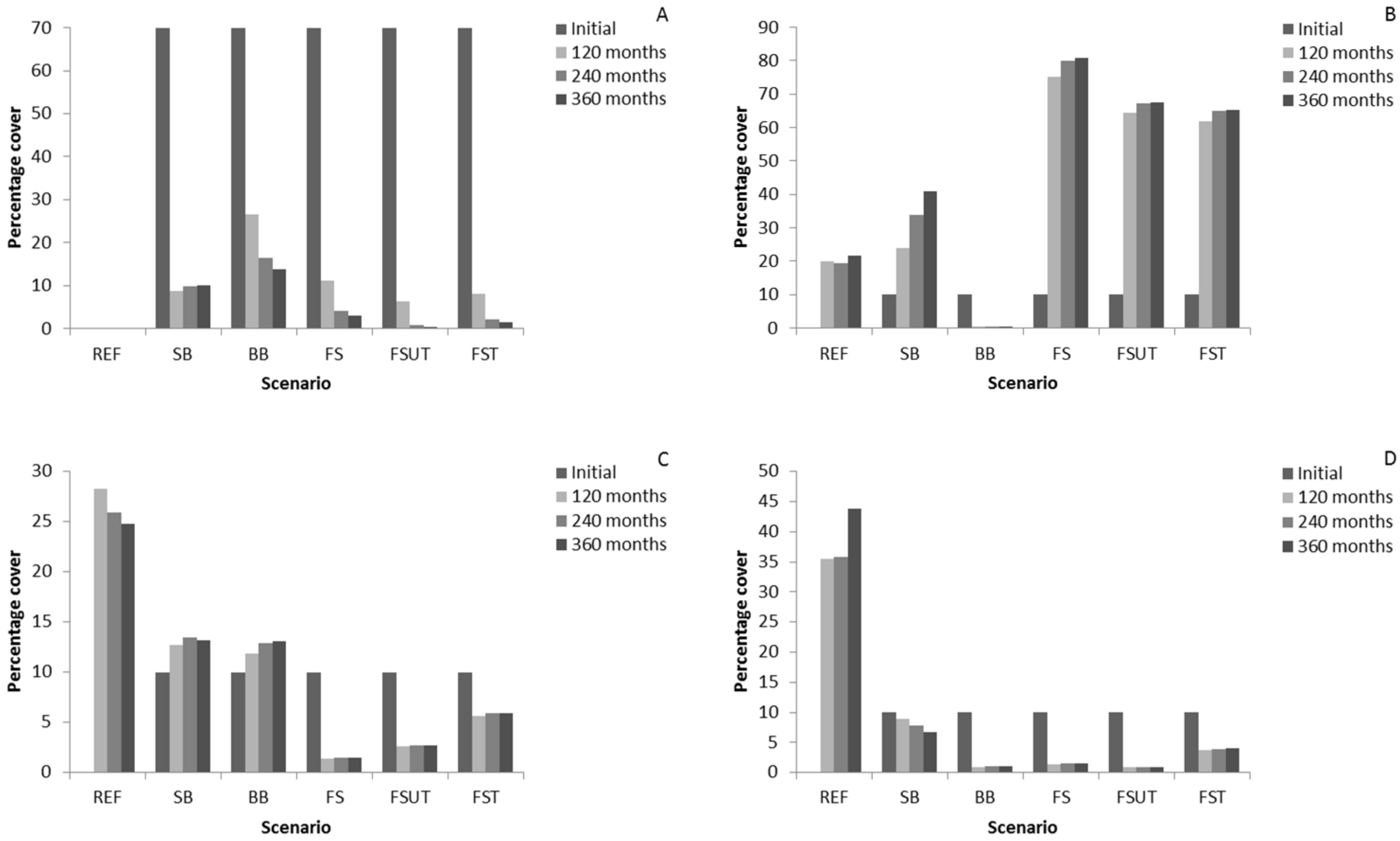


Figure 5. Percentage cover of acacia (A), Non-sprouting shrubs (B), Resprouting shrubs (C) and Restios (D), according to 4 time frames (t = 1, t = 120, t = 240 and t = 360) in each scenario considered: Scenario 0 - reference site (REF), Scenario 1 – Stack-block (SB), Scenario 2 – Burn-block (BB), Scenario 3 - Initial Fynbos-sown (FS), Scenario 4 - Delayed untreated seeds Fynbos-sown (FSUT), Scenario 5 - Delayed pretreated seeds Fynbos-sown (FST).

4.4.2 Cause-effect relationships between acacia control treatments and emergent indicators of community structure and soil composition

Results of the correlation analysis within soil chemistry (Table 3) showed that moisture, carbon (C), ammonium (NH_4), nitrate (NO_3) and phosphate (P) were explained to at least some extent by the modelled vegetation components with a minimum correlation value of 24%. Only soil ammonium increased while all other variables decreased with increasing overall vegetation cover. Apart from geophyte richness, species richness and plant density of all vegetation components showed a minimum correlation value of 27% with cover of the modelled vegetation components.

Table 3. Percentage correlation of parameters estimated from the modelled vegetation components, as well as effect on parameters of an increase in native and alien cover. Parameters tagged * had higher than 20% correlation value and were considered to be explained by the model vegetation components.

Parameter	model code	correlation %	acacia cover	native cover	total cover
log total carbon	log C	26% *	negative	negative	N
electrical conductivity	EC	13%	NA	NA	
log soil moisture	log Moist	35% *	negative	negative	N
log total nitrogen	log N	9%	NA	NA	
ammonium	NH_4^+	38% *	positive	positive	P
log nitrate	log NO_3^-	24% *	negative	negative	N
log phosphate	log P	46% *	negative	negative	N
log pH	log pH	<1%	NA	NA	
restio spp richness	ERich	54% *	negative	positive	X
resprouting shrub spp richness	RRich	47% *	negative	positive	X
non-sprouting shrub spp richness	SRich	27% *	positive	positive	P
geophyte spp richness	BRich	19%	negative	positive	X
graminoid spp richness	GRich	30% *	negative	negative	N
herbaceous spp richness	HRich	38% *	positive	NA	P
restio plant density	EDens	74% *	negative	positive	X
resprouting shrub plant density	RDens	76% *	negative	X	X
non-sprouting shrub plant density	SDens	42% *	positive	positive	P
geophyte plant density	BDens	43% *	0	positive	P
graminoid plant density	GDens	31% *	positive	0	P
herbaceous plant density	HDens	37% *	positive	0	X

Species richness, plant density and soil chemistry differed in all treatments from the reference vegetation, based on estimations of these variables from vegetation cover. The resulting estimated values of these variables at the end of the simulation are shown in Table 4. All treatments had lower richness of restios (maximum 2 vs. 3 spp.) and resprouters (maximum 2 vs. 5 spp.) than in reference sites. Fynbos-sown plots had the highest richness (16 spp.) although mostly due to non-sprouting shrubs (9 spp.), while Burn-block treatment resulted in lowest richness overall (9 spp.), apart from graminoids (4 spp.). Lower shrub species richness was predicted in delayed sowing treatments (8-10 vs. 12 spp.). The Burn-block treatment had lowest plant density including all components (21 plants in total). Non-sprouting shrub density was comparable between Stack-block treatment (21 plants) and the reference site (20 plants), while all sown treatments had much higher density than the reference site (31-54 vs. 20 plants). All sowing treatments also had increased restio and herbaceous density but not that of resprouters. For soil chemistry, C (2.07-2.17 vs. 1.88%), NO_3^- (4.49-5.81 vs. 2.65mg/kg) and P (3.37-4.81 vs. 1.56mg/kg) were similar for all invaded treatments but higher than the reference. NH_4^+ was lower in the Burn-block treatment (5.55mg/kg) but higher in all other treatments (42.95-83.34mg/kg) than the reference, especially in all sowing treatments (67.1-83.34mg/kg). Soil moisture content was higher for all treatments (0.32-1.10%) than the reference (0.15%), but particularly high for the Burn-block treatment (1.10%).

4.4.3 Economic assessment

Cost accumulation of different treatments under scenarios is illustrated in Figure 6 and total cost Figures are shown in Table 4. In terms of costs per treatment, after the first clearing cycle Stack-block was the cheapest method at R17,505 ($1,347) per ha, followed by Burn-block at R44,536 ($3,426) per ha, and active sowing treatments were most expensive at R52,520 ($4,040) per ha. However, the accumulated cost after three clearing cycles in Stack-block came to R24,277 ($1,867) per ha, while the active sowing treatment with pre-treated seeds came to R75,173 ($5,783) per ha and the Burn-block treatment was the most expensive treatment in the long term at R85,044 ($6,542) per ha.

Table 4. Results of different treatments at the end of 360 months simulated. Cover is expressed by the percentage (%) of the plot area, richness is the average number of species per plot, plant density is number of plants per m^2, soil chemistry is expressed by % for C, P and moisture, and mg/kg for NH_4^+ and NO_3^-. Follow-up cost is calculated in South African Rands.

	Cover %				Species richness					Plant Density					Soil chemistry					Treatment cost in Rands	
Treatment	Acacia	S	R	E	E	R	S	G	H	E	R	S	G	H	C	NH_4^+	NO_3^-	P	moist	1 follow-up	3 follow-ups
Reference site	0	22	27	44	3	5	5	2	2	28	13	20	12	11	1.88	16.51	2.65	1.56	0.15	NA	NA
Stack-block SB	9.98	40.91	13.20	6.68	1	2	5	2	2	8	7	21	4	10	2.07	42.95	4.49	3.37	0.47	17505	24277
Burn-block BB	13.72	0.49	13.12	1.05	0	2	1	4	2	1	5	4	5	6	2.17	5.55	5.59	4.81	1.10	44536	85044
Fynbos-sown FS	3.06	80.79	1.44	1.53	2	1	9	1	3	12	5	54	3	19	2.10	83.34	5.38	4.11	0.32	52546	78497
Delayed sowing untreated FSUT	0.31	67.6	2.72	0.9	1	1	6	1	3	8	5	31	4	17	2.15	70.2	5.81	4.37	0.52	52520	73538
Delayed sowing pretreated FST	1.51	65.3	5.93	3.97	2	1	7	1	3	11	6	35	4	15	2.12	67.1	5.27	3.82	0.45	52520	75173

Key

Restioid shrub	E
Resprouting shrub	R
Non-sprouting shrub	S
Graminoid	G
Herbaceous	H
Soil Carbon	C
Soil Nitrate	NH_4^+
Soil Ammonia	NO_3^-
Phosphorous	P
Effective soil moisture	moist

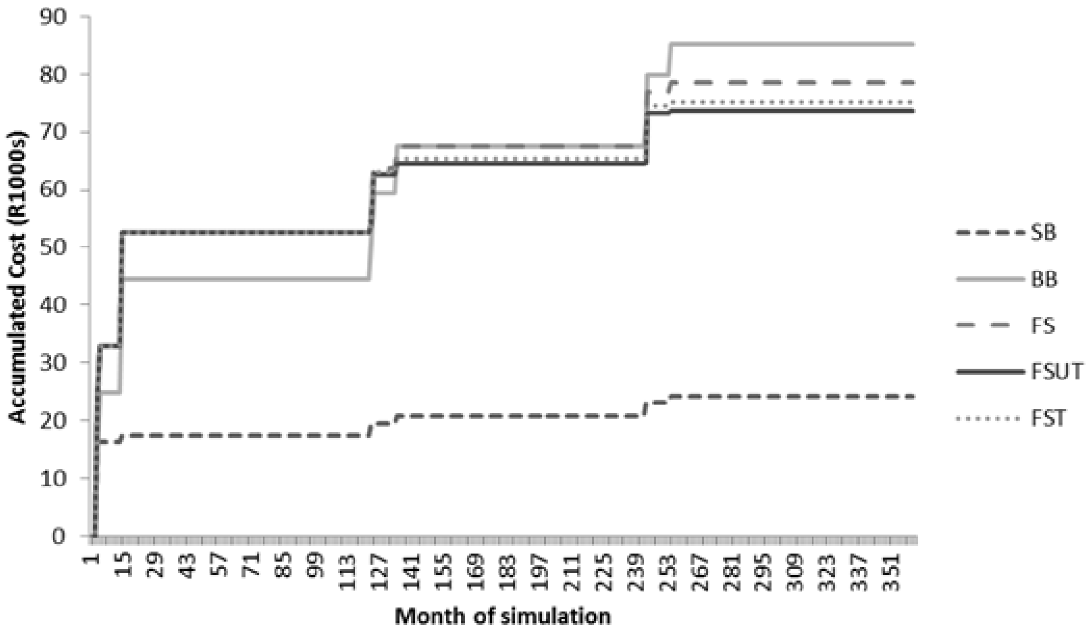


Figure 6. The average economic expenditure (R1000/ha) predicted for each scenario considered, throughout 360 months of simulation. SB – Stack-block treatment, BB – Burn-block treatment, FS – initial Fynbos-sowing, FSUT – follow-up untreated Fynbos-sowing, FST – follow-up pre-treated Fynbos-sowing.

4.5 Discussion

The main aim of this study was to demonstrate how an innovative dynamic modelling approach can be applied to compare and optimise the effectiveness of five alien plant clearing treatments in terms of fynbos recovery and acacia control, as well as costs of each method.

4.5.1 Simulated ecological succession and recovery after invasive plant control

It is important that models of ecosystem dynamics can be used to support management decision-making on a broader scale, as hypothesized by Le Maitre *et al.* (2011) and demonstrated for example by Rastetter *et al.* (2003). The model developed using our data showed that the reference scenario was capable of simulating the system dynamics of pristine fynbos in terms of key structural components and their response to periodic wildfires. Vegetation cover was shown to be within the range of that recorded for mature fynbos plots, and compared well with that found by Hoffman *et al.* (1987). At community level, the emergent richness of modelled components and soil chemistry were also predicted within what would be expected based on plot data from the field experiments in this study. However, plant density was not well estimated, likely because of the large change in number of plants within a plot over time as vegetation matures.

In acacia-invaded vegetation, the Burn-block treatment showed the highest rate of increase in acacia cover following clearing, which was expected since *Acacia saligna* is adapted to recruit after fire (Richardson and Kluge 2008). The sowing treatment, although also burnt, had the lowest rate of increase in acacia cover, since the high shrub cover provided competition against colonization by acacias or herbaceous weeds. This agrees with several studies from around the world which found that active revegetation can prevent further invasion (Kettenring and Adams 2011; Vranjic *et al.* 2012). Other studies found seeding after wildfires to decrease the abundance of invasive annuals (Pyke *et al.* 2013), and cover of invasive plants (Falk *et al.* 2013) although this was dependent on establishment success and post-fire age at assessment.

4.5.2 Impact of restoration treatments on native vegetation recovery and costs of treatments

Restoration treatments have been compared in terms of vegetation recovery in several other studies (Wilson and Gerry 1995; Ruwanza *et al.* 2013; Daehler and Goergen 2005). However, these studies only compared treatments up to at most four years after treatment initiation. In our study, the Stack-block treatment resulted in highest percentage cover of restios and resprouting shrubs in the long term, but this was due to persistence of plants that were present before clearing. Where these species have been lost they will likely remain absent due to a lack of fire, since fire is necessary for stimulating germination of many fynbos species where seeds are present in the soil (Holmes and Cowling 1997). However, there was limited native vegetation recovery especially of non-sprouting shrubs in the Burn-block treatment, which is likely due to a combination of a depleted indigenous seed bank (Holmes 2002) and competition from acacia on the few native species re-establishing from seed (Musil 1993). The high establishment success of shrub cover from the sowing treatment was furthermore sustained over the long term, assuming follow-up clearing. An active seed sowing treatment was also found to benefit restoration in studies from other regions (Wilkerson *et al.* 2014), since propagule limitation was otherwise a barrier to ecosystem restoration following invasive alien plant removal (Kettenring and Adams 2011).

Restoration studies do not often evaluate cost effectiveness of different treatments being compared (Kettenring and Adams 2011), which makes it hard to determine which method should be chosen when budgets are limited.

A key objective of this model is to determine the most ecologically- and cost-effective fynbos restoration treatment. Although the Stack-block treatment was the cheapest option, a greater long-term investment will likely be required for secondary invasive control in areas lacking indigenous shrub cover (Blanchard and Holmes 2008; French *et al.* 2008), or else the area may revert to a highly invaded state thus failing in the treatment objective as found in numerous restoration studies by Pearson *et al.* (2016). Since cost of control of secondary invaders was not included, factoring in this aspect would likely make the stacking treatment significantly more expensive (Loo *et al.* 2009).

The fynbos sowing treatments were initially the most expensive methods. However, the increased establishment success of shrub cover resulted in decreased potential for establishment of invasive alien acacias, and by the second follow-up clearing this treatment became cheaper than burning alone. This agrees with Le Maitre *et al.* (2011) who indicate that longer term cumulative costs following seed sowing could be lower than continued higher management costs of removing acacia or secondary invaders.

4.5.3 Anticipating restoration thresholds and using modelled treatments in decision-making to facilitate their reversal

The long-term projected low post-clearance recovery in treatments without sowing shows that restoration is constrained by seed-limitation, and is suggestive that an ecological threshold has been crossed given the data incorporated into the model from the present study. Gaertner *et al.* (2012) describe different thresholds, including biotic and abiotic as well as structural and functional. Passive treatments resulted in limited recovery even over an extended period of time. In the unburnt treatment, the lack of shrub cover left a niche in which secondary invasive species established with time. This has been found in many restoration studies (e.g., Pearson *et al.* 2016) where removal of a target species resulted in recovery by secondary invaders rather than the desired native species. Secondary invaders, including alien grasses, tend to accumulate biomass faster than indigenous shrub species and increase the risk of too-frequent fires, negatively impacting native vegetation recovery (Vilà *et al.* 2001). This prevents native shrub cover from building up an adequate seed bank, favouring domination by fast-maturing grasses and resulting in an alternative stable state of herbaceous cover rather than perennial shrubs.

Active sowing is able to at least partially overcome the constraint of seed limitation and reverse the biotic and structural thresholds if these have been crossed, by restoring some of the structural elements and diversity of the vegetation as well as decreasing acacia recovery potential. However, initial fynbos sowing resulted in poor recovery of resprouting shrub and restio cover even after a long period of time. Delayed sowing resulted in better recovery of resprouting shrub cover and decreased acacia cover. Pre-treating seeds using appropriate heat and smoke cues (Brown 1993; Jeffery *et al.* 1988; Hall *et al.* 2016) further improved recovery of resprouting shrub as well as restio cover relative to initial fynbos sowing, but these components still never reestablished a level of cover or diversity comparable to a reference site. Effectively restoring these components will likely require planting out rooted material in addition to seed, which is more costly but would decrease the risk of failure during early seedling establishment (Godefroid *et al.* 2011; Davy 2002).

Abiotic and functional thresholds may also have been crossed due to the changes in soil chemistry which are sustained over the long term as predicted by the model. This was also found by Marchante et al. (2009) in spite of attempting to reduce excess soil C and N, which suggests a legacy effect of invasive plant impact on soil chemistry (Gaertner, Holmes, *et al.* 2012; Corbin and D'Antonio 2012; Von Holle *et al.* 2013). However, the fact that shrub cover reestablished in sowing treatments suggests that abiotic thresholds were not crossed.

It may not be feasible to expect to restore a degraded site to a reference condition, and perhaps the short-term goal should rather be to reinstate vegetation structure in support of key ecosystem functions (Gaertner, Nottebrock, *et al.* 2012). This would still be important for conservation since representative structure will provide suitable habitat for reintroduction of range-restricted species and those of conservation concern, such as *Erica verticillata* and *E. turgida* which are extinct in the wild and being reintroduced to structurally representative Cape Flats Sand Fynbos habitat (Hitchcock *et al.* 2012).

4.5.4 Use of this model approach to inform future management and alien clearing protocol

Models have been used to inform management related to invasive alien plant clearing protocols, and planning where to focus clearing efforts most effectively (Higgins *et al.* 2000). Restoration treatments have also been compared from projected outcomes using models to simulate long-term trends (Arosa *et al.* 2017). In this case the simulation was extrapolated over 100 years, which showed treatments to follow trends not evident over short time periods.

It is important to stipulate the desired outcomes of the restoration action. In the case of the study used here, the goal was fynbos biodiversity conservation, as well as resilience to future invasion. Vegetation cover of indigenous shrub species as well as species richness are linked with resilience (Peterson *et al.* 1998) since this decreases opportunities for invasive alien plant establishment, and these measures are therefore a potentially useful proxy for long term ecosystem stability and resilience.

The results from application of our modelling approach can provide management recommendations with the use of longer term projections of how vegetation will likely respond to different treatments when only short term data are available. Another goal when developing methods for assessing changes in the ecological status of natural ecosystems is the feasibility of application and extent to which the results can be applied in other areas. Different site conditions e.g. initial vegetation cover or rates of increase in cover can also be incorporated into the model where this data exists, in order to make assessments over a wider range of conditions, as well as determining where restoration is likely to be unsuccessful.

When compared to other methodologies, dynamic modelling has the advantage of being adaptable to local management requirements (objectives and parameters) in specific contexts. Although Species Distribution Models (SDMs) have been widely applied in predicting species distributions under global change scenarios, their deterministic assumptions and the lack of integration with dynamic and/or stochastic processes limit the accuracy in capturing ecological responses under scenarios of more local changes (Kandziora *et al.* 2013; Zurell *et al.* 2009). In contrast, our approach represents a step forward in anticipating the regional consequences of invasive tree control treatments on fynbos recovery under dynamic scenarios of post-fire ecological succession.

4.5.5 Conclusions and implications for fynbos conservation

The analysis of long-term fynbos dynamics under realistic scenarios represents a big challenge to optimise conservation management strategies, namely by anticipating future ecological consequences associated with invasive tree species. Therefore, since the best treatment is site-dependent, the benefit of this type of modelling can be determined by incorporating data from sites in different locations or ecosystems. This model provides a more effective tool to determine restoration potential than direct comparison of field data, since long-term competitive effects between native and alien vegetation components (e.g. the effect of non-sprouting shrub on acacia reestablishment) are not apparent in the initial dataset. Furthermore, these long-term effects translate into changes in follow-up clearing costs between different treatments, and in this case predicted that the most expensive treatment initially is not the most expensive over a longer time-span. .

According to our model simulation results, the forthcoming conservation actions are advised for the management of acacia-invaded fynbos vegetation:

- Presence of native vegetation cover and diversity post-clearing is dependent on its presence within the site before initial clearing, and therefore Stack-block treatment would only be advisable in such situations where all native vegetation components are still abundant.
- Areas of low native cover and diversity show poor recovery of vegetation components under both passive treatments; therefore active sowing treatment would be the best method to use in such cases in order to increase indigenous diversity and cover as well as resilience to secondary invasions.

- Delaying seed sowing until after one follow-up clearing as well as pre-treatment of seeds facilitates establishment of an increased diversity of vegetation components and at a decreased long-term cost due to poorer acacia recovery.

Moreover, the delineation of the specific actions outlined above, focused on successful acacia removal and restoration of perennial fynbos shrub cover, must be mandatory to prevent loss of fynbos and development of an alternate stable state. In conclusion, we highlight the interplay between dynamic model-based research and ecological monitoring, namely by testing and validating the resultant simulations with real future ecological trends associated with restoration treatments to mitigate the impacts of invasive alien species, which will make our proposal more instructive and credible to decision-makers and environmental managers.

4.6 References

Arosa, M. L., Bastos, R., Cabral, J. A., Freitas, H., Costa, S. R., Santos, M. (2017) Long-term sustainability of cork oak agro-forests in the Iberian Peninsula: A model-based approach aimed at supporting the best management options for the montado conservation. *Ecol. Modell.*. **343**, 68–79.

Bastos, R., Santos, M., Ramos, J. A., Vicente, J., Guerra, C., Alonso, J., Honrado, J., Ceia, R. S., Timóteo, S., Cabral, J. A. (2012) Testing a novel spatially-explicit dynamic modelling approach in the scope of the laurel forest management for the endangered Azores bullfinch (*Pyrrhula murina*) conservation. *Biol. Conserv.*. **147**, 243–254.

Blackwood, J., Hastings, A., Costello, C. (2010) Cost-effective management of invasive species using linear-quadratic control. *Ecol. Econ.*. **69**, 519–527.

Blanchard, R., Holmes, P. M. (2008) Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. *South African J. Bot.*. **74**, 421–431.

Brown, N. A. C. (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytol.*. **123**, 575–83.

Burnham, K. P., Anderson, D. R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* 2nd edn. Springer.

Corbin, J. D., D'Antonio, C. M. (2012) Gone but Not Forgotten? Invasive Plants' Legacies on Community and Ecosystem Properties. *Invasive Plant Sci. Manag.*. **5**, 117–124.

D'Antonio, C., Meyerson, L. A. (2002) Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis. *Restor. Ecol.*. **10**, 703–713.

Daehler, C. C., Goergen, E. M. (2005) Experimental Restoration of an Indigenous Hawaiian Grassland after Invasion by Buffel Grass (*Cenchrus ciliaris*). *Restor. Ecol.*. **13**, 380–389.

Davy, A. J. (2002) Establishment and manipulation of plant populations and communities in terrestrial systems. In: *Handbook of Ecological Restoration. Principles of Restoration, vol. 1.* (eds M. R. Perrow & A. J. Davy) pp. 223–241 Cambridge University Press, Cambridge.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., Ewers, R. M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.*. **22**, 489–96.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Esler, K. J., Pierce, S. M., De Villiers, C. (2014) *Fynbos : ecology and management*. Briza Publications, Pretoria.

Falk, A. D., Fulbright, T. E., Smith, F. S., Brennan, L. a., Ortega-Santos, A. J., Benn, S. (2013) Does Seeding a Locally Adapted Native Mixture Inhibit Ingress by Exotic Plants? *Restor. Ecol.*. **21**, 474–480.

French, K., Ens, E., Gosper, C. R., Lindsay, E., Mason, T., Owers, B., Sullivan, N. (2008) Management implications of recent research into the effect of bitou bush invasion. *Plant Prot. Q.*. **23**, 24–28.

Gaertner, M., Holmes, P. M., Richardson, D. M. (2012) Biological invasions, resilience and restoration. In: *Restoration Ecology: The new frontier* (eds J. Andel & J. Aronson) pp. 265–280 Oxford: Wiley-Blackwell.

Gaertner, M., Nottebrock, H., Fourie, H., Privett, S. D. J., Richardson, D. M. (2012) Plant invasions, restoration, and economics: Perspectives from South African fynbos. *Perspect. Plant Ecol. , Evol. Syst.*. **14**, 341–353.

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R., Cowell, C., Weekley, C. W., Vogg, G., Iriondo, J. M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjureke, K., Koopman, R., Vicens, M., Virevaire, M., Vanderborght, T. (2011) How successful are plant species reintroductions? *Biol. Conserv.*. **144**, 672–682.

Guisan, A., Zimmermann, N. E. (2000) Predictive habitat distribution models in ecology. *Ecol. Modell.*. **135**, 147–186.

Hall, S. A., Newton, R. J., Holmes, P. M., Gaertner, M., Esler, K. J. (2016) Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type. *Austral Ecol.*. **42**, 354–366.

Hewitt, C. L., Campbell, M. L., McEnnulty, F., Moore, K. M., Murfet, N. B., Robertson, B., Schaffelke, B. (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. *Biol. Invasions*. **7**, 251–263.

Higgins, S. I., Richardson, D. M., Cowling, R. M. (2000) Using a dynamic landscape model for planning the management of alien plant invasions. *Ecol. Appl.*. **10**, 1833–1848.

Hitchcock, A., Cowell, C., Rebelo, T. (2012) The lost fynbos of Tokai Park. *Veld Flora*. **98**, 30–33.

Hoffman, M. T., Moll, E. J., Boucher, C. (1987) Post-fire succession at Pella, a South African lowland fynbos site. *South African J. Bot.*. **53**, 370–374.

Von Holle, B., Neill, C., Largay, E. F., Budreski, K. A., Ozimec, B., Clark, S. A., Lee, K. (2013) Ecosystem legacy of the introduced N_2-fixing tree *Robinia pseudoacacia* in a coastal forest. *Oecologia*. **172**, 915–924.

Holmes, P. M. (2002) Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecol.*. **27**, 110–120.

Holmes, P. M., Cowling, R. M. (1997) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrubland. *J. Appl. Ecol.*. **34**, 317–332.

Holmes, P. M., Macdonald, I. A. W., Juritz, J. (1987) Effects of Clearing Treatment on Seed Banks of the Alien Invasive Shrubs *Acacia saligna* and *Acacia cyclops* in the Southern and South-Western Cape, South Africa. *J. Appl. Ecol.*. **24**, 1045–1051.

Holmes, P. M., Richardson, D. M., Van Wilgen, B. W., Gelderblom, C. (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecol.*. **25**, 631–639.

Hulme, P. E. (2006) Beyond control: wider implications for the management of biological invasions. *J. Appl. Ecol.*. **43**, 835–847.

Hurvich, C. M., Tsai, C.-L. (1989) Regression and time series model selection in small samples. *Biometrika*. **76**, 297–307.

Jeffery, D. J., Holmes, P. M., Rebelo, A. G. (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. *South African J. Bot.*. **54**, 28–34.

Jørgensen, S. E. (1994) Models as instruments for combination of ecological theory and environmental practice. *Ecol. Modell.*. **75**–**76**, 5–20.

Jørgensen, S. E., Bendoricchio, G. (2001) *Fundamentals of Ecological Modelling*. third ed. Elsevier, Amsterdam.

Jørgensen, S. E., de Bernardi, R. (1997) The application of a model with dynamic structure to simulate the effect of mass fish mortality on zooplankton structure in Lago di Annone. *Hydrobiologia*. **356**, 87–96.

Kandziora, M., Burkhard, B., Müller, F. (2013) Interactions of ecosystem properties, ecosystem integrity and ecosystem service indicators—A theoretical matrix exercise. *Ecol. Indic.*. **28**, 54–78.

Keeley, J. E., Bond, W. J. (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecol.*. **133**, 153–167.

Kettenring, K. M., Adams, C. R. (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *J. Appl. Ecol.*. **48**, 970–979.

Kruger, F. J. (1984) Fire in fynbos. In: *Ecological Effects of Fire in South African Ecosystems, Ecological Studies* (eds P. de V. Booysen & N. M. Tainton) pp. 68–114Springer-Verlag, Berlin.

Krupek, A., Gaertner, M., Holmes, P. M., Esler, K. J. (2016) Assessment of post-burn removal methods for *Acacia saligna* in Cape Flats Sand Fynbos, with consideration of indigenous plant recovery. *South African J. Bot.*. **105**, 211–217.

Levine, J. M., Vilà, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. Biol. Sci.*. **270**, 775–781.

Loo, S. E., Mac Nally, R., O'Dowd, D. J., Lake, P. S. (2009) Secondary Invasions: Implications of Riparian Restoration for In-Stream Invasion by an Aquatic Grass. *Restor. Ecol.*. **17**, 378–385.

Le Maitre, D. C. (1992) The relative advantages of seeding and sprouting in fire-prone environments: a comparison of life histories of Protea neriifolia and Protea nitida. In: *Fire in South African Mountain Fynbos* (eds B. W. van Wilgen, D. M. Richardson, F. J. Kruger, & H. J. van Hensbergen) pp. 123–144 Springer-Verlag, Berlin.

Le Maitre, D. C., Gaertner, M., Marchante, E., Ens, E. J., Holmes, P. M., Pauchard, A., O'Farrell, P. J.,

Marchante, E., Kjøller, A., Struwe, S., Freitas, H. (2009) Soil recovery after removal of the N_2-fixing invasive *Acacia longifolia*: Consequences for ecosystem restoration. *Biol. Invasions*. **11**, 813–823.

Musil, C. F. (1993) Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. *J. Appl. Ecol.*. **30**, 361–372.

Musil, C. F., Milton, S. J., Davis, G. W. (2005) The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. *S. Afr. J. Sci.*. **101**, 337–344.

Nakazawa, Y., McC. Overton, J. M., Townsend Peterson, A., Phillips, S. J., *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.).*. **29**, 129–151.

Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., Palma, A. De, Ferrier, S., Hill, S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C. W. T., Emerson, S., Gao, D., Pask-hale, G., Hutton, J., Jung, M., Sanchez-ortiz, K., Simmons, B. I., Whitmee, S., *et al.* (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science (80-.).*. **353**, 288–291.

Nsikani, M. M., Novoa, A., Van Wilgen, B., Keet, J., Gaertner, M. (2017) *Acacia saligna's* soil legacy effects persist up to 10 years after clearing: Implications for ecological restoration. *South African J. Bot.* **42**, 880-889.

Ortega, Y. K., Pearson, D. E. (2005) Weak vs. Strong Invaders of Natural Plant Communities: Assessing Invasibility and Impact. *Ecol. Soc. Am.*. **15**, 651–661.

Pearson, D. E., Ortega, Y. K., Runyon, J. B., Butler, J. L. (2016) Secondary invasion: The bane of weed management. *Biol. Conserv.*. **197**, 8–17.

Peterson, G., Allen, C. R., Holling, C. S. (1998) Ecological Resilience, Biodiversity, and Scale. *Ecosystems*. **1**, 6–18.

Pyke, D. A., Wirth, T. A., Beyers, J. L. (2013) Does Seeding After Wildfires in Rangelands Reduce Erosion or Invasive Species? *Restor. Ecol.*. **21**, 415–421.

R Core Team (2015). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Rastetter, E. B., Aber, J. D., Peters, D. P. C., Ojima, D. S., Burke, I. C. (2003) Using Mechanistic Models to Scale Ecological Processes across Space and Time. *Bioscience*. **53**, 68–76.

Rebelo, A. G., Boucher, C., Helme, N., Mucina, L., Rutherford, M. C. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland.* (eds L. Mucina & M. C. Rutherford) pp. 52–219 South African National Biodiversity Institute, Pretoria.

Reid, A. M., Morin, L., Downey, P. O., French, K., Virtue, J. G. (2009) Does invasive plant management aid the restoration of natural ecosystems? *Biol. Conserv.*. **142**, 2342–2349.

Richardson, D. M., Kluge, R. L. (2008) Seed banks of invasive Australian *Acacia* species in South Africa: Role in invasiveness and options for management. *Perspect. Plant Ecol. Evol. Syst.*. **10**, 161–177.

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., West, C. J. (2000) Naturalization and invasion of alien plants : concepts and definitions. *Divers. Distrib.*. **6**, 93–107.

Rogers, A. M., Blanchard, R., Blignaut, J., Richardson, D. M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Divers. Distrib.*. **17**, 1015–1029.

Ruwanza, S., Gaertner, M., Esler, K. J., Richardson, D. M. (2013) The effectiveness of active and passive restoration on recovery of indigenous vegetation in riparian zones in the Western Cape, South Africa: A preliminary assessment. *South African J. Bot.*. **88**, 132–141.

Santos, M., Freitas, R., Crespí, A. L., Hughes, S. J., Cabral, J. A. (2011) Predicting trends of invasive plants richness using local socio-economic data: an application in North Portugal. *Environ. Res.*. **111**, 960–6.

Scheffer, M., Bakema, A. H., Wortelboer, F. G. (1993) MEGAPLANT: a simulation model of the dynamics of submerged plants. *Aquat. Bot.*. **45**, 341–356.

Sterman, J. D. (2001) System dynamics modelling: tools for learning in a complex world. *Calif. Manage. Rev.*. **43**, 8-25.

Taylor, H. C. (1984) A vegetation survey of the Cape of Good Hope Nature Reserve. I. The use of association-analysis and Braun-Blanquet methods*. *Bothalia*. **15**, 245–258.

Ter Braak, C. J. F., Smilauer, P. (2002) CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Micro-computer Power, Ithaca.

Vilà, M., Lloret, F., Ogheri, E., Terradas, J. (2001) Positive fire-grass feedback in Mediterranean Basin woodlands. *Ecol. Manag.*. **147**, 3–14.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmánek, M., Westbrooks, R. (1997) Introduced species: A significant component of human-caused global change. *N. Z. J. Ecol.*. **21**, 1–16.

Vranjic, J. A., Morin, L., Reid, A. M., Groves, R. H. (2012) Integrating revegetation with management methods to rehabilitate coastal vegetation invaded by Bitou bush (*Chrysanthemoides monilifera ssp. rotundata*) in Australia. *Austral Ecol.*. **37**, 78–89.

Wilkerson, M. L., Ward, K. L., Williams, N. M., Ullmann, K. S., Young, T. P. (2014) Diminishing Returns from Higher Density Restoration Seedings Suggest Trade-offs in Pollinator Seed Mixes. *Restor. Ecol.*. **22**, 782–789.

Wilson, S. D., Gerry, A. K. (1995) Strategies for Mixed-Grass Prairie Restoration: Herbicide, Tilling, and Nitrogen Manipulation. *Restor. Ecol.*. **3**, 290–298.

Wisz, M. S., Guisan, A. (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecol.*. **9**, 8.

Yelenik, S. G., Stock, W. D., Richardson, D. M. (2004) Ecosystem Level Impacts of Invasive *Acacia saligna* in the South African Fynbos. . **12**, 44–51.

Zurell, D., Jeltsch, F., Dormann, C. F., Schröder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography (Cop.)*. **32**, 733–744.

Chapter 5: Synthesis of findings and implications for management following alien invasion

5.1 Bridging the gap between knowledge and practical implementation

Restoration Ecology and Invasion Biology are synergistic fields, but there is a gap between knowledge and practical implementation within these fields (Gaertner *et al.* 2012; Sitas *et al.* 2014). Although science can inform best practise, there are also many constraints from a management and resource perspective (e.g. Hewitt *et al.* 2005; Krupek *et al.* 2016). This can be solved through transdisciplinary collaborations between scientists and management practitioners (Naveh 2005; Cabin 2007). The present study has helped to close the gap by advancing the current knowledge of how to effectively manage alien-invaded lowland fynbos to optimize the restoration of degraded habitat. This chapter aims to make findings from a research project on restoration following clearing of invasive species accessible to managers involved in invasive species management and biodiversity conservation programmes.

This study covered different aspects of the processes involved in restoring a lowland fynbos ecosystem following alien clearing. Experiments were initiated in the field, which determined the effectiveness of different passive treatments, followed by active restoration interventions involving sowing seeds. Many fynbos species have very specific dormancy breaking cues, and optimal heat and smoke pre-treatments were determined through testing these in the lab on germination success of key structural species used in the active restoration treatments. Recovery trends under different passive and active restoration treatments in the field were simulated using a dynamic model in order to predict long-term (multiple fire intervals time-span) recovery trajectories and potentially determine where ecological thresholds may have been crossed, and which treatments can reverse them.

5.2 Assessing limitations to restoration and potential ecological thresholds

It is valuable to determine constraints to restoration, in order to determine the most effective restoration method to use in a specific site (Kimball *et al.* 2015), or whether restoration is feasible at all (Aronson *et al.* 1993). Sites can therefore be prioritized for management based on restoration potential. The use of a dynamic model to extrapolate the recovery trends following treatments (results of chapter 4) over the longer term (30 years) suggested that biotic thresholds may have been crossed at the study site due to the long duration (> 5 decades) of invasion and multiple fire events resulting in depleted native seed bank and low potential for autogenic recovery. However, the relative success of active sowing treatments (chapter 3) shows that restoration across the site is still feasible, albeit more resource-intensive, in more degraded sites lacking any native seed bank and/or containing a larger primary or secondary invasive alien seed bank. Such sites were usually those lacking any substantial native shrub cover or diversity at the time of initial alien clearing.

In general, where cover and diversity representing the main fynbos structural components persists at the time of initial clearing, there is still a native seed bank remaining, and clearing alone (Figure 1a) or clearing and burning (Figure 1d) is sufficient to facilitate native vegetation recovery and replenishment of the native seed bank (Gaertner *et al*. 2012). However, serotinous proteas will likely have disappeared by this time and since they do not have a soil seed bank they will need to be reintroduced following the next planned management burn (Holmes and Cowling 1997a). Other guilds are less likely to require re-introduction.

Where native cover and diversity is very limited or non-existent, autogenic recovery will likely not take place, since the native seed bank has been depleted (Downey and Richardson 2016) and invasive alien species dominate the seed bank. Such areas are evident where only a few scattered native shrubs are still present (Figure 1b, e), and in some cases there may be no native cover remaining at all (Figure 1c and f). In these cases there will be no autogenic recovery after alien clearing, since most fynbos species are only capable of short dispersal distances (Holmes and Cowling 1997b) and active restoration of all vegetation guilds will be required. This can be done by means of sowing seeds (preferably pre-treated) into these areas (Figure 1g). Soil chemistry has been altered as a result of acacia invasion, as was found by Yelenik *et al.* (2004) and Marchante *et al.* (2009). However, sowing of fynbos seeds still resulted in reestablishment of cover and diversity within certain shrub components suggesting limited detrimental effects if any from altered soil chemistry. Therefore, abiotic thresholds appear not to have been crossed. The process of ecosystem degradation across potential biotic and abiotic thresholds is further illustrated in Figure 2 using the findings from chapters 3 and 4, noting features associated with these thresholds that may be evident in lowland fynbos, as well as necessary interventions for restoring sites in each state.

5.3 Seed ecology considerations

Seed ecology is a vitally important aspect to consider in the process of active restoration (Commander *et al.* 2009). Since alien-invaded lowland habitats are in many cases sufficiently degraded for the native seed bank to have been depleted, seed sowing will be necessary to facilitate shrub and graminoid/restioid recovery, but seeds of most fynbos species will also require pre-treatment in order to stimulate germination. Species should be selected based on their importance as structural components of the vegetation, as well as germination success relative to effort involved in collecting and processing seeds (Waller *et al.* 2015). In terms of practicality it is necessary to also focus on species that produce lots of seeds which are easy to collect. It is important to collect seeds of species in sufficient numbers from a local source within the same habitat as the restoration site, as well as from a range of plants in the population in order to maximise genetic diversity introduced to the restoration site (Vander Mijnsbrugge *et al.* 2010).

Species have specific optimal treatments in terms of enhancing germination, as shown in chapter 2, and making use of these treatments could greatly enhance germination and therefore make more efficient use of often limited quantities of seeds to restore the largest area possible. However, results from the active restoration studies in chapter 3 show that even with optimal seed pre-treatment (as shown in chapter 2) this does not guarantee that these species will necessarily establish successfully in the field. Factors which might play a role here include low seed viability, drought sensitivity or competition from invasive species, as discussed below.

Some species may require higher sowing densities in spite of pre-treatment due to low viability, which was found in *Passerina corymbosa* by Pierce and Moll (1994), while other species may be better able to germinate under nursery conditions to be planted out as seedlings in the field (e.g. *Phylica cephalantha, Trichocephalus stipularis* and *Leucadendron salignum*). This is more labour and resource intensive but would increase likelihood of successful re-establishment of these species, especially in the case of these structurally important resprouting shrubs, as well as any species of conservation concern.

Competition from invasive species is an important issue to consider when sowing seeds (Adams and Galatowitsch 2008), especially resulting from acacia recruitment after burning or increased herbaceous cover without burning. Follow-up control of acacia and secondary invasive species will result in significantly improved establishment success from active sowing intervention (Waller *et al.* 2016; Krupek *et al.* 2016). However, while manual clearing is least detrimental to native establishment, herbicide spraying is more feasible and while it is better than not removing invasive alien seedlings, this treatment does negatively impact native recovery (Krupek *et al.* 2016).

Some species are sensitive to drought stress, as found by Mukundamago (2016) and Mustart et al. (2012). Supplemental irrigation could facilitate more effective establishment, but is unlikely to be feasible on a large scale due to resource limitation. Irrigation does not necessarily have a positive influence on native vegetation establishment (Daehler and Goergen 2005; Clary *et al.* 2004), but rather the absence of competition from invasive species is more important for successful native establishment. Planning restoration work to coincide with wetter years where possible can also facilitate better results (Holmgren and Scheffer 2001).

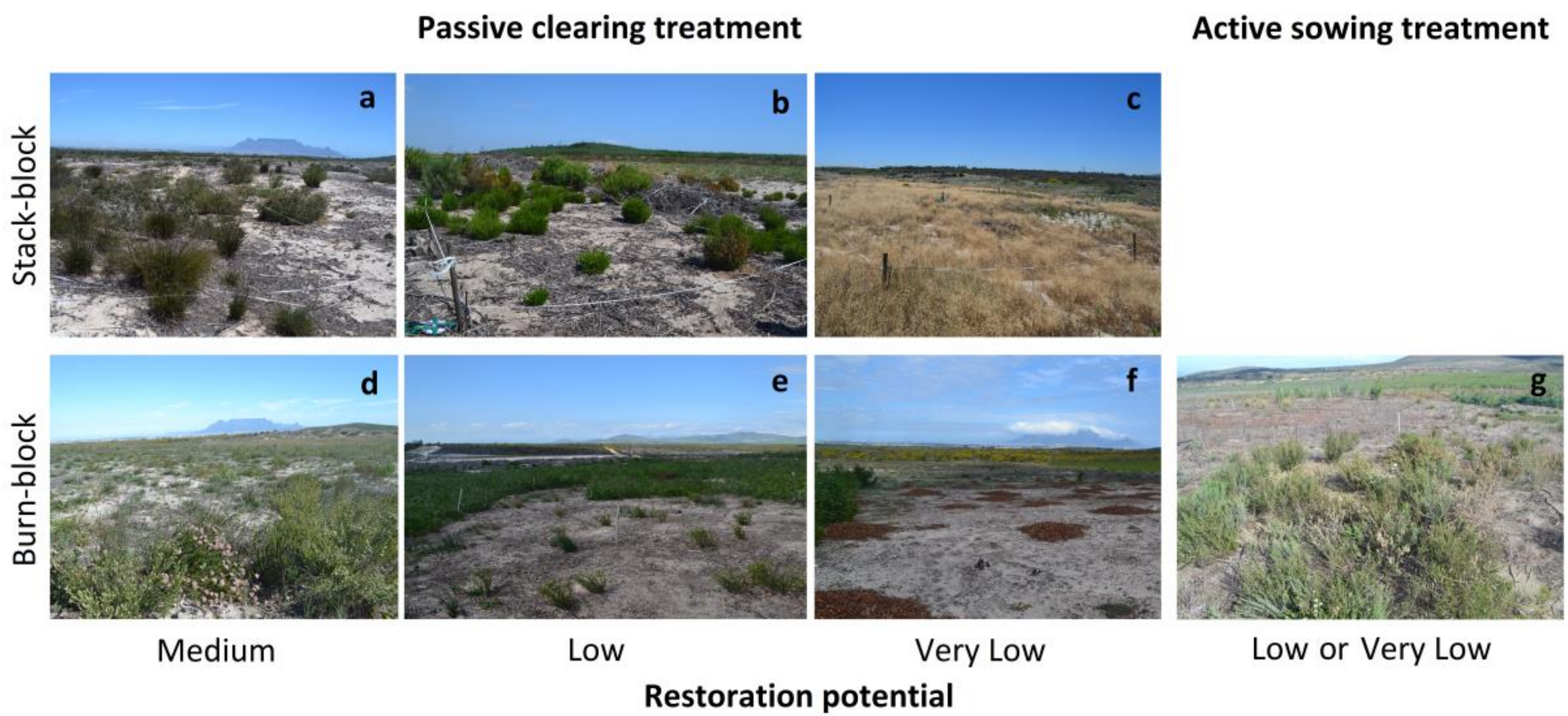


Figure 1. Resulting vegetation recovery under different initial levels of vegetation degradation (restoration potential) following Stack-block and Burn-block passive treatments (after follow-up acacia clearing) and active sowing treatment: (a and d) medium restoration potential - relatively intact vegetation with guilds other than serotinous proteas still present (autogenic recovery possible), recovery of reasonable diversity after burning; (b and e) low restoration potential - highly degraded vegetation with only scattered shrubs of mostly a single ericoid shrub species *Passerina corymbosa* remaining without burning, and few resprouting shrubs present after burning (active restoration necessary); (c and f) extremely degraded and containing no native shrub cover or diversity, secondary invasives dominant without burning but barren after burning apart from acacia recruitment (active restoration necessary); (g) recovery of fynbos vegetation structure after active sowing intervention in either low or very low restoration potential sites.

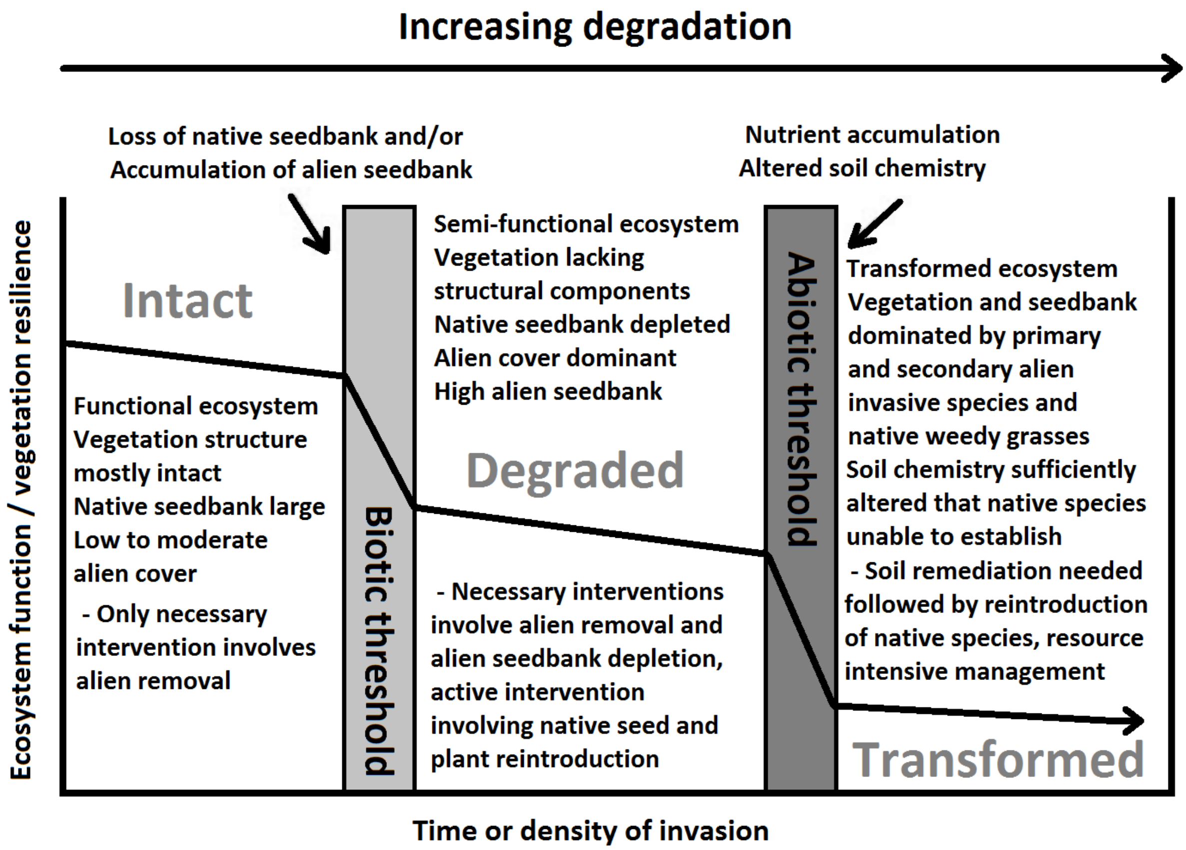


Figure 2. Conceptual threshold model showing what features are associated with biotic and abiotic thresholds being crossed, using the present study site as an example, and the necessary interventions required to reverse these thresholds. Modified from Whisenant (2002).

5.4 Implications for vegetation restoration and conservation

The best restoration treatment to use in the field will depend on the characteristics of the site in question (See Figure 3 for decision tree). Where there is a higher cover of fynbos and higher level of plant diversity representing key vegetation components, then clearing alone will likely be sufficient, with only limited follow-up clearing necessary as long as fire is excluded until invasive alien seed banks have been reduced and indigenous seed banks have recovered (Figure 3a). Clearing alone was also found to be successful for recently invaded vegetation in Portuguese coastal dune systems, although longer invaded sites did not recover as well (Marchante *et al.* 2011). Ideally a site should never be allowed to become degraded to the point that certain vegetation components disappear (Holmes and Cowling 1997a), other than perhaps the overstorey proteoid component. This component is the first to be lost but is possible to restore by seeding just after a managed fire or onto bare soil post-clearance (Holmes 2001). However, in reality much of the remaining fynbos habitat on the lowlands is far beyond this state. It is therefore important to decide firstly where to prioritise restoration efforts based on likely outcomes and chances of success (Holl and Aide 2011), and secondly which treatments work best in different states of degradation.

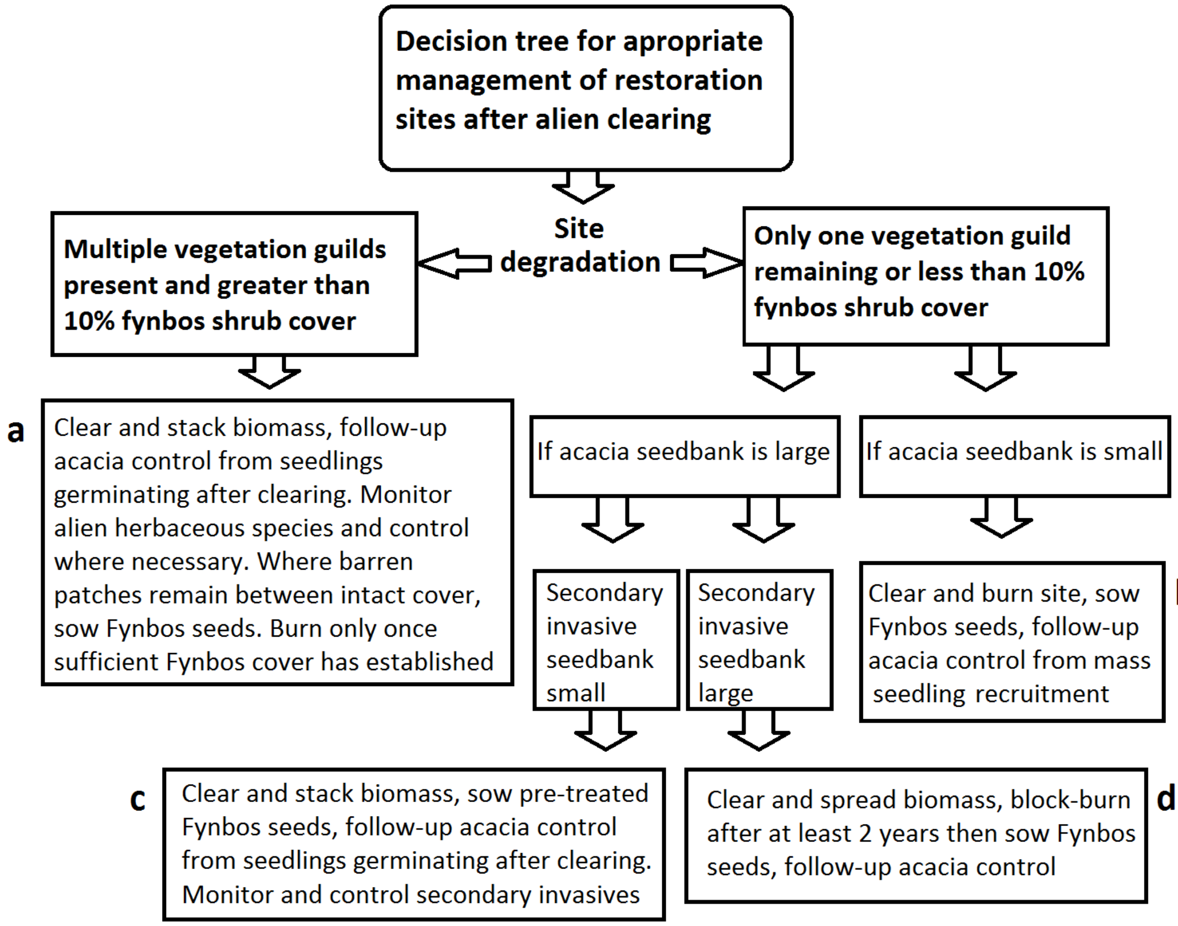


Figure 3. Decision tree for determining best protocol for restoration of lowland fynbos vegetation after initial alien clearing.

In general it is not advisable to burn after clearing acacia without further intervention, since this results in very high rates of acacia regrowth making follow-up clearing extremely labour and resource intensive, which will often make restoration unfeasible unless the acacia seed bank is small, such as in old acacia stands (Strydom *et al.* 2017). The seed bank under Stack-block treatment also becomes reduced by a similar amount as with burning after two years (average 6445 to 1453 seeds/m^2 or almost an 80% reduction) (Chapter 3), and without the mass acacia recruitment observed when burning a few months after initial clearing (Krupek *et al.* 2016).

Burning controls invasive alien annual grasses, but can still allow invasive alien perennial herbaceous species to proliferate from the second winter post-fire if no shrub cover has established during this window period. Sowing of annual herbaceous species can unintentionally spread invasive alien annual species into previously burnt areas if seed collection was done using suction harvester machinery, and therefore care should be taken to limit inclusion of invasive alien species in seed mixes. Sowing of annuals can help to suppress acacia growth initially, but this effect does not persist once the annuals die down in summer, as shown by chapter 3. While this study showed annual sowing to have no positive effect on native shrub establishment success, this may have been negated by the competitive ability of the acacias. When sowing seeds in the absence of mass acacia recruitment, following no burning, or following burning where acacia seed banks are small, including native annuals in the seed mix may be beneficial in providing additional protection to shrub seedlings in the absence of resprouting native shrubs which would usually provide rapid post-fire cover and shelter. Furthermore, when not burning, sowing of native annuals could compete against secondary invasive graminoids (Herron *et al.* 2013).

Sowing a seed mix of fynbos species after burning facilitates better recovery of perennial cover and species richness than either passive treatments or sowing annuals alone. Long-term ecological modelling showed that recovery of vegetation cover is sustained for active sowing treatments of fynbos seed. In contrast, passive treatments fail to recover autogenically even after prolonged periods unless there was already existing fynbos cover at the time of initial clearing (Chapter 4). Pre-treatment of seeds before sowing was beneficial in increasing the number of shrubs establishing as well as species richness for minimal additional cost. The main problem with clearing, burning and sowing seeds at Blaauwberg Nature Reserve was the mass acacia recruitment. In other sites with a smaller acacia seed bank, acacia recruitment may be less of an issue and therefore this treatment would be the best management option (Figure 3b). Delaying sowing by a year after clearing and burning (Fell and Burn treatment) can also be beneficial in that acacia seedlings can be cleared without risking damage to establishing shrubs. However, especially where acacia seed banks are high, delaying burning by at least two years facilitates reduction of the acacia seed bank by a similar proportion to that after burning. After this period of time, burning followed by sowing native shrub seeds will likely be more beneficial since there should be less acacia recruitment competing with shrub seedlings while the burn clears the soil surface facilitating better fynbos establishment.

To conclude, even under sowing treatments, follow-up clearing is vital to prevent establishment of acacias as well as secondary invasives, as was found by Adams and Galatowitsch (2008) in a study on native and invasive alien propagule pressure. Burning after clearing as well as burning followed by active fynbos sowing is much more expensive than passive clearing treatments without initial burning. However, active fynbos sowing with pre-treated seed decreases the long term reinvasion potential of acacias or secondary invasives, and this will in turn significantly decrease the long-term costs of follow-up clearing relative to passive burning treatment.

5.5 Alternative restoration actions to consider

Since clearing without burning leads to much lower rates of acacia recovery, and burning immediately after clearing results in limited fynbos recruitment when acacia seed banks are large, active intervention with sowing pre-treated seeds or planting seedlings after clearing alone (i.e. without initial burning) may be a more economically viable restoration option in sites with a long history of acacia invasion (Figure 3c). Active restoration using pre-treated seeds without incorporating burning into management has been utilised in restoration projects in other Mediterranean-climate regions such as California (Wilkin *et al.* 2013) and South-western Australia (Roche *et al.* 1997). The main problem with this treatment is the potential proliferation of secondary invasive species, and therefore this treatment would work best where seed banks of secondary invasives are relatively small. These species are able to grow quickly and proliferate during the winter/spring growing season when native perennial species require optimal growing conditions in order to establish before the dry summer season. Secondary invasives may be controlled using temporary summer irrigation to reduce exotic seed banks by initiating premature germination of these species (Funk *et al.* 2015; Wainwright *et al.* 2012), or through the use of pre-emergence herbicides (Waller *et al.* 2016). Both interventions would however be resource-intensive and so only viable on a small scale. Alternatively, if both invasive alien annual graminoid and acacia seed banks are in high abundance on a large scale, the site could be left after initial alien acacia clearing for at least two years in order to allow time for acacia seed bank reduction, after which the site can be burnt to reduce the seed bank of annual graminoids and then sown with a fynbos seed mix (Figure 3d). This would facilitate more manageable follow-up control of acacia than burning sooner after initial clearing. Failure to break the cycle of grass dominance will otherwise result in persistence of invasive alien annual grasses (Cox and Allen 2008). Once intact shrub cover has been established this will prevent further invasion by alien grasses (Cione *et al.* 2002; Lindig-Cisneros and Zedler 2002) thus reversing the biotic threshold. Once an indigenous soil seed bank has built up under intact shrub cover, then controlled burning can be implemented.

If restoration is done in a phased approach as opposed to implementing one large-scale project, initial work can be assessed to see if treatments are working and what species are successful at recovering autogenically or establishing from sown seed. Monitoring feedback can therefore adaptively inform management of the best protocol under specific conditions. For fast maturing perennial species, initial treatments can furthermore be used to provide seeds for further sowing treatments. This management approach has been utilized for restoration work in California whereby initial results are used to assess and improve the effectiveness of seed mixtures, active vs. passive restoration, as well as density and clustering of plantings (Harwayne *et al.* 2008).

If it is necessary to initiate restoration at a large site in one season, then it will be important to source sufficient seeds or material for propagation in order to treat the whole site sufficiently, and in order to limit opportunities for secondary invasions or erosion of barren soil. This can be compared to post-mining restoration work in Western Australia, which is underpinned with a scientifically based understanding of all the components involved including: nature of vegetation dynamics, processes of plant community assembly, interaction of the restored biotic community with its environment, technological tools utilized, and application of scientific knowledge and technology in formulating and executing the rehabilitation plan (Mucina *et al.* 2017).

5.6 Concluding remarks

It may not be possible to restore the entire suite of species representative of Cape Flats Sand Fynbos vegetation. Focus should rather be on initially restoring vegetation structure to provide resilience against invasive species establishment, facilitating an appropriate fire regime and providing suitable habitat for reintroduction of rare or threatened species at a later stage. In this case, focus could be given to fewer species that are easy to collect in bulk and that establish well, so long as they represent sufficient structural diversity, to outcompete invasive species and facilitate the return of an appropriate fire regime. Further diversity can be subsequently introduced through planting of seedlings or seeding of less opportunistic species once herbaceous weeds have been outcompeted and acacia follow-up control is more manageable.

5.7 References

Adams, C. R., Galatowitsch, S. M. (2008) The transition from invasive species control to native species promotion and its dependence on seed density thresholds. *Appl. Veg. Sci.*. **11**, 131–138.

Aronson, J., Floret, C., Floc'h, E., Ovalle, C., Pontanier, R. (1993) Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. I. A View from the South. *Restor. Ecol.*. **1**, 8–17.

Cabin, R. J. (2007) Science-Driven Restoration: A Square Grid on a Round Earth? *Restor. Ecol.*. **15**, 1–7.

Cione, N. K., Padgett, P. E., Allen, E. B. (2002) Restoration of a Native Shrubland Impacted by Exotic Grasses, Frequent Fire, and Nitrogen Deposition in Southern California. *Restor. Ecol.*. **10**, 376–384.

Clary, J., Robert, S., Biel, C., Herralde, F. (2004) Water relations in competitive interactions of Mediterranean grasses and shrubs. *Ann. Appl. Biol.*. **144**, 149–155.

Commander, L. E., Merritt, D. J., Rokich, D. P., Dixon, K. W. (2009) Seed biology of Australian arid zone species: Germination of 18 species used for rehabilitation. *J. Arid Environ.*. **73**, 617–625.

Cox, R. D., Allen, E. B. (2008) Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *J. Appl. Ecol.*. **45**, 495–504.

Daehler, C. C., Goergen, E. M. (2005) Experimental Restoration of an Indigenous Hawaiian Grassland after Invasion by Buffel Grass (*Cenchrus ciliaris*). *Restor. Ecol.*. **13**, 380–389.

Downey, P. O., Richardson, D. M. (2016) Alien plant invasions and native plant extinctions : a six- threshold framework. *AoB Plants*. **8**, plw047.

Funk, J. L., Hoffacker, M. K., Matzek, V. (2015) Summer irrigation, grazing and seed addition differentially influence community composition in an invaded serpentine grassland. *Restor. Ecol.*. **23**, 122–130.

Gaertner, M., Fisher, J., Sharma, G., Esler, K. (2012) Insights into invasion and restoration ecology: Time to collaborate towards a holistic approach to tackle biological invasions. *NeoBiota*. **12**, 57–76.

Gaertner, M., Holmes, P. M., Richardson, D. M. (2012) Biological invasions, resilience and restoration. In: *Restoration Ecology: The new frontier* (eds J. Andel & J. Aronson) pp. 265–280 Oxford: Wiley-Blackwell.

Harwayne, J., Worcester, S., Detka, J., Lienk, L. L. (2008) *Draft Final Habitat Restoration Plan Site 39 Inland Ranges Former Fort Ord, California*. Monterey, CA.

Herron, C. M., Jonas, J. L., Meiman, P. J., Paschke, M. W. (2013) Using native annual plants to restore post-fire habitats in western North America. *Int. J. Wildl. Fire*. **22**, 815–821.

Hewitt, C. L., Campbell, M. L., McEnnulty, F., Moore, K. M., Murfet, N. B., Robertson, B., Schaffelke, B. (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. *Biol. Invasions*. **7**, 251–263.

Holl, K. D., Aide, T. M. (2011) When and where to actively restore ecosystems? *For. Ecol. Manage.*. **261**, 1558–1563.

Holmes, P. M. (2001) Shrubland restoration following woody alien invasion and mining: Effects of topsoil depth, seed source, and fertilizer addition. *Restor. Ecol.*. **9**, 71–84.

Holmes, P. M., Cowling, R. M. (1997a) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *J. Appl. Ecol.*. **34**, 317–332.

Holmes, P. M., Cowling, R. M. (1997b) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecol.*. **133**, 107–122.

Holmes, P. M., Cowling, R. M. (1997c) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrubland. *J. Appl. Ecol.*. **34**, 317–332.

Holmgren , M. and Scheffer , M. (2001) El niño as a window of opportunity for the restoration of degraded arid ecosystems . *Ecosystems.* **4**, 151 – 159.

Kimball, S., Lulow, M., Sorenson, Q., Balazs, K., Fang, Y.-C., Davis, S. J., O'Connell, M., Huxman, T. E. (2015) Cost-effective ecological restoration. *Restor. Ecol.*. **23**, 800–810.

Krupek, A., Gaertner, M., Holmes, P. M., Esler, K. J. (2016) Assessment of post-burn removal methods for *Acacia saligna* in Cape Flats Sand Fynbos, with consideration of indigenous plant recovery. *South African J. Bot.*. **105**, 211–217.

Lindig-Cisneros, R., Zedler, J. B. (2002) *Phalaris arundinacea* seedling establishment: effects of canopy complexity in fen, mesocosm, and restoration experiments. *Can. J. Bot.*. **80**, 617–624.

Marchante, E., Kjøller, A., Struwe, S., Freitas, H. (2009) Soil recovery after removal of the N_2-fixing invasive *Acacia longifolia*: Consequences for ecosystem restoration. *Biol. Invasions*. **11**, 813–823.

Marchante, H., Freitas, H., Hoffmann, J. H. (2011) Post-clearing recovery of coastal dunes invaded by *Acacia longifolia*: is duration of invasion relevant for management success? *J. Appl. Ecol.*. **48**, 1295–1304.

Vander Mijnsbrugge, K., Bischoff, A., Smith, B. (2010) A question of origin: Where and how to collect seed for ecological restoration. *Basic Appl. Ecol.*. **11**, 300–311.

Mucina, L., Bustamante-Sánchez, M. A., Duguy, B., Holmes, P., Keeler-Wolf, T., Armesto, J. J., Dobrowolski, M., Gaertner, M., Smith-Ramírez, C., Vilagrosa, A. (2017) Ecological restoration in mediterranean-type shrublands and woodlands. In: *Routledge Handbook of Ecological and Environmental Restoration.* (eds S. Allison & S. Murphy) pp. 173–196 Taylor & Francis, Abingdon, UK.

Mukundamago, M. (2016) *Restoration of Cape Flats Sand Fynbos : The significance of pre-germination treatments and moisture regime.* Stellenbosch University.

Mustart, P. J., Rebelo, A. G., Juritz, J., Cowling, R. M. (2012) Wide variation in post-emergence desiccation tolerance of seedlings of fynbos proteoid shrubs. *South African J. Bot.*. **80**, 110–117.

Naveh, Z. (2005) Epilogue: Toward a Transdisciplinary Science of Ecological and Cultural Landscape Restoration. *Restor. Ecol.*. **13**, 228–234.

Pierce, S. M., Moll, E. J. (1994) Germination Ecology of Six Shrubs in Fire-Prone Cape Fynbos. *Vegetatio*. **110**, 25–41.

Roche, S., Koch, J. M., Dixon, K. W. (1997) Smoke Enhanced Seed Germination for Mine Rehabilitation in the Southwest of Western Australia. *Restor. Ecol.*. **5**, 191–203.

Sitas, N., Prozesky, H., Esler, K., Reyers, B. (2014) Exploring the Gap between Ecosystem Service Research and Management in Development Planning. *Sustainability*. **6**, 3802–3824.

Strydom, M., Veldtman, R., Ngwenya, M. Z., Esler, K. J. (2017) Invasive Australian Acacia seed banks: Size and relationship with stem diameter in the presence of gall-forming biological control agents (ed C. E. Coleman). *PLoS One*. **12**, 1–16.

Wainwright, C. E., Wolkovich, E. M., Cleland, E. E. (2012) Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *J. Appl. Ecol.*. **49**, 234–241.

Waller, P. A., Anderson, P. M., Holmes, P. M., Newton, R. J. (2015) Developing a species selection index for seed-based ecological restoration in Peninsula Shale Renosterveld, Cape Town. *South African J. Bot.*. **99**, 62–68.

Waller, P. A., Anderson, P. M. L., Holmes, P. M., Allsopp, N. (2016) Seedling recruitment responses to interventions in seed-based ecological restoration of Peninsula Shale Renosterveld, Cape Town. *South African J. Bot.*. **103**, 193–209.

Whisenant, S. G. (2002) Terrestrial Ecosystems. In: *Handbook of ecological restoration. Volume 1. Principles of restoration.* (eds M. R. Perrow & A. J. Davy) pp. 83–105 Cambridge University Press, New York.

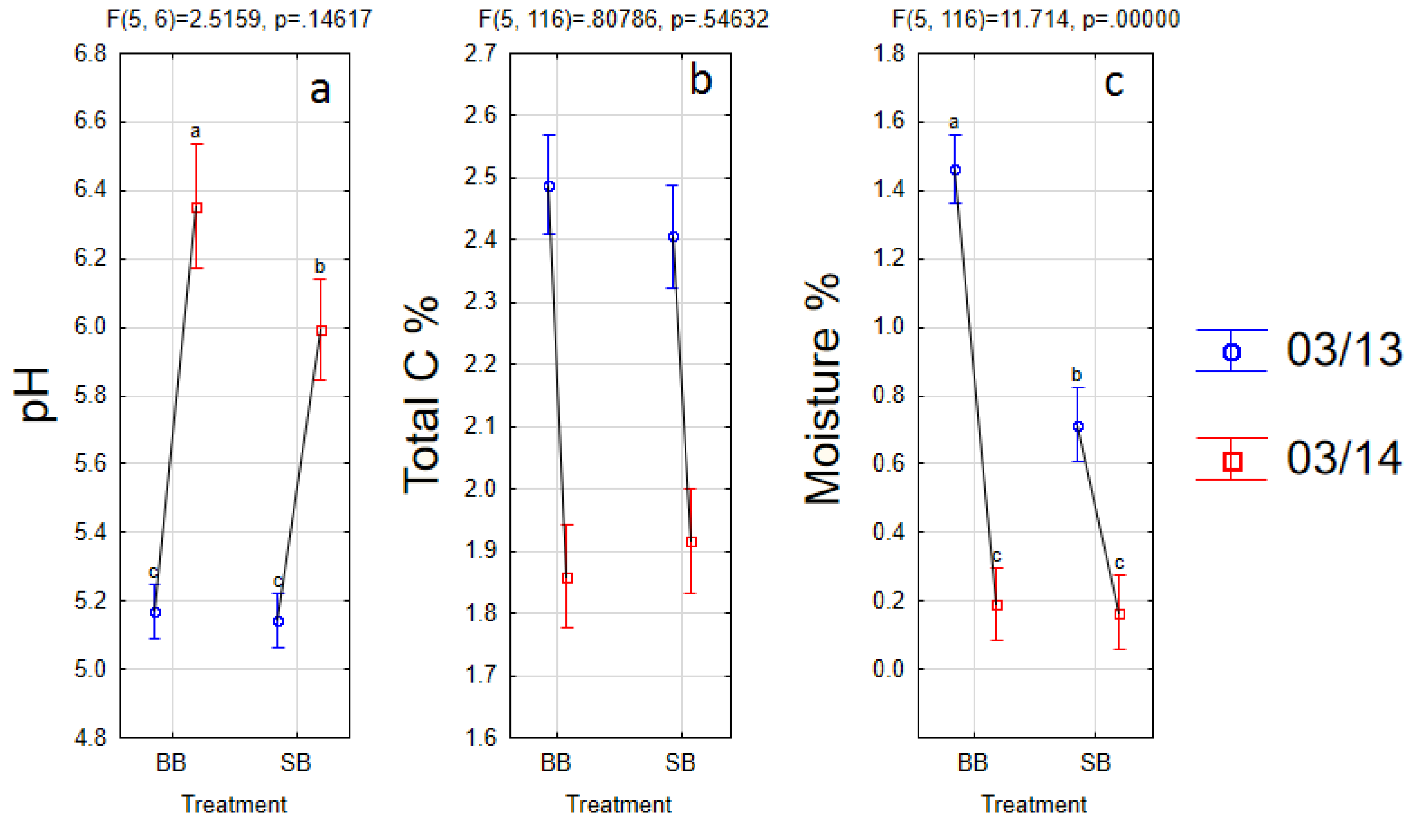
Wilkin, K. M., Holland, V. L., Keil, D., Schaffner, A. (2013) Mimicking Fire for Successful Chaparral Restoration. *Madroño*. **60**, 165–172.

Yelenik, S. G., Stock, W. D., Richardson, D. M. (2004) Ecosystem Level Impacts of Invasive *Acacia saligna* in the South African Fynbos. *Restor. Ecol.*. **12**, 44–51.

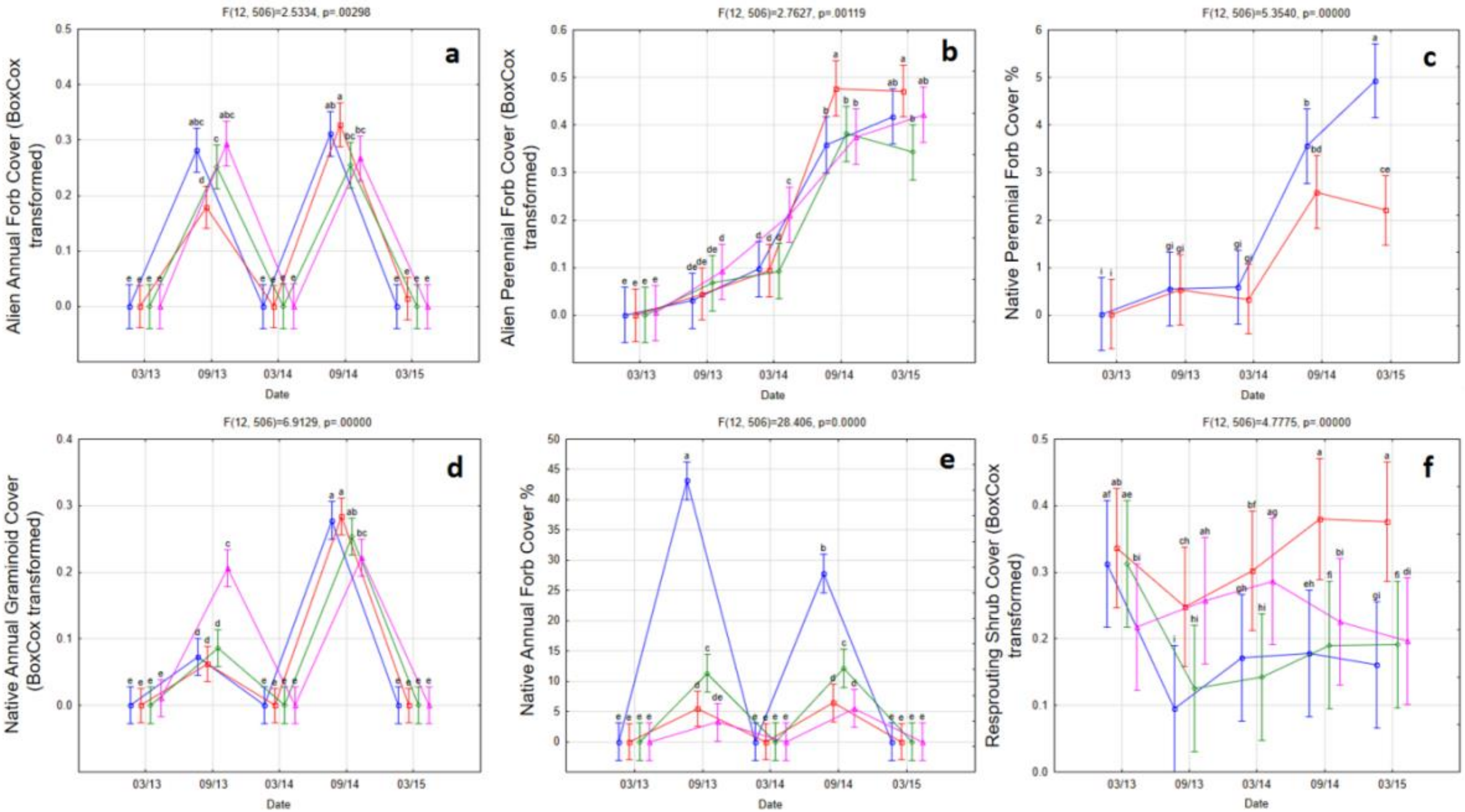
6.1 Appendix 1 – Additional figures for Chapter 3

Appendix 1a. List of species included in active sowing treatments, classified by vegetation guild, seed morphology and pre-treatment used in follow-up sowing experiment.

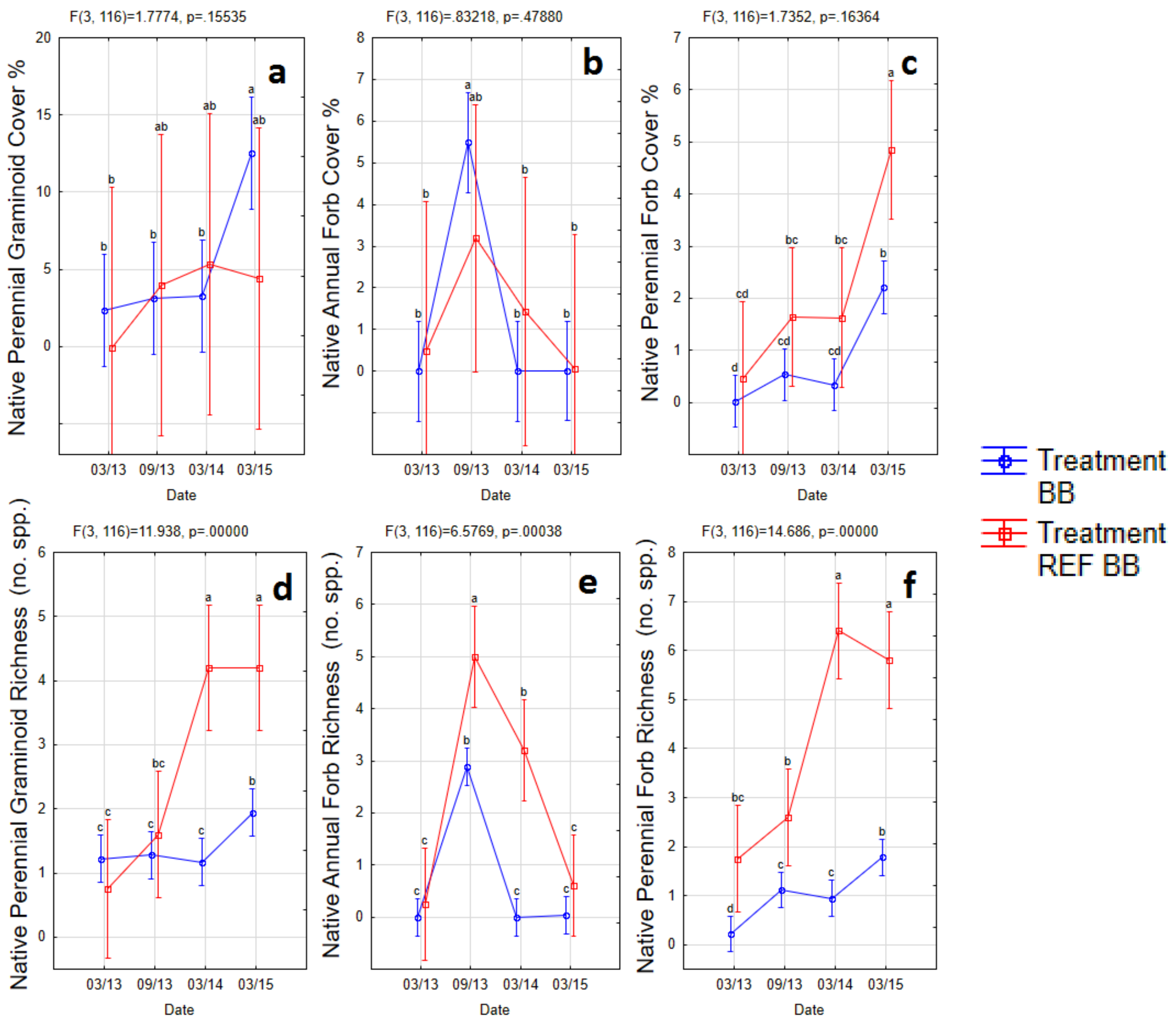
Species	Vegetation guild	Seed Morphology	Pre-treatment
Agathosma imbricata	Resprouting shrub	Small, thin seed coat	Smoke and heat
Anthospermum aethiopicum	Nonsprouting shrub	Small, thin seed coat	Smoke and heat
Chrysocoma ciliata	Nonsprouting shrub	Small seeded	Smoke and heat
Cliffortia juniperina	Nonsprouting shrub	Small seeded	Smoke and heat
Cliffortia polygonifolia	Nonsprouting shrub	Small seeded	Smoke and heat
Diosma oppositifolia	Reprouting shrub	Large, thick seed coat	Smoke and heat
Leucadendron salignum	Reprouting shrub	Large seeded	Smoke and heat
Phylica cephalantha	Reprouting shrub	Large, thick seed coat	Smoke and heat
Thamnochortus fruticosus	Restioid shrub	Small, thin seed coat	Smoke and heat
Thamnochortus punctatus	Restioid shrub	Small, thin seed coat	Smoke and heat
Bobartia indica	Geophyte	Large seeded	Smoke
Erica ferrea	Nonsprouting shrub	Small seeded	Smoke
Erica mammosa	Resprouting shrub	Small, thin seed coat	Smoke
Helichrysum sp.	Nonsprouting shrub	Small seeded	Smoke
Lampranthus reptans	Perennial Forb	Small, thick seed coat	Smoke and heat
Moraea cf. fugax	Geophyte	Small seeded	Smoke
Passerina corymbosa	Nonsprouting shrub	Small, medium seed coat	Smoke
Protea repens	Nonsprouting shrub	Large seeded	Smoke
Protea scolymocephala	Nonsprouting shrub	Large seeded	Smoke
Stoebe plumosa	Nonsprouting shrub	Small seeded	Smoke
Watsonia meriana	Geophyte	Large, thin seed coat	Smoke
Ifloga repens	Nonsprouting shrub	Small seeded	Smoke
Metalasia densa	Nonsprouting shrub	Small, thin seed coat	Smoke
Trichocephalus stipularis	Resprouting shrub	Medium, thick seed coat	Smoke and heat



Appendix 1b. Soil chemistry variables analysed for passive treatments burn-block (BB) and stack-block (SB) at time of initial clearing (03/13) and a year after clearing (03/14): a) Soil pH; b) Total C (%); c) Moisture (%). Same letters or no letters (Total C %) show which samples do not differ significantly based on repeat measures ANOVA.



Appendix 1c. Comparison of vegetation components over five survey times between passive clearing treatments burn-block (BB) and stack-block (SB), and initial sowing treatments Annual sowing (AS) and Fynbos sowing (FS): a) Alien annual forb cover; b) Alien perennial forb cover; c) Native perennial forb cover; d) Native annual graminoid cover; e) Native annual forb cover; f) Resprouting shrub cover. Cover represented as percent cover where not BoxCox transformed. Same letters show which samples do not differ significantly based on repeat measures ANOVA.



Appendix 1d. Comparison of vegetation percentage cover and species richness of selected vegetation components between burn-block treatment (BB) and burnt reference site (REF BB): a) Native perennial graminoid cover; b) Native annual forb cover; c) Native perennial forb Cover; d) Native perennial graminoid richness; e) Native annual forb richness; f) Native perennial forb richness. Same letters show which samples do not differ significantly based on repeat measures ANOVA.

6.2 Appendix 2 - Full explanation of processes and parameters included in the dynamic model, and the original conceptual diagram of the sub-models considered.

STOCHASTIC DYNAMIC MODEL

A) PURPOSE

The model was developed to simulate recovery of invasive *Acacia saligna* and native fynbos vegetation components under different alien vegetation clearing scenarios.

B) STRUTURE AND FUNCTIONING

1. LAND/VEGETATION COVER DYNAMICS

2. ENVIRONMENTAL PREDICTORS AND COMMUNITY EMERGENT INDICATORS

---

1. LAND/VEGETATION COVER DYNAMICS

The sub-model was designed to simulate the dynamics of land/vegetation covers for Cape Flats Sand Fynbos at Blaauwberg Nature Reserve, taking into account 6 scenarios of land/vegetation cover change which result in different rates of vegetation growth and competition.

1. 1. SCENARIOS

In order to recreate changes in the prevalent land/vegetation covers for the experimental site of interest, six scenarios were considered: (1) Reference condition - Vegetation consists of fynbos shrub components alone and the only impact is stochastic wildfire events after which fynbos components recover and experience competitive interactions (since no alien clearing or managed fire is activated, there are no costs involved); (2) Stack Block - Invaded vegetation is cleared of acacia without managed fire, so any fynbos cover present at each clearing event is left to recover based on the recovery rates recorded for this treatment; (3) Burn-block - Invaded vegetation is cleared of acacia followed by managed fire, after which the resulting burnt ground (occupying the entire site) is colonized by fynbos and acacia based on the recovery rates recorded for this treatment; (4) Initial Seed Sowing – This scenario follows the same initial path as the Burn-block treatment but the rates of acacia and fynbos recovery change immediately after managed fire whereas in the delayed sowing treatments or pre-treated seed sowing depending on scenario; (5) Delayed sowing with untreated seeds – This treatment follows the same initial path as the Burn-block treatment but the vegetation recovery rates change a year after managed fire to rates recorded for sowing with un-treated seed; and (6) Delayed sowing with pre-treated seeds – This treatment follows the same path as for scenario (5) but the growth rates are those recorded for sowing with pre-treated seed. When selected (i.e. option = 1), specific rates of land/vegetation cover transitions are activated in order to reproduce the trends considered in each scenario.

MODELING ELEMENTS

- *scenario 1* (Appendix 3 – "Constants")
- *scenario 2* (Appendix 3 – "Constants")
- *scenario 3* (Appendix 3 – "Constants")
- *scenario 4* (Appendix 3 – "Constants")
- *scenario 5* (Appendix 3 – "Constants")
- *scenario 6* (Appendix 3 – "Constants")

1.2. FIRE EVENTS

Wildfires were included in the model as stochastic occurrences, in order to simulate fire regimes that represent this typical phenomenon affecting fynbos vegetation (Kruger 1984).

MODELING ELEMENTS

- *fire occurrence* (Appendix 3 – "Composed Variables")

1.2.1. FIRE PROBABILITY

Fire events were simulated by generating random probabilities of fire occurrence. This was based on a random probability within a given number of chances for a fire to occur.

MODELING ELEMENTS

- *fire probability* (Appendix 3 – "Random Variables")
- *chances for fire to occur* (Appendix 3 – "Constants")

1.2.2. FIRE INTENSITY

The overall possible range concerning the percentage of area of each vegetation component liable to be burnt (i.e. Acacia cover, restio cover, resprouting shrub and non-sprouting shrub cover) was considered (i.e. from 0% to 100%), assuming that the correspondent cover being modelled is prone to be burned totally.

MODELING ELEMENTS

- *fire intensity* (Appendix 3 – "Random Variables")

1.2.3. FIRE SEASON

The fire season was determined to be between November and March (Esler *et al.* 2014), and therefore fires would only occur if the chance of a fire event took place during a month that was within the fire season.

MODELING ELEMENTS

- *seasonality* (Appendix 3 – "Constants")

1.3. MAIN LAND/VEGETATION COVERS

To model the vegetation dynamics of Cape Flats Sand Fynbos, six principal categories of cover were assumed: Bare ground, Burnt area, Acacia cover, Non-sprouting shrub cover, Resprouting shrub cover, and Restio cover.

STATE VARIABLES

1.3.1. **BARE GROUND:** (*Bare ground %*) (Figure 1 and Appendix 3 – "Difference and Process Equations")

1.3.2. **BURNT GROUND:** (*Burnt area %*) (Figure 2 and Appendix 3 – "Difference and Process Equations")

1.3.3. **ACACIA COVER:** (*Acacia cover %*) (Figure 3 and Appendix 3 – "Difference and Process Equations")

1.3.4. **NON-SPROUTING SHRUB COVER:** (*Nonsprouting shrub cover S %)* (Figure 4 and Appendix 3 – "Difference and Process Equations")

1.3.5. **RESPROUTING SHRUB COVER:** (*Resprout cover R %*) (Figure 5 and Appendix 3 – "Difference and Process Equations")

1.3.6. **RESTIO COVER:** (*Restio cover E %*) (Figure 6 and Appendix 3 – "Difference and Process Equations")

1.3.1. **BARE GROUND**

Areas lacking woody vegetation cover after acacia clearing in invaded sites.

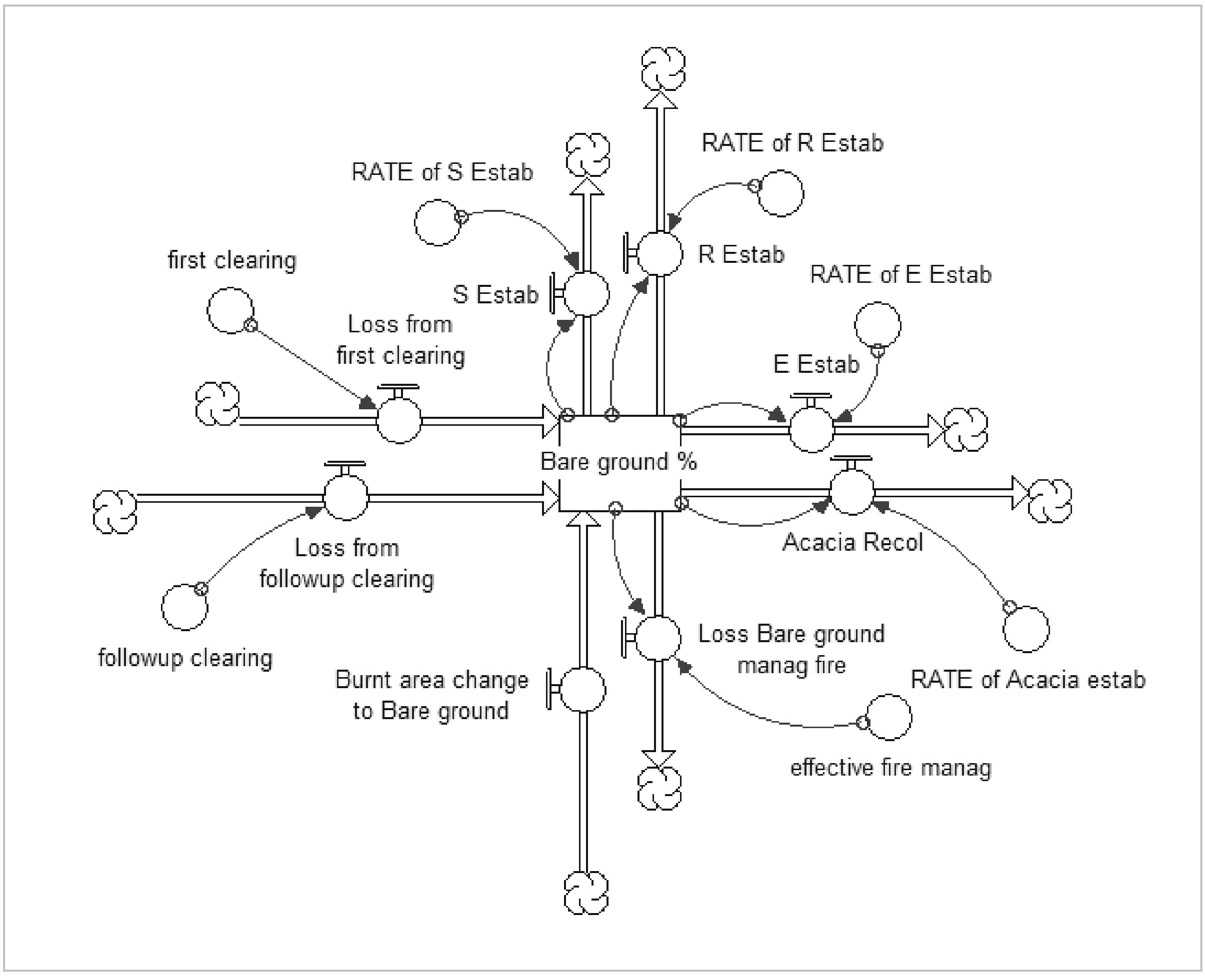


Figure 1. Stella conceptual diagram of the sub-model to simulate the dynamics of bare ground. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

PROCESSES

1.3.1.1. **RECONVERSION FROM ACACIA COVER**

Loss from first clearing (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.2. **RECONVERSION FROM ACACIA COVER**

Loss from followup clearing (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.3. **RECONVERSION FROM BURNT AREA**

Burnt area change to Bare ground (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.4. **RECONVERSION INTO BURNT AREA**

Loss Bare ground manag fire (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.5. **<u>RECONVERSION INTO ACACIA COVER</u>**

Acacia Recol (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.6. **<u>RECONVERSION INTO RESTIO COVER</u>**

E Estab (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.7. **<u>RECONVERSION INTO RESPROUTING SHRUB COVER</u>**

R Estab (Figure 1 and Appendix 3 – "Process Equations")

1.3.1.8. **<u>RECONVERSION INTO NON-SPROUTING SHRUB COVER</u>**

S Estab (Figure 1 and Appendix 3 – "Process Equations")

FUNCTIONING

1.3.1.1. <u>RECONVERSION FROM ACACIA COVER</u>

Conversion of acacia cover to bare ground from initial alien clearing.

MODELING ELEMENTS

- *first clearing* (Appendix 3 – "Composed Variables")

1.3.1.2. <u>RECONVERSION FROM ACACIA COVER</u>

Conversion of acacia cover to bare ground from followup alien clearing.

MODELING ELEMENTS

- *followup clearing* (Appendix 3 – "Composed Variables")

1.3.1.3. <u>RECONVERSION FROM BURNT AREA</u>

Conversion of burnt area once alien clearing takes place.

MODELING ELEMENTS

- *Burnt area change to Bare ground* (Figure 2 and Appendix 3 – "Process Equations")

1.3.1.4. <u>RECONVERSION INTO BURNT AREA</u>

Conversion of bare ground into burnt area following a fire.

MODELING ELEMENTS

- *effective fire manag* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.1.5. **RECONVERSION INTO ACACIA COVER**

Colonisation of bare ground by acacia cover.

MODELING ELEMENTS

- *RATE of acacia estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.1.6. **RECONVERSION INTO RESTIO COVER**

Colonisation of bare ground by restio cover.

MODELING ELEMENTS

- *RATE of E Estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.1.7. **RECONVERSION INTO RESPROUTING SHRUB COVER**

Colonisation of bare ground by resprouting shrub cover.

MODELING ELEMENTS

- *RATE of R Estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.1.8. **RECONVERSION INTO NON-SPROUTING SHRUB COVER**

Colonisation of bare ground by non-sprouting shrub cover.

MODELING ELEMENTS

- *RATE of S Estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.2. **BURNT GROUND**

Areas lacking woody vegetation cover after fire.

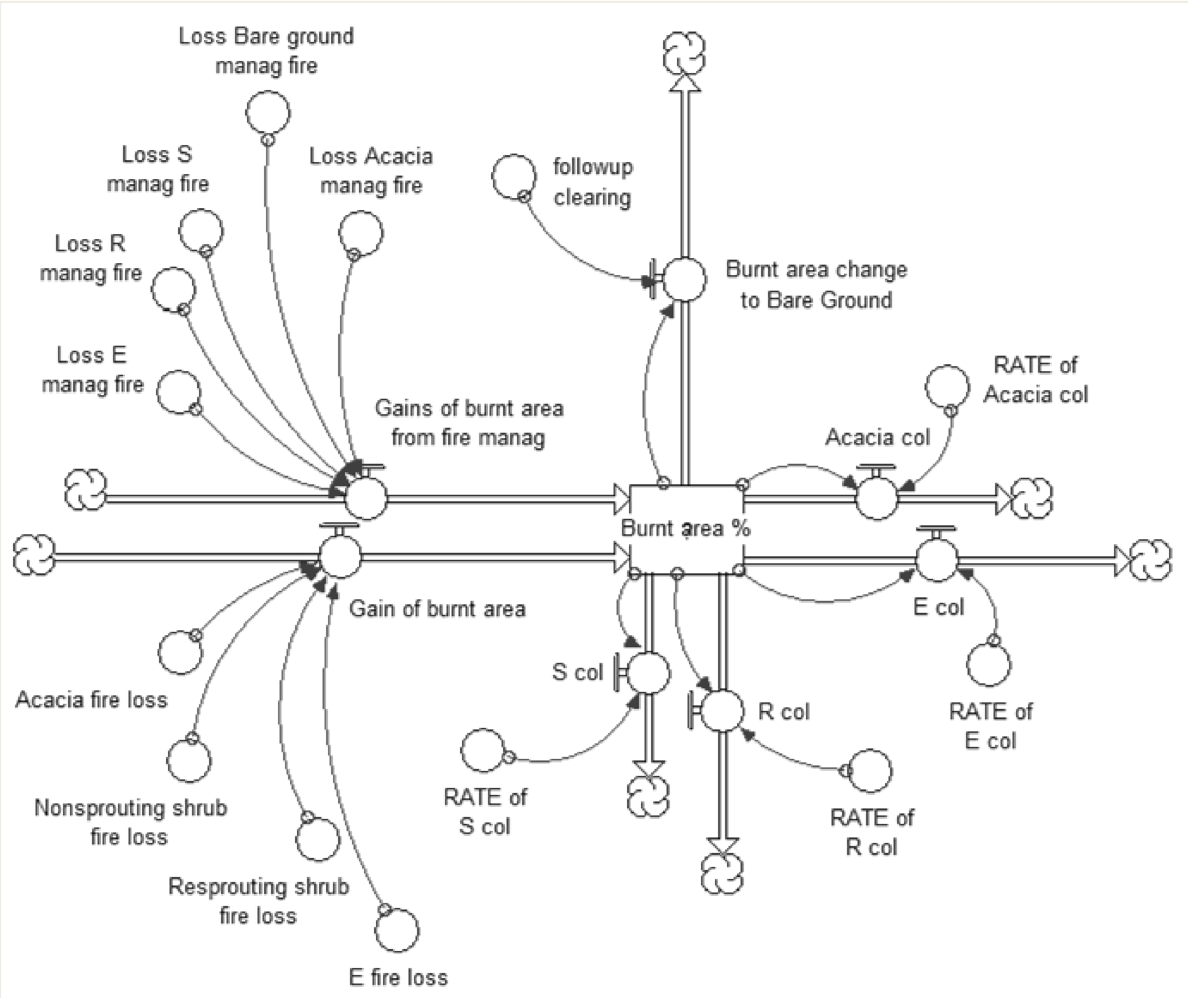


Figure 2. Stella conceptual diagram of the sub-model to simulate the dynamics of burnt ground. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

PROCESSES

1.3.2.1. **RECONVERSION FROM VEGETATION COVER**

Gains of burnt area fire manag (Figure 2 and Appendix 3 – "Process Equations")

1.3.2.2. **RECONVERSION FROM VEGETATION COVER**

Gain of burnt area (Figure 2 and Appendix 3 – "Process Equations")

1.3.2.3. **RECONVERSION INTO BARE GROUND**

Burnt area change to Bare ground (Figure 2 and Appendix 3 – "Process Equations")

1.3.2.4. **RECONVERSION INTO ACACIA COVER**

Acacia col (Figure 2 and Appendix 3 – "Process Equations")

1.3.2.5. **<u>RECONVERSION INTO RESTIO COVER</u>**

E col (Figure 2 and Appendix 3 – "Process Equations")

1.3.2.6. **<u>RECONVERSION INTO RESPROUTING SHRUB COVER</u>**

R col (Figure 2 and Appendix 3 – "Process Equations")

1.3.2.7. **<u>RECONVERSION INTO NON-SPROUTING SHRUB COVER</u>**

S col (Figure 2 and Appendix 3 – "Process Equations")

FUNCTIONING

1.3.2.1. <u>RECONVERSION FROM VEGETATION COVER</u>

Conversion of all vegetation cover into burnt area following managed fire.

MODELING ELEMENTS

- *Loss Acacia manag fire* (Figure 3 and Appendix 3 – "Process Equations")
- *Loss Bare ground manag fire* (Figure 1 and Appendix 3 – "Process Equations")
- *Loss E manag fire* (Figure 4 and Appendix 3 – "Process Equations")
- *Loss R manag fire* (Figure 5 and Appendix 3 – "Process Equations")
- *Loss S manag fire* (Figure 6 and Appendix 3 – "Process Equations")

1.3.2.2. <u>RECONVERSION FROM VEGETATION COVER</u>

Conversion of all vegetation cover into burnt area following wildfire.

MODELING ELEMENTS

- *Acacia fire loss* (Figure 3 and Appendix 3 – "Process Equations")
- *Non-sprouting shrub fire loss* (Figure 6 and Appendix 3 – "Process Equations")
- *Resprouting shrub fire loss* (Figure 5 and Appendix 3 – "Process Equations")
- *E fire loss* (Figure 5 and Appendix 4 – "Process Equations")

1.3.2.3. <u>RECONVERSION INTO BARE GROUND</u>

Conversion of burnt area into bare ground with follow-up clearing.

MODELING ELEMENTS

- *followup clearing* (Figure 6 and Appendix 3 – "Composed Variables")

1.3.2.4. <u>RECONVERSION INTO ACACIA GROUND</u>

Colonisation of burnt ground by acacia cover.

MODELING ELEMENTS

- *RATE of Acacia col* (Figure 7 and Appendix 3 – “Composed Variables”)

1.3.2.5. <u>RECONVERSION INTO RESTIO GROUND</u>

Colonisation of burnt ground by restio cover.

MODELING ELEMENTS

- *RATE of E col* (Figure 2 and Appendix 3 – “Composed Variables”)

1.3.2.6. <u>RECONVERSION INTO RESPROUTING GROUND</u>

Colonisation of burnt ground by resprouting cover.

MODELING ELEMENTS

- *RATE of R col* (Figure 2 and Appendix 3 – “Composed Variables”)

1.3.2.7. <u>RECONVERSION INTO NON-SPROUTING GROUND</u>

Colonisation of burnt ground by non-sprouting cover.

MODELING ELEMENTS

- *RATE of S col* (Figure 2 and Appendix 3 – “Composed Variables”)

1.3.3. **ACACIA COVER**

Areas occupied by *Acacia saligna* trees.

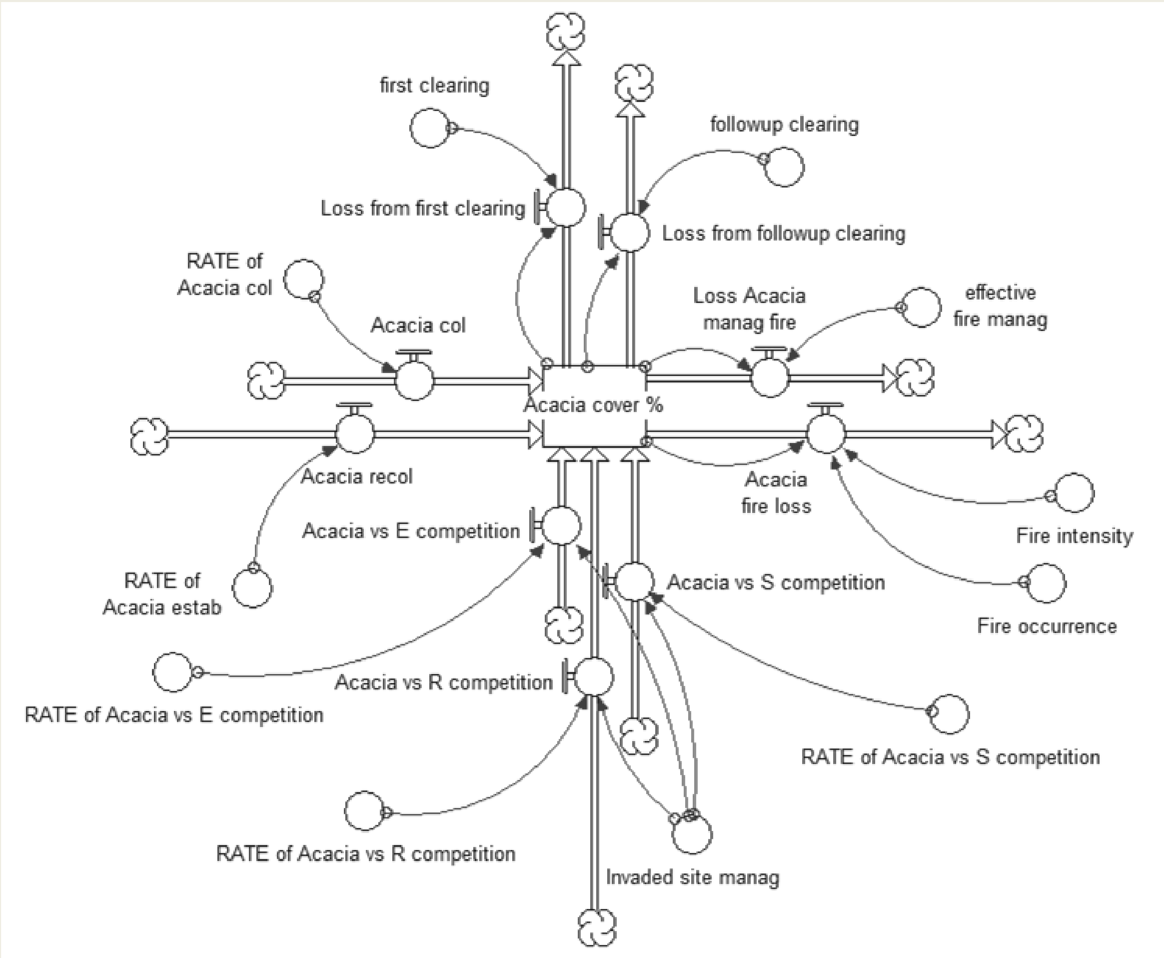


Figure 3. Stella conceptual diagram of the sub-model to simulate the dynamics of acacia. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

PROCESSES

1.3.3.1. **<u>RECONVERSION FROM BURNT GROUND</u>**

Acacia col (Figure 2 and Appendix 3 – "Process Equations")

1.3.3.2. **<u>RECONVERSION FROM BARE GROUND</u>**

Acacia recol (Figure 1 and Appendix 3 – "Process Equations")

1.3.3.3. **<u>RECONVERSION FROM RESTIO COVER</u>**

Acacia vs E competition (Figure 4 and Appendix 3 – "Process Equations")

1.3.3.4. **<u>RECONVERSION FROM RESPROUTING SHRUB COVER</u>**

Acacia vs R competition (Figure 5 and Appendix 3 – "Process Equations")

1.3.3.5. **<u>RECONVERSION FROM NON-SPROUTING SHRUB COVER</u>**

Acacia vs S competition (Figure 6 and Appendix 3 – "Process Equations")

1.3.3.6. **RECONVERSION INTO BURNT GROUND**

Acacia fire loss (Figure 3 and Appendix 3 – "Process Equations")

1.3.3.7. **RECONVERSION INTO BURNT GROUND**

Loss Acacia manag fire (Figure 3 and Appendix 3 – "Process Equations")

1.3.3.8. **RECONVERSION INTO BARE GROUND**

Loss from first clearing (Figure 3 and Appendix 3 – "Process Equations")

1.3.3.9. **RECONVERSION INTO BARE GROUND**

Loss from followup clearing (Figure 3 and Appendix 3 – "Process Equations")

FUNCTIONING

1.3.3.1. RECONVERSION FROM BURNT GROUND

Conversion of burnt ground into acacia cover.

MODELING ELEMENTS

- *RATE of acacia col* (Figure 2 and Appendix 3 – "Composed Variables")

1.3.3.2. RECONVERSION FROM BARE GROUND

Conversion of bare ground into acacia cover.

MODELING ELEMENTS

- *RATE of acacia Estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.3.3. RECONVERSION FROM RESTIO COVER

Conversion of restio cover in acacia cover due to competitive effect.

MODELING ELEMENTS

- *RATE of Acacia vs E competition* (Figure 4 and Appendix 3 – "Composed Variables")

1.3.3.4. RECONVERSION FROM RESPROUTING SHRUB COVER

Conversion of resprouting shrub cover in acacia cover due to competitive effect.

MODELING ELEMENTS

- *RATE of Acacia vs R competition* (Figure 5 and Appendix 3 – "Composed Variables")

1.3.3.5. <u>RECONVERSION FROM NON-SPROUTING SHRUB COVER</u>

Conversion of non-sprouting shrub cover in acacia cover due to competitive effect.

MODELING ELEMENTS

- *RATE of Acacia vs S competition* (Figure 6 and Appendix 3 – "Composed Variables")

1.3.3.6. <u>RECONVERSION INTO BURNT GROUND</u>

Conversion of acacia into burnt ground through wildfire.

MODELING ELEMENTS

- *Fire intensity* (Figure 3 and Appendix 3 – "Random Variables")
- *Fire occurrence* (Figure 3 and Appendix 3 – "Composed Variables")

1.3.3.7. <u>RECONVERSION INTO BURNT GROUND</u>

Conversion of acacia into bare ground through managed fire.

MODELING ELEMENTS

- *effective fire management* (Figure 3 and Appendix 3 – "Composed Variables")

1.3.3.8. <u>RECONVERSION INTO BARE GROUND</u>

Conversion of acacia into bare ground from first clearing.

MODELING ELEMENTS

- *first clearing* (Figure 3 and Appendix 3 – "Composed Variables")

1.3.3.9. <u>RECONVERSION INTO BARE GROUND</u>

Conversion of acacia into bare ground from followup clearing.

MODELING ELEMENTS

- *followup clearing* (Figure 3 and Appendix 3 – "Composed Variables")

1.3.4. **RESTIO COVER**

Areas occupied by cover of graminoid shrubs within the family Restionaceae.

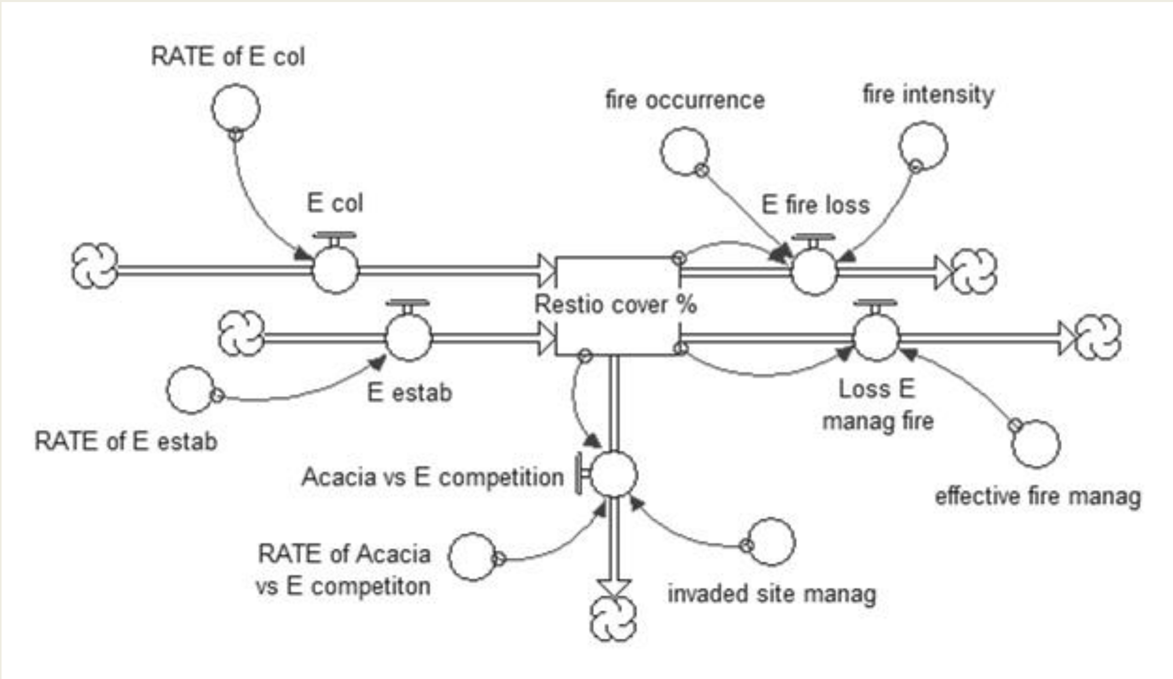


Figure 4. Stella conceptual diagram of the sub-model to simulate the dynamics of restio cover. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

PROCESSES

<u>1.3.4.1. **RECONVERSION FROM BURNT GROUND**</u>

E col (Figure 2 and Appendix 3 – “Process Equations”)

<u>1.3.4.2. **RECONVERSION FROM BARE GROUND**</u>

E estab (Figure 1 and Appendix 3 – “Process Equations”)

<u>1.3.4.3. **RECONVERSION INTO ACACIA**</u>

Acacia vs E competition (Figure 4 and Appendix 3 – “Process Equations”)

<u>1.3.4.4. **RECONVERSION INTO BURNT GROUND**</u>

Loss E manag fire (Figure 4 and Appendix 3 – “Process Equations”)

<u>1.3.4.5. **RECONVERSION INTO BURNT GROUND**</u>

E fire loss (Figure 4 and Appendix 3 – “Process Equations”)

FUNCTIONING

<u>**1.3.4.1. RECONVERSION FROM BURNT GROUND**</u>

Conversion of burnt ground into restio cover.

MODELING ELEMENTS

- *RATE of E col* (Figure 2 and Appendix 3 – "Composed Variables")

1.3.4.2. RECONVERSION FROM BARE GROUND

Conversion of bare ground into restio cover.

MODELING ELEMENTS

- *RATE of E estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.4.3. RECONVERSION INTO ACACIA

Conversion of restio cover into acacia cover.

MODELING ELEMENTS

- *RATE of Acacia vs E competition* (Figure 4 and Appendix 3 – "Composed Variables")
- *Invaded site manag* (Figure 4 and Appendix 3 – "Process Equations")

1.3.4.4. RECONVERSION INTO BURNT GROUND

Conversion of restio cover into burnt ground through managed fire.

MODELING ELEMENTS

- *Effective fire manag* (Figure 4 and Appendix 3 – "Composed Variables")

1.3.4.5. RECONVERSION INTO BURNT GROUND

Conversion of restio cover into burnt ground through wildfire

MODELING ELEMENTS

- *fire occurrence* (Figure 4 and Appendix 3 – "Composed Variables")
- *fire intensity* (Figure 4 and Appendix 3 – "Random Variables")

1.3.5. **RESPROUTING SHRUB COVER**

Areas occupied by cover of shrub species that can resprout after fire.

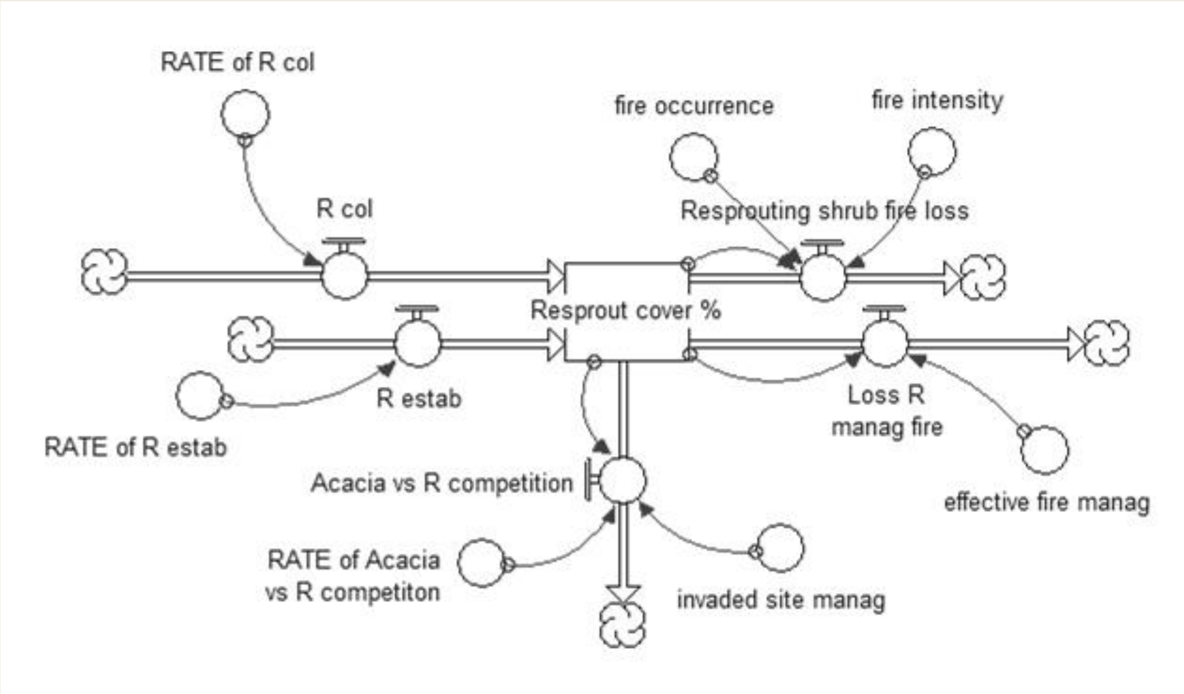


Figure 5. Stella conceptual diagram of the sub-model to simulate the dynamics of resprouting shrub cover. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

PROCESSES

<u>1.3.5.1. **RECONVERSION FROM BURNT GROUND**</u>

R col (Figure 2 and Appendix 3 – "Process Equations")

<u>1.3.5.2. **RECONVERSION FROM BARE GROUND**</u>

R estab (Figure 1 and Appendix 3 – "Process Equations")

<u>1.3.5.3. **RECONVERSION INTO ACACIA**</u>

Acacia vs R competition (Figure 4 and Appendix 3 – "Process Equations")

<u>1.3.5.4. **RECONVERSION INTO BURNT GROUND**</u>

Loss R manag fire (Figure 4 and Appendix 3 – "Process Equations")

<u>1.3.5.5. **RECONVERSION INTO BURNT GROUND**</u>

Resprouting shrub fire loss (Figure 4 and Appendix 3 – "Process Equations")

FUNCTIONING

<u>**1.3.5.1. RECONVERSION FROM BURNT GROUND**</u>

Conversion of burnt ground into resprouting shrub cover.

MODELING ELEMENTS

- *RATE of R col* (Figure 2 and Appendix 3 – "Composed Variables")

<u>1.3.5.2. RECONVERSION FROM BARE GROUND</u>

Conversion of bare ground into resprouting shrub cover.

MODELING ELEMENTS

- *RATE of R estab* (Figure 1 and Appendix 3 – "Composed Variables")

<u>1.3.5.3. RECONVERSION INTO ACACIA</u>

Conversion of resprouting shrub cover into acacia cover.

MODELING ELEMENTS

- *RATE of Acacia vs R competition* (Figure 4 and Appendix 3 – "Composed Variables")
- *Invaded site manag* (Figure 4 and Appendix 3 – "Composed Variables")

<u>1.3.5.4. RECONVERSION INTO BURNT GROUND</u>

Conversion of resprouting shrub cover into burnt ground through managed fire.

MODELING ELEMENTS

- *Effective fire manag* (Figure 4 and Appendix 3 – "Composed Variables")

<u>1.3.5.5. RECONVERSION INTO BURNT GROUND</u>

Conversion of resprouting shrub cover into burnt ground through wildfire

MODELING ELEMENTS

- *fire occurrence* (Figure 4 and Appendix 3 – "Composed Variables")
- *fire intensity* (Figure 4 and Appendix 3 – "Random Variables")

1.3.6. **NON-SPROUTING SHRUB COVER**

Areas occupied by cover of shrub species that do not resprout after fire.

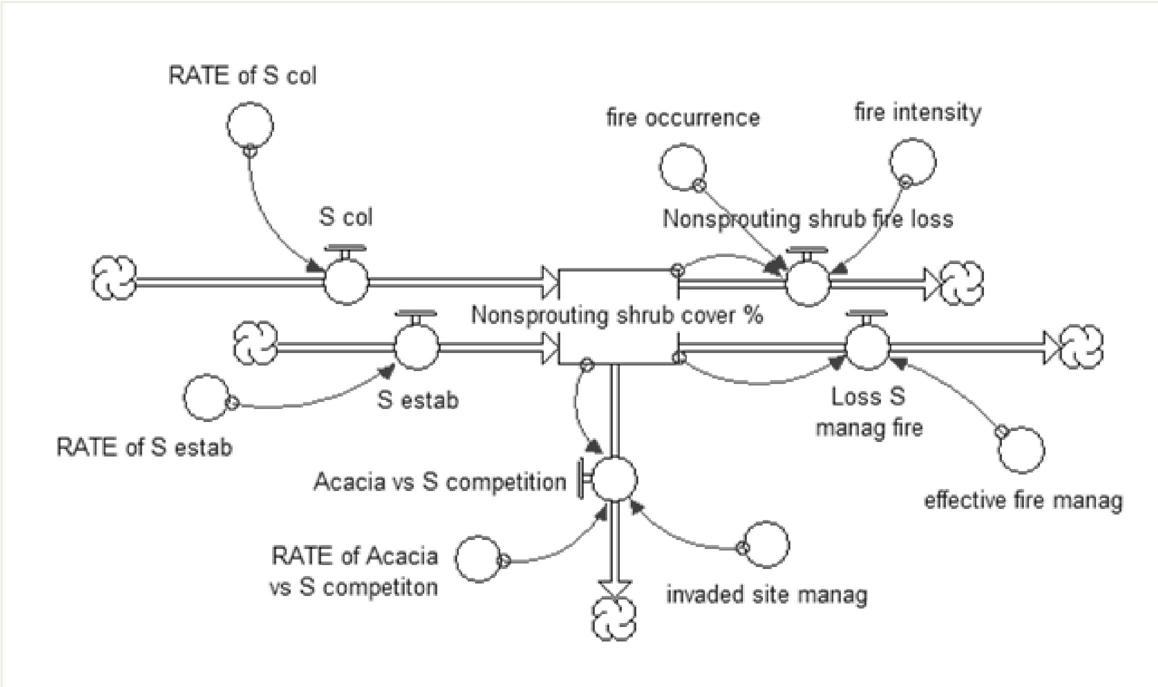


Figure 6. Stella conceptual diagram of the sub-model to simulate the dynamics of non-sprouting shrub cover. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

PROCESSES

1.3.6.1. **RECONVERSION FROM BURNT GROUND**

S col (Figure 2 and Appendix 3 – “Process Equations”)

1.3.6.2. **RECONVERSION FROM BARE GROUND**

S estab (Figure 1 and Appendix 3 – “Process Equations”)

1.3.6.3. **RECONVERSION INTO ACACIA**

Acacia vs S competition (Figure 4 and Appendix 3 – “Process Equations”)

1.3.6.4. **RECONVERSION INTO BURNT GROUND**

Loss S manag fire (Figure 4 and Appendix 3 – “Process Equations”)

1.3.6.5. **RECONVERSION INTO BURNT GROUND**

Nonsprouting shrub fire loss (Figure 4 and Appendix 3 – “Process Equations”)

FUNCTIONING

1.3.6.1. RECONVERSION FROM BURNT GROUND

Conversion of burnt ground into nonsprouting shrub cover.

MODELING ELEMENTS

- *RATE of S col* (Figure 2 and Appendix 3 – "Composed Variables")

1.3.6.2. RECONVERSION FROM BARE GROUND

Conversion of bare ground into nonsprouting shrub cover.

MODELING ELEMENTS

- *RATE of S estab* (Figure 1 and Appendix 3 – "Composed Variables")

1.3.6.3. RECONVERSION INTO ACACIA

Conversion of non-sprouting shrub cover into acacia cover.

MODELING ELEMENTS

- *RATE of Acacia vs S competition* (Figure 4 and Appendix 3 – "Composed Variables")
- *Invaded site manag* (Figure 4 and Appendix 3 – "Composed Variables")

1.3.6.4. RECONVERSION INTO BURNT GROUND

Conversion of non-sprouting shrub cover into burnt ground through managed fire.

MODELING ELEMENTS

- *Effective fire manag* (Figure 4 and Appendix 3 – "Composed Variables")

1.3.6.5. RECONVERSION INTO BURNT GROUND

Conversion of nonsprouting shrub cover into burnt ground through wildfire

MODELING ELEMENTS

- *fire occurrence* (Figure 4 and Appendix 3 – "Composed Variables")
- *fire intensity* (Figure 4 and Appendix 3 – "Random Variables")

----

2. ENVIRONMENTAL PREDICTORS AND COMMUNITY EMERGENT INDICATORS

The environmental predictors and community emergent indicators responses to land/vegetation cover changes occurring at the study unit level (i.e. 50m^2) were given by the respective positive and negative partial regression coefficients of the selected land/vegetation cover independent variables (Santos and Cabral 2004).

MODELING ELEMENTS

- *management costs* (Figure 7 and Appendix 3– "Composed Variables")
- *species richness* (Figure 8 and Appendix 3– "Composed Variables")
- *plant density* (Figure 9 and Appendix 3– "Composed Variables")
- *soil chemistry* (Figure 10 and Appendix 3– "Composed Variables")

2.1 MANAGEMENT COSTS

Cost of different treatments calculated over the total timespan of the scenario selected.

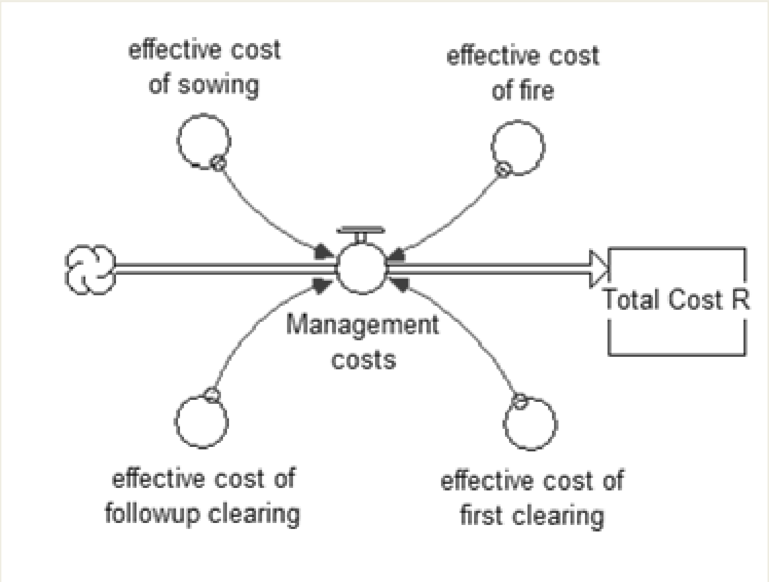


Figure 7 - Stella conceptual diagram of the sub-model to estimate management costs. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

MODELING ELEMENTS

- *effective cost of sowing* (Appendix 3 – "Composed Variables")
- *effective cost of fire* (Appendix 3 – "Composed Variables")
- *effective cost of first clearing* (Appendix 3 – "Composed Variables")
- *effective cost of followup clearing* (Appendix 3 – "Composed Variables")

2.2. SPECIES RICHNESS

Number of species within each of six vegetation structural components.

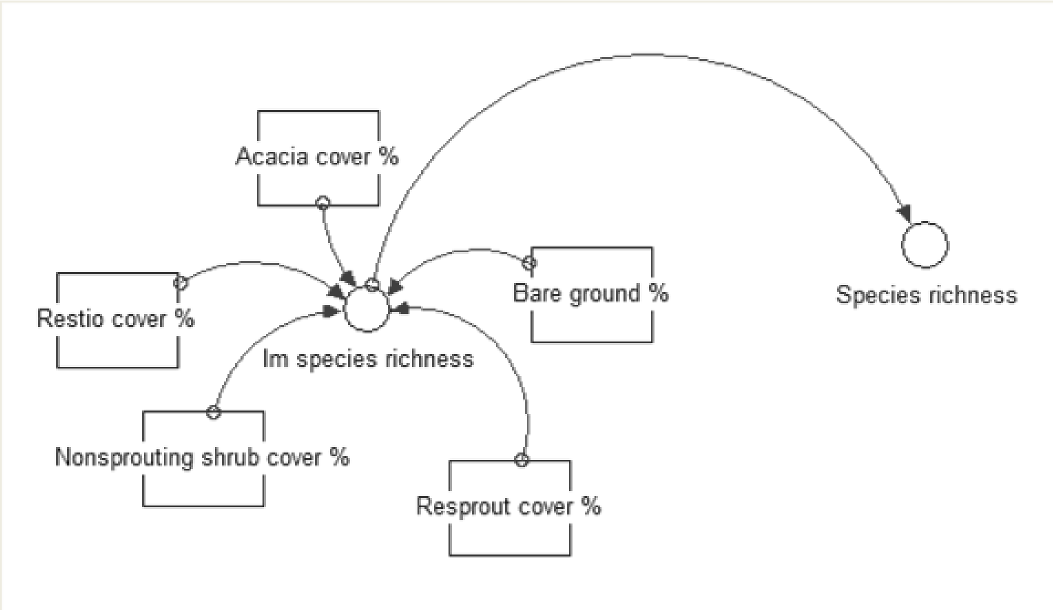


Figure 8 - Stella conceptual diagram of the sub-model to estimate species richness within vegetation structural components. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

MODELING ELEMENTS

- *Bare ground %* (Figure 1 and Appendix 3 – "Difference and Process Equations")
- *Acacia cover %* (Figure 3 and Appendix 3 – "Difference and Process Equations")
- *Restio cover %* (Figure 4 and Appendix 3 – "Difference and Process Equations")
- *Resprout cover %* (Figure 5 and Appendix 3 – "Difference and Process Equations")
- *Nonsprouting shrub cover %* (Figure 6 and Appendix 3 – "Difference and Process Equations")

2.3. PLANT DENSITY

Number of plants per $5m^2$ within each of six vegetation structural components.

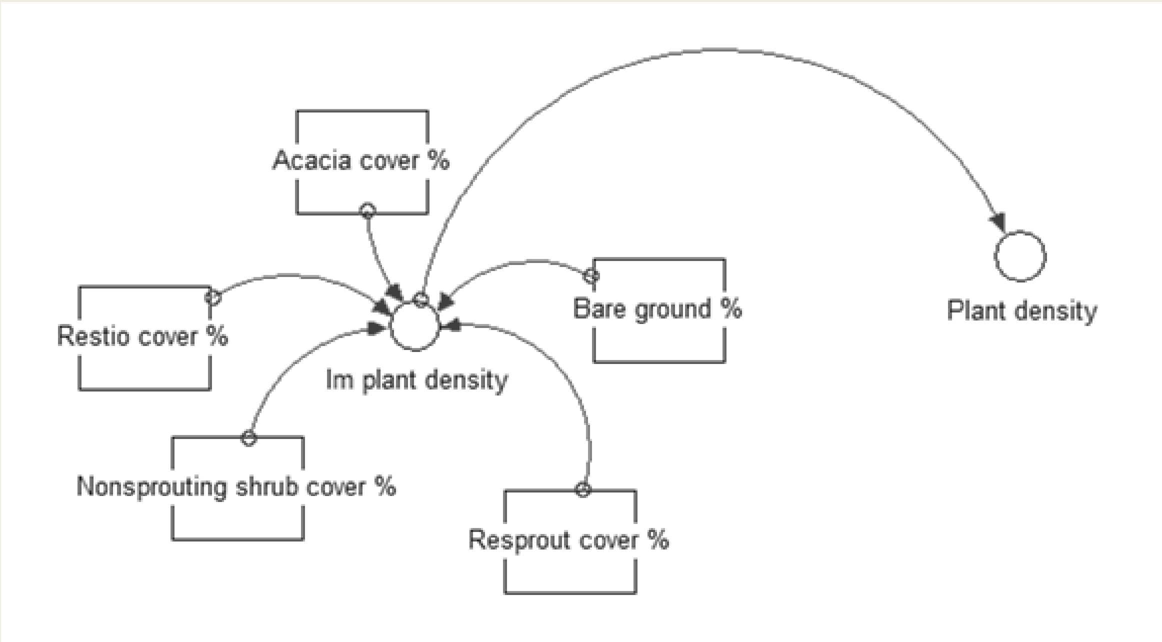


Figure 9 - Stella conceptual diagram of the sub-model to estimate plant density within vegetation structural components. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

MODELING ELEMENTS

- *Bare ground %* (Figure 1 and Appendix 3 – "Difference and Process Equations")
- *Acacia cover %* (Figure 3 and Appendix 3 – "Difference and Process Equations")
- *Restio cover %* (Figure 4 and Appendix 3 – "Difference and Process Equations")
- *Resprout cover %* (Figure 5 and Appendix 3 – "Difference and Process Equations")
- *Nonsprouting shrub cover %* (Figure 6 and Appendix 3 – "Difference and Process Equations")

2.4. SOIL CHEMISTRY

Values of five soil chemistry variables related to vegetation.

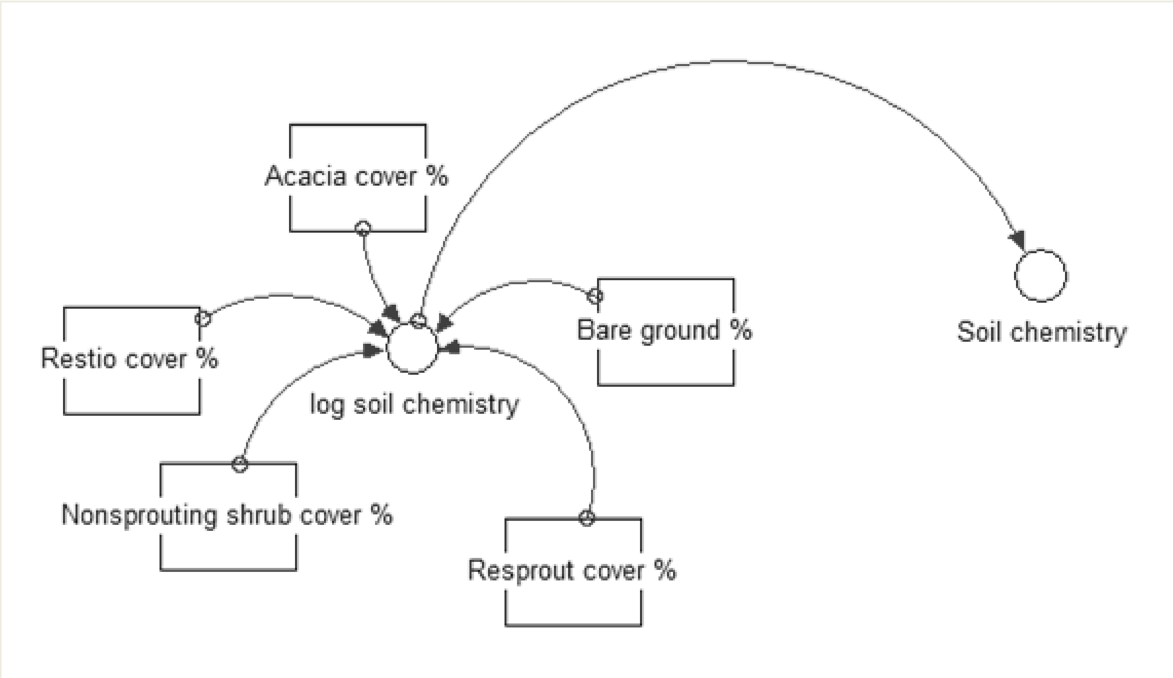


Figure 10 - Stella conceptual diagram of the sub-model to estimate soil chemistry variables. Rectangles represent state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

MODELING ELEMENTS

- *Bare ground %* (Figure 1 and Appendix 3 – "Difference and Process Equations")
- *Acacia cover %* (Figure 3 and Appendix 3 – "Difference and Process Equations")
- *Restio cover %* (Figure 4 and Appendix 3 – "Difference and Process Equations")
- *Resprout cover %* (Figure 5 and Appendix 3 – "Difference and Process Equations")
- *Nonsprouting shrub cover %* (Figure 6 and Appendix 3 – "Difference and Process Equations")

References

Esler, K. J., Pierce, S. M., De Villiers, C. (2014) *Fynbos : ecology and management*. Briza Publications, Pretoria.

Kruger, F. J. (1984) Fire in fynbos. In: *Ecological Effects of Fire in South African Ecosystems, Ecological Studies* (eds P. de V. Booysen & N. M. Tainton) pp. 68–114 Springer-Verlag, Berlin.

Santos, M., Cabral, J. A. (2004) Development of a stochastic dynamic model for ecological indicators' prediction in changed Mediterranean agroecosystems of north-eastern Portugal. *Ecol. Indic.* **3**, 285-303

6.3 Appendix 3 – Specification of all mathematic equations included in the dynamic model

DIFFERENCE EQUATIONS:

Land use/Land cover dynamics

Bare ground %(t) = Initial Bare cover(t - dt) + (Loss from first clearing + Loss from followup clearing + Burnt area change to Bare Ground - Loss Bare ground manag fire - Acacia recol - E Estab - R Estab - S Estab) * dt

Burnt area %(t) = Initial Burnt cover(t - dt) + (Gains of burnt area from fire manag + Gain of burnt area –Burnt area change to Bare Ground – Acacia col – E col – R col – S col) * dt

Acacia cover %(t) = Initial Acacia cover(t - dt) + (Acacia col + Acacia recol + Acacia vs E competition + Acacia vs R competition + Acacia vs S competition – Acacia fire loss – Loss Acacia manag fire – Loss from first clearing – Loss from followup clearing) * dt

Nonsprouting shrub cover S %(t) = Initial S cover(t - dt) + (S col + S Estab – Nonsprouting shrub fire loss – Loss S manag fire – Acacia vs S competition) * dt

Resprout cover R %(t) = Initial R cover(t - dt) + (R col + R Estab – Resprouting shrub fire loss – Loss R manag fire – Acacia vs R competition) * dt

Restio cover E %(t) = Initial E cover(t - dt) + (E col + E Estab – E fire loss – Loss E manag fire – Acacia vs E competition) * dt

PROCESS EQUATIONS:

Initial Bare cover = 0

INFLOWS:

Loss from first clearing = IF first clearing = 1 THEN first clearing *Acacia cover % ELSE 0

Loss from RATE = IF followup clearing = 1 THEN followup clearing * Acacia cover % ELSE 0

Burnt area change to Bare Ground = IF followup clearing = 1 THEN followup clearing * Burnt area % ELSE 0

OUTFLOWS:

Loss Bare ground manag fire = effective fire manag * Bare ground %

Acacia recol = RATE of Acacia estab * Bare ground %

E Estab = RATE of E estab * Bare ground %

R Estab = RATE of R estab * Bare ground %

S Estab = RATE of S estab * Bare ground %

Initial Burnt cover = 0

INFLOWS:

Gains of burnt area from fire manag = *Loss from first clearing* + Loss S manag fire + Loss R

manag fire + Loss Bare ground manag fire + Loss E manag fire Gain of burnt area = Resprouting shrub fire loss + Acacia fire loss + Nonsprouting shrub fire loss + E fire loss OUTFLOWS: Burnt area change to Bare Ground = IF followup clearing = 1 THEN followup clearing * Burnt area % ELSE 0 Acacia col = Burnt area % * RATE of Acacia col E col = RATE of E col * Burnt area % R col = RATE of R col * Burnt area % S col = RATE of S col * Burnt area %
Initial Acacia cover = 0 INFLOWS: Acacia col = Burnt area % * RATE of Acacia col Acacia recol = RATE of Acacia estab * Bare ground % Acacia vs E competition = IF Invaded site manag = 1 THEN RATE of Acacia vs E comp * Restio cover E % ELSE 0 Acacia vs R competition = IF Invaded site manag = 1 THEN RATE of Acacia vs R comp * Resprout cover R % ELSE 0 Acacia vs S competition = IF Invaded site manag = 1 THEN RATE of Acacia vs S comp * Nonsprouting shrub cover S % ELSE 0 OUTFLOWS: Acacia fire loss = IF Fire occurrence = 1 THEN Fire intensity * Acacia cover % ELSE 0 Loss Acacia manag fire = effective fire manag * Acacia cover % Loss from first clearing = IF first clearing = 1 THEN first clearing * Acacia cover % ELSE 0 Loss from followup clearing = IF followup clearing = 1 THEN followup clearing * Acacia cover % ELSE 0
Initial E cover = 0 INFLOWS: E col = RATE of E col * Burnt area % E Estab = RATE of E estab * Bare ground % OUTFLOWS: E fire loss = IF Fire occurrence = 1 THEN Fire intensity * Restio cover E % ELSE 0 Loss E manag fire = effective fire manag * Restio cover E % Acacia vs E competition = IF Invaded site manag = 1 THEN RATE of Acacia vs E comp *

Restio cover E % ELSE 0

Initial R cover = 0

INFLOWS:

R col = RATE of R col * Burnt area %

R Estab = RATE of R estab * Bare ground %

OUTFLOWS:

Resprouting shrub fire loss = IF Fire occurrence = 1 THEN Fire intensity * Resprout cover R % ELSE 0

Loss R manag fire = effective fire manag * Resprout cover R %

Acacia vs R competition = IF Invaded site manag = 1 THEN RATE of Acacia vs R comp * Resprout cover R % ELSE 0

Initial S cover = 0

INFLOWS:

S col = RATE of S col * Burnt area %

S Estab = RATE of S estab * Bare ground %

OUTFLOWS:

Nonsprouting shrub fire loss = IF Fire occurrence = 1 THEN Fire intensity * Nonsprouting shrub cover S % ELSE 0

Loss S manag fire = effective fire manag * Nonsprouting shrub cover S %

Acacia vs S competition = IF Invaded site manag = 1 THEN RATE of Acacia vs S comp * Nonsprouting shrub cover S % ELSE 0

COMPOSED VARIABLES:

Management costs = Effective cost of fire + Effective cost of first clearing + Effective cost of followup clearing + Effective cost of sowing

lm R richness = -0.831016+0.00625 * Acacia cover % + 0.027751 * Restio cover E %+0.008178 * Nonsprouting shrub cover S % + 0.051295 * Resprout cover R % + 0.008552 * Bare ground %

lm E richness = -1.615051-0.02036686 * Acacia cover %+0.04098734 * Restio cover E %+0.005243138 * Bare ground %+0.03630238 * Resprout cover R %+0.02484453 * Nonsprouting shrub cover S %

lm S richness = 0.364181+0.003825 * Acacia cover %+0.011909 * Restio cover E %+0.023297 * Nonsprouting shrub cover S %+0.020705 * Resprout cover R %-0.006342 * Bare ground %

lm G richness = 2.092516-0.01703704 * Acacia cover %-0.01713903 * Restio cover E %-0.02645817 * Nonsprouting shrub cover S %-0.01018492 * Resprout cover R %-0.003133070 * Bare ground %

lm H richness = 3.145265-0.0185944 * Acacia cover %-0.0408624 * Restio cover E %-0.0185045 *

Nonsprouting shrub cover S %-0.0277861 * Resprout cover R %-0.0238734 * Bare ground %
Richness R = EXP(lm R Richness)
Richness E = EXP(lm E Richness)
Richness S = EXP(lm S Richness)
Richness G = EXP(lm G Richness)
Richness H = EXP(lm H Richness)
lm R Density = -2.298977+0.008200 * Acacia cover %+0.052176 * Restio cover E %+0.039104 * Nonsprouting shrub cover S %+0.099396 * Resprout cover R %+0.032868 * Bare ground %
lm E Density =   -0.831083-0.009263 * Acacia cover %+0.063840 * Restio cover E %+0.037842 * Nonsprouting shrub cover S %+0.060301 * Resprout cover R %+0.006550 * Bare ground %
lm S Density =   0.5610423+0.0141418 * Acacia cover %+0.0224023 * Restio cover E %+0.0407681 * Nonsprouting shrub cover S %+0.0398175 * Resprout cover R %-0.0001019 * Bare ground %
lm B Density =   1.241032-0.005250941 * Acacia cover %-0.01724106 * Restio cover E %+0.06939348 * Nonsprouting shrub cover S %+0.004682193 * Resprout cover R %-0.0011003381 * Bare ground %
lm G Density =   4.3381065-0.0295592 * Acacia cover %-0.0143860 * Restio cover E %-0.0324658 * Nonsprouting shrub cover S %-0.0330021 * Resprout cover R %-0.0250445 * Bare ground %
lm H Density =   4.7805668-0.0335004 * Acacia cover %-0.0447871 * Restio cover E %-0.0152236 * Nonsprouting shrub cover S %-0.0306029 * Resprout cover R %-0.0278427 * Bare ground %
Density R = EXP(lm R Density)
Density E = EXP(lm E Density)
Density S = EXP(lm S Density)
Density B = EXP(lm B Density)
Density G = EXP(lm G Density)
Density H = EXP(lm H Density)
Log Moist = -0.04552578+0.004161059 * Restio cover E %+0.005271602 * Bare ground %-0.0014933343 * Resprout cover R %+0.0011432401 * Nonsprouting shrub cover S %+3.461120e-04 * Acacia cover %
Log C = 0.4121105+0.001129587 * Restio cover E %+0.001193364 * Bare ground %+0.0007561044 * Nonsprouting shrub cover S %+1.276605e-04 * Acacia cover %
calc NH4 = 12.94841+0.06901565 * Acacia cover %-0.3536587 * Resprout cover R %+0.8860505 * Nonsprouting shrub cover S %-0.0924375 * Restio cover E %-0.05650016 * Bare ground %
Log NON = 0.6299669+0.003644587 * Bare ground %-0.005055868 * Resprout cover R %+0.0016544550 * Nonsprouting shrub cover S %+0.0012632703 * Restio cover E %-0.0005942024 * Acacia cover %
Log P = 0.8172256-0.00348796 * Restio cover E %+0.001118295 * Bare ground %-0.01058244 *

Resprout cover R %+0.0006992905 * Acacia cover %-0.0012990042 * Nonsprouting shrub cover S %
Soil Moist = (10^Log Moist)-1
Soil C = (10^Log C)-1
Soil NH4 = calc NH4
Soil NON = (10^Log NON)-1
Soil P = (10^Log P)-1
Fire Occurrence = IF Wildfire_option = 1 AND Fire_probability = Chances_for_fire_to_occur AND Fire_season = 1 THEN 1 ELSE 0
After followup clearing interval = IF first clearing option = 1 AND followup clearing option = 1 AND clearing cycle > followup clearing time THEN 1 ELSE 0
After followup without fire = IF Fire management option = 0 AND followup clearing option = 1 THEN After followup clearing interval + Converter 3 ELSE 0
After followup with fire = IF Fire management option = 1 AND followup clearing option = 1 THEN After followup clearing interval + Converter 3 ELSE 0
Before first clearing interval = IF first clearing option=1 AND TIME<cleaning time after initial THEN 1 ELSE 0
clearing time after initial = COUNTER(1,periodicity of clearing months)
effective Acacia recol BB = (1+Acacia recol trans rate BB)^(1/months from 2nd to 3rd clearing)-1
effective Acacia recol FS = (1+Acacia recol trans rate FS)^(1/months from 2nd to 3rd clearing)-1
effective Acacia recol SB 3 = (1+Acacia col trans rate SB 3)^(1/months after clearing SB)-1
effective Acacia recol SB 5 = (1+Acacia recol trans rate SB 5)^(1/months after clearing SB)-1
Effective cost of fire = IF effective fire manag = 1 THEN Cost of fire ELSE 0
Effective cost of first clearing = IF first clearing = 1 THEN Cost of first clearing ELSE 0
Effective cost of followup clearing = IF followup clearing = 1 THEN Cost of followup clearing ELSE 0
Effective cost of sowing = IF effective sowing manag = 1 THEN Cost of sowing ELSE 0
effective E estab BB = (1+E estab trans rate BB)^(1/months from 2nd to 3rd clearing)-1
effective E estab FS = (1+E estab trans rate FS)^(1/months from 2nd to 3rd clearing)-1
effective E estab SB 3 = (1+E estab trans rate SB 3)^(1/months after clearing SB)-1

effective E estab SB 5 = (1+E estab trans rate SB 5)^(1/months after clearing SB)-1
effective fire manag = IF clearing cycle = fire effective time AND first clearing option = 1 THEN 1 ELSE 0
effective rate Acacia col BB = (1+Acacia col trans rate BB)^(1/months from 1st to 2nd clearing)-1
effective rate Acacia col FS = (1+Acacia col trans rate FS)^(1/months from 1st to 2nd clearing)-1
effective rate Aca vs E comp BB 3 = (1+Acacia vs E trans rate BB 3)^(1/months of competition)-1
effective rate Aca vs E comp BB 5 = (1+Acacia vs E trans rate BB 5)^(1/months of competition)-1
effective rate Aca vs E comp FS 3 = (1+Acacia vs E trans rate FS 3)^(1/months of competition)-1
effective rate Aca vs E comp FS 5 = (1+Acacia vs E trans rate FS 5)^(1/months of competition)-1
effective rate Aca vs E comp SB 3 = (1+Acacia vs E trans rate SB 3)^(1/months of competition)-1
effective rate Aca vs E comp SB 5 = (1+Acacia vs E trans rate SB 5)^(1/months of competition)-1
effective rate Aca vs R comp BB 3 = (1+Acacia vs R trans rate BB 3)^(1/months of competition)-1
effective rate Aca vs R comp BB 5 = (1+Acacia vs R trans rate BB 5)^(1/months of competition)-1
effective rate Aca vs R comp FS 3 = (1+Acacia vs R trans rate FS 3)^(1/months of competition)-1
effective rate Aca vs R comp FS 5 = (1+Acacia vs R trans rate FS 5)^(1/months of competition)-1
effective rate Aca vs R comp SB 3 = (1+Acacia vs R trans rate SB 3)^(1/months of competition)-1
effective rate Aca vs R comp SB 5 = (1+Acacia vs R trans rate SB 5)^(1/months of competition)-1
effective rate Aca vs S comp BB 3 = (1+Acacia vs S trans rate BB 3)^(1/months of competition)-1
effective rate Aca vs S comp BB 5 = (1+Acacia vs S trans rate BB 5)^(1/months of competition)-1
effective rate Aca vs S comp FS 3 = (1+Acacia vs S trans rate FS 3)^(1/months of competition)-1
effective rate Aca vs S comp FS 5 = (1+Acacia vs S trans rate FS 5)^(1/months of competition)-1
effective rate Aca vs S comp SB 3 = (1+Acacia vs S trans rate SB 3)^(1/months of competition)-1
effective rate Aca vs S comp SB 5 = (1+Acacia vs S trans rate SB 5)^(1/months of competition)-1
effective rate E col BB = (1+E col trans rate BB)^(1/months from 1st to 2nd clearing)-1
effective rate E col FS = (1+E col trans rate FS)^(1/months from 1st to 2nd clearing)-1
effective rate E col Ref = (1+E col trans rate Ref)^(1/months after burn in Ref site)-1

effective rate R col BB = (1+R col trans rate BB)^(1/months from 1st to 2nd clearing)-1
effective rate R col FS = (1+R col trans rate FS)^(1/months from 1st to 2nd clearing)-1
effective rate R col Ref = (1+R col trans rate Ref)^(1/months after burn in Ref site)-1
effective rate S col BB = (1+S col trans rate BB)^(1/months from 1st to 2nd clearing)-1
effective rate S col FS = (1+S col trans rate FS)^(1/months from 1st to 2nd clearing)-1
effective rate S col Ref = (1+S col trans rate Ref)^(1/months after burn in Ref site)-1
effective rate S estab BB = (1+S estab trans rate BB)^(1/months from 2nd to 3rd clearing)-1
effective rate S estab FS = (1+S estab trans rate FS)^(1/months from 2nd to 3rd clearing)-1
effective rate S estab SB 3 = (1+S estab trans rate SB 3)^(1/months after clearing SB)-1
effective rate S estab SB 5 = (1+S estab trans rate SB 5)^(1/months after clearing SB)-1
effective R estab BB = (1+R estab trans rate BB)^(1/months from 2nd to 3rd clearing)-1
effective R estab FS = (1+R estab trans rate FS)^(1/months from 2nd to 3rd clearing)-1
effective R estab SB 3 = (1+R estab trans rate SB 3)^(1/months after clearing SB)-1
effective R estab SB 5 = (1+R estab trans rate SB 5)^(1/months after clearing SB)-1
Effective soil moisture = IF Soil Moist < 0 THEN 0 ELSE Soil Moist
effective sowing manag = IF clearing cycle= fire effective time AND Sowing management option = 1 THEN 1 ELSE 0
fire effective time = IF Fire management option = 1 THEN cleaning time after initial+Management fire time after first clearing ELSE 0
Fire season = IF seasonality >= 11 OR seasonality< 4 THEN 1 ELSE 0
Fire to followup clearing interval = IF first clearing option = 1 AND Fire management option = 1 AND followup clearing option=1 AND clearing cycle > fire effective time AND clearing cycle <= followup clearing time THEN 1 ELSE IF first clearing option = 1 AND Fire management option = 1 AND followup clearing option=0 AND clearing cycle > fire effective time THEN 1 ELSE 0
first clearing = IF first clearing option = 1 THEN periodic clearing ELSE 0
First clearing to fire interval = IF first clearing option = 1 AND clearing cycle >= cleaning time after initial AND clearing cycle <= fire effective time THEN 1 ELSE 0
First clearing to followup clearing interval without fire = IF first clearing option = 1 AND Fire management option = 0 AND followup clearing option = 1 AND clearing cycle >= cleaning time

after initial AND clearing cycle <= followup clearing time THEN 1 ELSE 0

First clearing without fire or followup = IF first clearing option=1 AND Fire management option = 0 AND followup clearing option = 0 AND TIME >= cleaning time after initial THEN 1 ELSE 0
followup clearing = If clearing cycle = followup clearing time AND followup clearing option = 1 THEN 1 ELSE 0
followup clearing time = cleaning time after initial+followup clearing time after first clearing
Invaded site manag = IF Invaded site option = 1 THEN 1 ELSE 0
periodic clearing = IF clearing cycle = cleaning time after initial+1 THEN 1 ELSE 0
RATE Aca vs E comp fire to followup interval FS = IF Sowing management option = 1 THEN First clearing to fire interval*effective rate Aca vs E comp SB 3+Fire to followup clearing interval*effective rate Aca vs E comp FS 3+After followup with fire*effective rate Aca vs E comp FS 5 ELSE 0
RATE Aca vs E comp fire to followup interval BB = IF Sowing management option = 0 THEN First clearing to fire interval*effective rate Aca vs E comp SB 3+Fire to followup clearing interval*effective rate Aca vs E comp BB 3+After followup with fire*effective rate Aca vs E comp BB 5 ELSE 0
RATE Aca vs E comp fire to followup interval SB = First clearing without fire or followup*effective rate Aca vs E comp SB 3+First clearing to followup clearing interval without fire*effective rate Aca vs E comp SB 3+After followup without fire*effective rate Aca vs E comp SB 5
RATE Aca vs R comp fire to followup interval BB = IF Sowing management option = 0 THEN First clearing to fire interval*effective rate Aca vs R comp SB 3+Fire to followup clearing interval*effective rate Aca vs R comp BB 3+After followup with fire*effective rate Aca vs R comp BB 5 ELSE 0
RATE Aca vs R comp fire to followup interval FS = IF Sowing management option = 1 THEN First clearing to fire interval*effective rate Aca vs R comp SB 3+Fire to followup clearing interval*effective rate Aca vs R comp FS 3+After followup with fire*effective rate Aca vs R comp FS 5 ELSE 0
RATE Aca vs R comp fire to followup interval SB = First clearing without fire or followup*effective rate Aca vs R comp SB 3+First clearing to followup clearing interval without fire*effective rate Aca vs R comp SB 3+After followup without fire*effective rate Aca vs R comp SB 5
RATE Aca vs S comp fire to followup interval BB = IF Sowing management option = 0 THEN First clearing to fire interval*effective rate Aca vs S comp SB 3+Fire to followup clearing interval*effective rate Aca vs S comp BB 3+After followup with fire*effective rate Aca vs S comp BB 5 ELSE 0

RATE Aca vs S comp fire to followup interval FS = IF Sowing management option = 1 THEN First clearing to fire interval*effective rate Aca vs S comp SB 3+Fire to followup clearing interval*effective rate Aca vs S comp FS 3+After followup with fire*effective rate Aca vs S comp FS 5 ELSE 0
RATE Aca vs S comp fire to followup interval SB = First clearing without fire or followup*effective rate Aca vs S comp SB 3+First clearing to followup clearing interval without fire*effective rate Aca vs S comp SB 3+After followup without fire*effective rate Aca vs S comp SB 5
RATE comp before initial clearing E = IF Invaded site manag = 1 THEN effective rate before clearing E ELSE 0
RATE comp before initial clearing R = IF Invaded site manag = 1 THEN effective rate before clearing R ELSE 0
RATE comp before initial clearing S = IF Invaded site manag = 1 THEN effective rate before clearing S ELSE 0
RATE of Acacia col = IF Fire management option=1 THEN RATE of Acacia col BB+RATE of Acacia col FS ELSE RATE of Acacia col no clearing
RATE of Acacia col BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN Fire to followup clearing interval*effective rate Acacia col BB ELSE 0
RATE of Acacia col FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN Fire to followup clearing interval*effective rate Acacia col FS ELSE 0
RATE of Acacia col no clearing = IF Wildfire option= 1 then 0.0111 else 0
RATE of Acacia estab = RATE of Acacia recol B+RATE of Acacia recol S+RATE of Acacia recol FS
RATE of Acacia recol BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN First clearing to fire interval*effective Acacia recol SB 3+After followup with fire*effective Acacia recol BB ELSE 0
RATE of Acacia recol FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN First clearing to fire interval*effective Acacia recol SB 3+After followup with fire*effective Acacia recol FS ELSE 0
RATE of Acacia recol SB = IF Invaded site manag = 1 THEN First clearing without fire or followup*effective Acacia recol SB 3+First clearing to followup clearing interval without fire*effective Acacia recol SB 3+After followup without fire*effective Acacia recol SB 5 ELSE 0
RATE of Acacia vs E comp = RATE Aca vs E comp fire to followup interval BB+RATE Aca vs E comp fire to followup interval SB+RATE Aca vs E comp 1st clearing to fire interval FS

RATE of Acacia vs E comp with first clearing = IF Before first clearing interval=1 THEN RATE comp before initial clearing E ELSE RATE Aca vs E comp fire to followup interval BB+RATE Aca vs E comp fire to followup interval FS+RATE Aca vs E comp fire to followup interval SB

RATE of Acacia vs R comp = IF first clearing option=1 THEN Converter 1 ELSE RATE comp before initial clearing R

RATE of Acacia vs R comp with first clearing = IF Before first clearing interval=1 THEN RATE comp before initial clearing R ELSE RATE Aca vs R comp fire to followup interval BB+RATE Aca vs R comp fire to followup interval FS+RATE Aca vs R comp fire to followup interval SB

RATE of Acacia vs S comp = RATE Aca vs S comp fire to followup interval BB+RATE Aca vs S comp fire to followup interval FS+RATE Aca vs S comp fire to follwup interval SB

RATE of Acacia vs S comp with first clearing = IF Before first clearing interval=1 THEN RATE comp before initial clearing S ELSE RATE Aca vs S comp fire to followup interval BB+RATE Aca vs S comp fire to followup interval FS+RATE Aca vs S comp fire to followup interval SB

RATE of E col = RATE of E col BB+RATE of E col FS+RATE of E col Ref

---

RATE of E col BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN Fire to followup clearing interval*effective rate E col BB ELSE 0

RATE of E col FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN Fire to followup clearing interval*effective rate E col FS ELSE 0

RATE of E col Ref = IF Invaded site manag = 0 THEN effective rate E col Ref ELSE 0

RATE of E estab = RATE of E estab BB+RATE of E estab FS+RATE of E estab SB

RATE of E estab BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN First clearing to fire interval*effective E estab SB 3+After followup with fire*effective E estab BB ELSE 0

RATE of E estab FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN First clearing to fire interval*effective E estab SB 3+After followup with fire*effective E estab FS ELSE 0

RATE of E estab SB = IF Invaded site manag = 1 THEN First clearing without fire or followup*effective E estab SB 3+First clearing to followup clearing interval without fire*effective E estab SB 3+After followup without fire*effective E estab SB 5 ELSE 0

RATE of R col = RATE of R col BB+RATE of R col FS+RATE of R col Ref

---

RATE of R col BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN Fire to followup clearing interval*effective rate R col BB ELSE 0

RATE of R col FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN Fire to followup clearing interval*effective rate R col FS ELSE 0
RATE of R col Ref = IF Invaded site manag = 0 THEN effective rate R col Ref ELSE 0
RATE of R estab = RATE of R estab BB+RATE of R estab FS+RATE of R estab SB
RATE of R estab BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN First clearing to fire interval*effective R estab SB 3+After followup with fire*effective R estab BB ELSE 0
RATE of R estab FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN First clearing to fire interval*effective R estab SB 3+After followup with fire*effective R estab FS ELSE 0
RATE of R estab SB = IF Invaded site manag = 1 THEN First clearing without fire or followup*effective R estab SB 3+First clearing to followup clearing interval without fire*effective R estab SB 3+After followup without fire*effective R estab SB 5 ELSE 0
RATE of S col = RATE of S col BB+RATE of S col FS+RATE of S col Ref
RATE of S col BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN Fire to followup clearing interval*effective rate S col BB ELSE 0
RATE of S col FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN Fire to followup clearing interval*effective rate S col FS ELSE 0
RATE of S col Ref = IF Invaded site manag = 0 THEN effective rate S col Ref ELSE 0
RATE of S estab = RATE of S estab BB+RATE of S estab FS+RATE of S estab SB

RANDOM VARIABLES:

Fire probability = ROUND(RANDOM(1,Chances_for_fire_to_occur))
Fire intensity = RANDOM(0,1)

CONSTANTS:

Chances for fire to occur = 0
Seasonality = COUNTER(0,12)
Scenario1 = 0
Scenario2 = 0
Scenario3 = 0

Scenario4 = 0
Scenario5 = 0
RATE of S estab BB = IF Sowing management option = 0 AND Invaded site manag = 1 THEN First clearing to fire interval*effective rate S estab SB 3+After followup with fire*effective rate S estab BB ELSE 0
RATE of S estab FS = IF Invaded site manag = 1 AND Sowing management option = 1 THEN First clearing to fire interval*effective rate S estab SB 3+After followup with fire*effective rate S estab FS ELSE 0
RATE of S estab SB = IF Invaded site manag = 1 THEN First clearing without fire or followup*effective rate S estab SB 3+First clearing to followup clearing interval without fire*effective rate S estab SB 3+After followup without fire*effective rate S estab SB 5 ELSE 0
Scenario6 = 0
Acacia col trans rate BB = 0.521599038395271
Acacia col trans rate FS = 0.503439116585814
Acacia col trans rate SB 3 = 0.0147202538232269
Acacia recol trans rate BB = 0.127451161607191
Acacia recol trans rate FS = 0.107804886228245
Acacia recol trans rate SB 5 = 0.0378401030761728
Acacia vs E trans rate BB 3 = 0.520769231241489
Acacia vs E trans rate BB 5 = 0.125171464161712
Acacia vs E trans rate FS 3 = 0.502381816519926
Acacia vs E trans rate FS 5 = 0.101013757216572
Acacia vs E trans rate SB 3 = 0.0232556409639907
Acacia vs E trans rate SB 5 = 0.0396702191049129
Acacia vs R trans rate BB 3 = 0.510219687467398
Acacia vs R trans rate BB 5 = 0.101165991689314
Acacia vs R trans rate FS 3 = 0.497254599319225
Acacia vs R trans rate FS 5 = 0.102085877750703

Acacia vs R trans rate SB 3 = 0
Acacia vs R trans rate SB 5 = 0.0395819585923386
Acacia vs S trans rate BB 3 = 0.517291085712172
Acacia vs S trans rate BB 5 = 0.126633281141432
Acacia vs S trans rate FS 3 = 0.47785970332092
Acacia vs S trans rate FS 5 = -0.123971825921716
Acacia vs S trans rate SB 3 = 0.00251745092295882
Acacia vs S trans rate SB 5 = 0.00819880657094906
E col trans rate BB = 0.000829807153781931
E col trans rate FS = 0.00105730006588832
E col trans rate Ref = 0.266410722264839
E estab trans rate BB = 0.00227969744547957
E estab trans rate FS = 0.00679112901167311
E estab trans rate SB 3 = 0.000847751552911241
E estab trans rate SB 5 = 0.00484418905096727
months after burn in Ref site = 24
months after clearing SB = 12
months from 1st to 2nd clearing = 12
months from 2nd to 3rd clearing = 12
months of competition = 12
R col trans rate BB = 0.0113793509278726
R col trans rate FS = 0.0061845172665895
R col trans rate Ref = 0.309175730501142
R estab trans rate BB = 0.0262851699178771
R estab trans rate FS = 0.00571900847754198
R estab trans rate SB 3 = 0.0186752443232551

R estab trans rate SB 5 = 0.0115458281084269
simulation periodicity = COUNTER(0,length_of_simulation+12)
S col trans rate BB = 0.00430795268309947
S col trans rate FS = 0.025579413264894
S col trans rate Ref = 0.17267576849813
S estab trans rate BB = 0.000817880465759004
S estab trans rate FS = 0.231776712149961
S estab trans rate SB 3 = 0.0122028029002681
S estab trans rate SB 5 = 0.0296412965052237
Chances for fire to occur = COUNTER(0,10)
clearing cycle = COUNTER(0,10)
Cost of fire = 0
Cost of first clearing = 0
Cost of followup clearing = 0
Cost of sowing = 0
Fire management option = COUNTER(0,1)
first clearing option = COUNTER(0,1)
followup clearing option = COUNTER(0,1)
followup clearing time after first clearing = COUNTER(1,36)
Invaded site option = COUNTER(0,1)
length of simulation = COUNTER(0,500)
Management fire time after first clearing = COUNTER(1,24)
periodicity of clearing months = COUNTER(1,36)
Sowing management option = COUNTER(0,1)
Wildfire option = COUNTER(0,1)