

Identifying priority areas for active restoration after alien plant clearing in the City of Cape Town

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(Department of Botany and Zoology)

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Declaration

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Date: March 2016

Thesis outline

Invasive alien plants (IAP) can have negative impacts on native ecosystems and in prolonged invasions, ecosystems can be transformed to a new alternative ecosystem state.

Clearing IAP (“passive” restoration) does not always initiate native vegetation and ecosystem function recovery, therefore additional restoration measures (“active” restoration) might be needed to set the ecosystem on the trajectory of recovery. Active restoration is more resource intensive compared to passive restoration. In some cases active restoration may be justified since, unsuccessful clearing may lead to the wasting of resources through re-invasion or secondary invasions. Restoring previously invaded or degraded vegetation can be motivated by using improved native biodiversity, ecosystem services or social benefits as incentives. To ensure the effective and efficient allocation of limited IAP control resources, some form of restoration prioritization is required. The aim of this study was thus to develop a framework to identify areas in need of active restoration and to prioritize areas for active restoration. The framework was illustrated in an urban setting by using Cape Town as a case study.

In the first part of my thesis I developed two frameworks. Firstly, a framework was developed to identify areas that may need active restoration. Results of this framework are illustrated in a map indicating areas that would likely need active restoration. A second framework was developed to prioritize areas for active restoration, with a map as an outcome, indicating priority areas for active restoration. Both frameworks were built using an approach called Multi-Criteria Analysis, which is a method to construct a goal, combine stakeholder opinions and facilitate spatial restoration planning. Frameworks consisted of different criteria and sub-criteria to identify and prioritize areas for active restoration such as the extent and density of invasion, invasive species’ ecosystem impacts and conservation status of vegetation types. Criteria and sub-criteria were scored in terms of their relative importance relating to effects on vegetation recovery post-alien clearing and prioritizing areas. The framework is simple to implement and to illustrate findings and can be applied spatially and updated if new information becomes available. It can also be applied at different scales and to different ecosystems around the world; the importance of some criteria might be altered according to the ecosystem dynamics.

In the second part of my thesis I conducted a field study investigating the impacts of invasions by two different types of invaders: pines and acacias; and compared their impacts on two different highly threatened lowland fynbos vegetation types. This study was also used to test the main assumptions made for the framework to identify areas for active restoration, developed in the first part of the thesis. Vegetation structure, composition and richness, and abiotic variables such as soil characteristics and litter biomass were used as criteria to determine whether ecosystems have been able to recover to a similar level than an uninvaded reference site post-clearing. Acacias changed abiotic and biotic variables after two cycles of invasion (and after one cycle of invasion in some cases) while lowland fynbos is resilient up to three rotations of pine planting. Pine-invaded areas generally had higher restoration potential than acacia-invaded areas. In terms of vegetation structure, perennial species and guild richness: acacias more

negatively impacted invaded sites, whereas pine plantations recovered better in comparison to the reference site. Follow-up clearing generally promoted better ecosystem recovery in terms of overall species richness and structure but care should be taken not to damage indigenous shrubs.

In conclusion, this study addressed two important aspects currently lacking in restoration, firstly by providing a framework for identifying and prioritizing areas for active restoration, to be used specifically in spatial IAP management. The two frameworks consider the multiple aspects involved in restoration, namely: biodiversity, ecosystem functioning and services, social and political aspects. Secondly, it is also a multi-species approach, considering the main woody transformers in the frameworks, testing the framework, and providing restoration recommendations for the two main lowland invaders: *Pinus radiata* and *Acacia saligna*. The overall outcomes of this study will serve as a tool for the City of Cape Town and land managers to improve active restoration efforts.

Opsomming

Uitheimse indringerplante kan 'n negatiewe impak op inheemse ekosisteme hê, en langdurige indringing kan ekosisteme tot 'n nuwe, alternatiewe toestand transformeer.

Die verwydering van uitheimse indringers ("passiewe" herstel) is nie altyd genoeg om die herstel van inheemse plantegroei en ekosisteemfunksionering teweeg te bring nie. Bykomende maatreëls ("aktiewe" herstel) kan nodig wees om die ekosisteem weer op die pad na herstel te plaas. Aktiewe herstel is meer hulpbronintensief as passiewe herstel. In sommige gevalle is aktiewe herstel egter geregverdig omdat onsuksesvolle verwydering van uitheimse indringers hulpbronne kan verkwis indien dit bloot tot hernude of sekondêre indringing lei. Verbeterde inheemse biodiversiteit, doeltreffende ekosisteemdienste of maatskaplike voordele kan as aansporing dien vir die herstel van plantegroei wat voorheen aan indringing of degradasie blootgestel was. Om te verseker dat die beperkte hulpbronne vir die beheer van uitheimse indringers doeltreffend en doelmatig toegewys word, word 'n vorm van prioritisering vereis. Die doel van hierdie studie was dus om 'n raamwerk te ontwikkel om gebiede waar aktiewe herstel nodig is uit te wys en te prioritiseer. Kaapstad dien as 'n gevallestudie om die toepassing van die raamwerk in 'n stedelike omgewing te demonstreer.

In die eerste deel van my tesis ontwikkel ek twee raamwerke. Eerstens word 'n raamwerk ontwikkel om gebiede uit te wys wat dalk aktiewe herstel vereis. Die resultate van hierdie raamwerk word voorgestel op 'n kaart wat dié gebiede aandui. 'n Tweede raamwerk word ontwikkel om gebiede vir aktiewe herstel te prioritiseer. Weereens word die prioriteitsgebiede op 'n kaart aangedui. Albei raamwerke word met behulp van 'n benadering genaamd Multikriteriaontleding ontwikkel. Dié benadering word gebruik om 'n doel vas te stel, die menings van belanghebbendes te kombineer en ruimtelike herstelbeplanning te fasiliteer. Die raamwerke gebruik verskillende kriteria en subkriteria om gebiede vir aktiewe herstel uit te wys en te prioritiseer, soos die omvang en digtheid van indringing, indringerspesies se impak op die ekosisteem, en die bewaringstatus van plantsoorte. Tellings word aan die kriteria en subkriteria toegeken op grond van hulle relatiewe belang vir plantegroeiherstel na die verwydering van indringers, sowel as vir gebiedsprioritisering. Die raamwerke is eenvoudig om te implementeer, en bevindinge word maklik geïllustreer. Dit kan ruimtelik toegepas en bygewerk word namate nuwe data beskikbaar kom. Boonop kan dit op verskillende skale en verskillende ekosisteme oor die hele wêreld toegepas word; die belang van sekere kriteria kan bloot aangepas word na gelang van die ekosisteemdinamiek.

In die tweede deel van my tesis onderneem ek 'n veldstudie om die indringingsimpak van twee soorte indringerplante, naamlik denne en akasias, te ondersoek. Die impak van dié twee spesies op twee hoogs bedreigde plantsoorte in die laaglandfynbosgroep word ook vergelyk. Die veldstudie word voorts gebruik vir die toetsing van die hoofaannames vir die raamwerke wat in die eerste deel van die tesis ontwikkel is. Plantegroeistruktuur, -samestelling en -rykheid sowel as abiotiese veranderlikes soos grondeienskappe en dooieplantbiomassa word gebruik as kriteria om vas te stel of ekosisteme ná die verwydering van indringers tot op dieselfde vlak kon herstel as 'n verwysingsterrein waar geen indringing plaasgevind het

nie. Met akasias het die abiotiese en biotiese veranderlikes ná twee indringingsiklusse (selfs na een indringersiklus in sommige gevalle) verander, terwyl laaglandfynbos tot drie rotasies denne-aanplanting kon weerstaan. Gebiede met denne-indringing beskik oor die algemeen oor sterker herstelpotensiaal as dié met akasia-indringing. Wat plantegroeistruktuur, die voorkoms van meerjarige plante en rykheid aan funksionele groepe betref, het akasias 'n groter negatiewe impak op indringingsgebiede gehad, terwyl denneplantasies beter herstel het in vergelyking met die verwysingsterrein. Opvolgverwydering van indringerplante het oor die algemeen beter ekosisteemherstel bevorder wat spesierykheid en -struktuur betref, maar daar moet versigtig te werk gegaan word om nie inheemse struik te beskadig nie.

Die navorsing vir hierdie tesis vul twee belangrike leemtes in huidige herstelaksies. Eerstens word raamwerke voorsien om gebiede vir aktiewe herstel uit te wys en te prioritiseer, wat bepaald vir die ruimtelike bestuur van uitheemse indringerplante gebruik kan word. Die twee raamwerke neem die veelvuldige aspekte van herstel in ag, naamlik biodiversiteit, ekosisteemfunksionering en -dienste, sowel as maatskaplike en politieke aspekte. Tweedens bied die navorsing 'n multispesiebenadering wat die vernaamste houtagtige transformatorspesies in die raamwerke bestudeer, die raamwerke toets, en dan aanbevelings doen oor herstel ná indringing deur die vernaamste twee laagland-indringers, *Pinus radiata* en *Acacia saligna*. Die algehele uitkomst van die studie dien as 'n instrument vir die Stad Kaapstad en grondbestuurders om aktiewe herstellings te verbeter.

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List of abbreviations

AHP: Analytical hierarchical process

CBA: Critical biodiversity areas

CESA: Critical ecological support areas

CFR: Cape Floristic Region

CFSF: Cape Flats Sand Fynbos

CI: Confidence interval

EC: Electrical conductivity

GIS: Geographic information system

GLM: Generalized linear models

GPS: Global positioning system

IAP: Invasive alien plants

MAT: Mean annual temperature

MCA: Multi-criteria approach

OESA: Other ecological support areas

PES: Payments for ecosystem services

SAF: Swartland Alluvium Fynbos

SAPIA: Southern African plant invaders atlas

WfW: Working for Water

Chapter 1: Introduction

1.1 Rationale

Invasive alien plants (IAP) can impact ecosystems negatively and in some extreme cases ecosystems can become transformed (van Andel and Aronson, 2012). South Africa has a comprehensive invasive species control programme, the Working for Water programme (WfW). It is a national programme sponsored by the government, private and international organizations. The WfW programme clears large areas of land of invasive alien vegetation, especially along waterways and in water catchment areas using mechanical, chemical and biological control measures. The programme is unique in the sense that it also provides employment and training to local communities (Van Wilgen et al., 1998; Koenig, 2009). The success of the programme lies in the fact that it considers the ecological, social, economic and hydrological aspects of invasions (Richardson and Van Wilgen, 2004). IAP control has previously been done opportunistically and with the main goal to improve water quantity and quality and ensure removal of alien biomass; whereas little attention was given to ensure or promote recovery of native vegetation (Turpie et al., 2008). The recovery of ecosystems (including native vegetation) is initiated and facilitated by restoration interventions. The aim of restoration is for ecosystems to recover structurally and functionally to a state similar to before invasions (Bradshaw, 1983). There are two types of restoration. Firstly, **passive** restoration is the removal of the stressor, in this example clearing IAP and limiting their regeneration (Le Maitre et al., 2011). The recovery of a native species-dominated, functional ecosystem is however not always realised (D'Antonio and Meyerson, 2002; Hulme, 2006; Reid et al., 2009). If the recovery of native vegetation post-clearing is slow or unlikely, additional restoration is needed (van Andel and Aronson, 2012). Any additional restoration is termed **active** restoration. Active restoration is, however, more resource intensive compared to passive restoration and when restoring invaded areas, some form of prioritization is required in order to use limited resources effectively and efficiently.

1.2 Knowledge Gap

Numerous studies have prioritized areas and species that should be targeted for alien vegetation control (Nel et al., 2004; van Wilgen et al., 2008), for example Forsyth et al. (2012) recently prioritized invasive plant species for control in the Cape Town municipal area. Additionally, a comprehensive protocol was described for restoration actions in the Cape Floristic Region, but this does not include a prioritization protocol for restoration (Holmes and Richardson, 1999). More recent work on restoration potential post-alien clearing has produced insights into ecosystem resilience and barriers to restoration (Aronson et al., 2007; Gaertner et al., 2012a). Conceptual models and theoretical frameworks have been developed (Holmes and Richardson, 1999; Gaertner et al., 2012b; Zhao et al., 2013) but have so far not been applied. There have been studies on restoration prioritization, but there is no universally accepted method. A common flaw in many restoration prioritization actions is that a clear goal does not precede

and guide the objectives and values of operations and often the wrong components are included to achieve the goal (Beechie et al., 2008; Richardson and Gaertner, 2013).

1.3 Problem Statement

I have identified two main gaps in the literature: firstly, selecting areas for restoration have for instance been done for reforestation (Kettle, 2012; Knowles, 2012), species habitat restoration (Beechie et al., 2008) and restoration after land transformation due to agriculture (Crossman and Bryan, 2006), but there is currently no protocol to distinguish between areas needing passive or active restoration and how to prioritize areas invaded by alien plants for restoration. Secondly, previous restoration prioritization usually focused on single or limited aspects (Esler et al., 2008), for example only considering economic aspects and not considering social and ecosystem service benefits in determining restoration priorities. However, in some situations, the biodiversity or ecosystem service significance of areas should be included, since those aspects might outweigh financially the low priority areas with their lower economic priority (Gaertner et al., 2012c; Crookes et al., 2013).

1.4 Research Aim

The overall aim of my study was to develop, illustrate and test a framework to distinguish between areas in need of active restoration in the City of Cape Town and to prioritize areas for restoration at a city scale.

Objectives

- To develop and illustrate a framework to identify areas in need of active restoration.
- To develop a framework to prioritize areas for active restoration, considering multiple aspects involved in restoration prioritization.
- To test assumptions developed in the frameworks in Chapter 3 by investigating the potential for passive recovery post-clearing of two different invasive transformer trees, namely acacias and pines, through a site-scale field study.

1.5 Brief Chapter Overview

This thesis comprises of a literature review and two research chapters, which are presented in the form of manuscripts to be submitted to scientific journals.

Firstly, the important concepts relating to restoration are reviewed, followed by a discussion on why it is important to consider whether areas cleared of invasive transformer species would recover after clearing (passive) or whether further active restoration would be required. Secondly, ways of how to go about prioritizing areas for active restoration are explored. Finally, the fields of restoration ecology and invasion biology are discussed with specific emphasis on fynbos shrubland, which is the main focus of this study (Chapter 2).

In Chapter 3 of this study, a framework was developed to identify areas that may need active restoration. The framework is illustrated at a city scale, using the City of Cape Town as a case study. Maps were produced indicating areas that would likely need active restoration. A second framework was developed

to prioritize areas for active restoration. The basic frameworks were developed during two workshops. The workshops drew from the experience and expert opinions of invited stakeholders on the impacts that woody alien transformer species have on fynbos regeneration ability and the criteria required to justify prioritizing areas for active restoration. For each of the criteria sub-criteria (such as under ‘invasion history’: density of invasion and duration of invasion/no of fire cycles since dense invasion) were identified and their relative importance scored in terms of effects on vegetation recovery post-alien clearing and prioritizing areas for active restoration. A map was produced as an outcome, indicating priority areas for active restoration in Cape Town.

Chapter 4 aimed to test some of the assumptions made in chapter 3 and to inform alien management practices by investigating the impact of invasions by two different types of invaders: pines and acacias; on highly threatened lowland fynbos ecosystems and the potential for passive recovery post-clearing. Vegetation structure, composition and richness, and abiotic variables such as soil characteristics and litter biomass were used as criteria to determine whether ecosystems have been able to recover to a similar level than an uninvaded reference site post-clearing. The impacts of acacia and pine invasion were also compared to each other.

Finally, I provide a synthesis of what the results of the work presented in the two research chapters add to our knowledge of restoration post alien clearing (Chapter 5).

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Chapter 2: Literature review

The ease of long-distance travel among areas, is purposefully or unintentionally introducing alien plants into new areas (Richardson and Van Wilgen, 2004; Mooney, 2005; Vallejo et al., 2012). Invasive alien plants (IAP) are of concern since they can change and negatively alter species composition, ecosystem structure and ecosystem functioning (Van Wilgen et al., 1998; Richardson et al., 2000; Mooney, 2005; Brownlie and Botha, 2009; Pejchar and Mooney, 2009; Vilà et al., 2009; Gaertner et al., 2012a; Handel et al., 2013). In South Africa, the number of naturalized alien invasive species exceeds 600 according to the Southern African Plant Invaders Atlas (SAPIA) and 379 species are listed invaders in the National Environmental Management: Biodiversity Act 2014 Invasive Species Regulations.

The negative impacts of IAP can lead to economic losses (Pimentel et al., 2001). The realization that it is more cost-effective to remove IAP and restore natural ecosystem functioning, than it is to source alternative ecosystem goods and services, led to the development of prevention strategies against introducing new species, controlling current invasions and developing supporting management plans and legislation (Van Wilgen et al., 1998; van Wilgen et al., 2012).

Managing IAP mostly includes manual clearing. Simply removing the dominant invader is sometimes not sufficient to address negative impacts that the species have on the ecosystem, such as altering soil conditions, or suppressing and eliminating native vegetation: additional restoration is hence often needed (Crossman and Bryan, 2006; Esler et al., 2008; Reid et al., 2009; Gaertner et al., 2012b; Ma et al., 2013). Restoration is aimed at speeding up the process of the recovery of ecosystems to an improved state concerning the vegetation structure, ecosystem functioning and community composition (D'Antonio and Meyerson, 2002; Trabucchi et al., 2012). Restoration actions can assist to control invasive alien species and restore native vegetation (Holmes et al., 2008; Gaertner et al., 2012c). **Passive** restoration refers to removing the cause of habitat degradation, in this case invasive alien vegetation, then leaving the ecosystem to self-repair, whereas **active** restoration includes additional measures such as re-introducing native species (Allen, 1995) and treating the altered physical processes, along with the biological processes (Tongway and Ludwig, 2012).

Restoration is labour-intensive and expensive. The cost of active restoration and associated activities can be prohibitive to some land owners; on the other hand, unsuccessful clearing may lead to the wasting of resources through re-invasion or secondary invasions (Hilderbrand et al., 2005; Holmes et al., 2008; Le Maitre et al., 2011). In some situations expenditure on restoration can reduce the long-term costs of IAP control by improving the efficiency of control while restoring the ecosystem (Le Maitre et al., 2011).

In general, resources for conservation and IAP control are limited (Crossman and Bryan, 2006) and managers must prioritize their actions in order to achieve their goals most efficiently and effectively (Aronson et al., 2007; Rew et al., 2007; Skurski, 2012; van Wilgen et al., 2012). Passive restoration usually requires the least amount of resources and areas only requiring passive restoration have the highest feasibility to restore natural vegetation and ecosystem functioning. Therefore one restoration strategy is to select areas with potential for passive restoration first (Beechie et al., 2008) until the budget is depleted or until all areas are controlled; selection will then move on to successive active restoration categories that require more resources. Therefore, those areas that do need active restoration should be identified.

2.2 Restoration

2.2.1 General concepts

Ecological restoration is based on the theory and science of restoration ecology. Bradshaw (1983) and Cairns (1988) were pioneers in this field which has grown over the last 30 years. Many times degradation and restoration studies are site specific, but ecological theories and conceptual models should be incorporated into a broad framework that can guide practitioners in ecological restoration decisions, as done by King and Hobbs (2006).

Whisenant (1999) made the distinction between two approaches to restoration: firstly a structural approach and secondly a functional approach. Which approach is chosen, depends on the desired outcome but also the current state of the ecosystem. The structural approach focusses on the static patterns of the ecosystem, restoring the ecosystem structural components, such as planting guilds missing due to degradation, to resemble an undisturbed state. This approach does not take into account the underlying dynamics and processes in the degraded ecosystem and some uncertainty will be created about the persistence of structural success. The functional approach however, takes into account the dynamic nature of ecosystems and the processes changed during degradation. Stromberg (2001) for example, places much emphasis on restoring the natural process to put ecosystems on the trajectory of restoration to maintain ecosystem functioning and biodiversity. Restoration using this approach takes more time (Stromberg 2001) but in the long term could lead to a decrease in uncertainty of restoration success.

Another distinction can be made, between biotic and abiotic components of the ecosystem and approaches to restoration. A combination of biotic/abiotic and either structural or functional can exist, e.g. biotic structural component. As the degradation continues, both biotic and abiotic structural and functional components are affected, with biotic structural changes occurring first, followed by either biotic functional or abiotic structural changes. Lastly, the extreme abiotic functional changes can occur. Abiotic components can affect biotic components and vice versa and structural components can

influence functional components and vice versa (i.e. re-enforcing feedback loops are established) (King and Hobbs, 2006). Restoration implications for different components are discussed below.

Once one has established which aspect to restore (e.g. structural/functional or biotic/abiotic), the next step is to decide how to approach restoration given the different ideas mentioned above. This is well illustrated in the threshold model. Restoration is challenging if the ecosystem has crossed one or more thresholds of degradation (Hobbs et al., 2006). Changes in vegetation dynamics can lead to the crossing of continuous and reversible thresholds while catastrophic events, multiple disturbances or ongoing disturbance can lead to the crossing of a discontinuous threshold (Briske et al., 2005). Continuous and reversible thresholds do not lead to a change to an alternative ecosystem state and with some input, ecosystems can be restored but once an irreversible threshold has been crossed, the ecosystem will change to an alternative ecosystem state which is difficult and often impossible to reverse (Briske et al., 2005). Thus after the crossing of several thresholds, including an irreversible threshold, ecosystems can shift to a new alternative stable state (Briske et al., 2005). The ecosystem processes that are changed and that lead to ecosystem transitions, should be restored in order to return to previous more desirable states (Stringham et al., 2003). As the ecosystem moves from one state to the next, the amount of resources needed to restore native vegetation increases (Holmes and Richardson, 1999; Gaertner et al., 2012a). At some stage, the resources required would be prohibitive. Where biotic structure and function is desired, abiotic processes need to be functioning (Stringham et al., 2003). Thus restoring the abiotic processes is critical to restoration and ecosystem functioning (Stringham et al., 2003). In some instances abiotic processes are still functioning, meaning autogenic biotic recovery is still possible; in other instances some input is necessary to achieve ecosystem recovery (Whisenant, 1999; Archer et al., 2001; Stringham et al., 2003; Gaertner et al., 2012a). Determining whether processes have been changed is however difficult, requiring data ranging over large time and spatial scales, and from different levels of degradation (Stringham et al., 2003). From these key ideas, one should carefully consider and choose restoration strategies that will benefit both the biotic (e.g. plant interactions, dispersal, pollination and soil microorganisms) and abiotic processes (e.g. hydrology, soil nutrients and stability) simultaneously in order to put the ecosystem on the trajectory of recovery. One should also keep the feedbacks between biotic and abiotic processes in mind (King and Hobbs, 2006). Ecosystem feedbacks (e.g. higher nutrient levels will lead to more invader biomass) re-inforce themselves and can lead to further dominance of invaders (Gaertner et al., 2012a)

2.2.2 Restoration post invasive species control

Conservation is focused on preventing damage to ecosystems, where ecological restoration aims to repair damage caused by disturbances such as IAP (Van Andel and Aronson, 2012). Conserving natural areas by itself is considered insufficient to achieve conservation targets in our highly altered and transformed environment (Young, 2000). Additionally, implementing invasive alien species

management to curb alien invasions and ecosystem transformations can be challenged by socio-economic impacts that influence every step (Mack et al., 2000), e.g. conflicts of interest over invasive alien species removal and budget allocation. Thus, conservation and restoration should be considered together. Ecological restoration aims to restore and protect the natural environment including biodiversity and the goods and services ecosystems provide (Aronson et al., 2006, 2007, 2010). Components that should be considered during restoration are: ecological, social, cultural, economic, political and legislative (Jackson et al., 1995; Aronson, 2010). The involvement of multiple disciplines means inter-professional cooperation as well as partnership and communication are essential, including local nonprofessional stakeholders. Communication and negotiation is crucial since some stakeholders see restoration as a waste of resources (financial, social and political) (Van Andel and Aronson, 2012). Priorities, ideas and criteria will however change over time (Van Andel and Aronson, 2012), influenced by dynamical socio-economic components of societies, such as changes in people's ideas, needs, desires, opinions, resource demands and budgets allocations.

2.2.3 Prioritization

The aim of IAP management is to reduce their impacts, eradicate or reduce their extent or contain them. Generally, the need for IAP management is recognized but how to achieve this is mostly debated. The reality is that conservation managers still need to implement restoration measures with limited budgets over large areas that require a variety of treatments (Parker-Allie et al., 2004). The need to prioritize IAP for management has therefore long been recognized. Kumschick et al. (2012) for example developed a species based approach to prioritize limited funding applications. They recognize the need to consider economy, environment and societal spheres and argue that the species that impact these aspects the most should receive most funding.

Part of restoration planning will have to include prioritizing restoration efforts to make the most efficient use of resources. Prioritization of areas for restoration can be done according to 'desirability', which is a subjective method of prioritization but one can use economic cost to justify this e.g. restoring areas requiring most benefit for least amount of input (Farley and Gaddis, 2007). There is an abundance of literature on restoration activities but less so that considers the economic implications of these; this makes it hard to perform a cost-benefit analysis of restoration activities (Figueroa, 2007). Even though passive restoration requires lower expenditure when compared to active restoration, the additional cost of active restoration might be offset by the gain in ecosystem goods and services (Farley and Gaddis, 2007). Payments for ecosystem services (PES) has been proposed in cases where a decline in ecosystem services (such as water quality and supply) can be used to motivate expenditure on restoration (Turpie et al., 2008; Crookes et al., 2013). Quantifying social benefit from ecosystem goods and services, in order to calculate economic factors and cost-benefit is difficult (Figueroa, 2007). Many studies have however found many social benefits linked to

ecosystem good and services, for example Sandifer et al. (2015) gives a review on the benefits of ecosystem services to human health and well-being.

Additionally prioritization can be done using ecosystem services, biodiversity or social benefits, without placing a quantitative monetary value on benefits. Restoration can be promoted as an investment in the future by maintaining and improving important ecosystem services such as water provision (Aronson et al., 2007; Handel et al., 2013). Social and economic benefits and outcomes from implementing restoration programs include opportunities for job creation and skills training and income from improved vegetation structure and function can be sourced from tourism and, the cut-flower industry (Vromans et al., 2010). Biodiversity benefits of restoration activities include improved conservation status of Red List threatened species and plant and animal communities with similar structure and functions as its pre-invasion state (Simberloff et al., 2011).

One can use certain criteria to identify and prioritize areas for active restoration such as: the extent and density of invasion, ease of control of species, life-history characteristics and ecosystem impacts. Different stakeholders should be included since there may be some conflict of interest e.g. In South Africa invasive Australian acacia species can have strong ecosystem impacts but are also known to have certain benefits such as providing fuel and timber (Wit et al., 2001). By including stakeholders these conflicts of interest can be addressed (De Lange et al., 2012; Forsyth et al., 2012). More recent attempts have been made to score overall species impact and also incorporates stakeholder involvement. Some prioritization schemes for species that considers conflict of interest can be time and resource consuming (Robertson et al., 2003; Roura-Pascual et al., 2010; De Lange et al., 2012; Forsyth et al., 2012). Through the proposed method used in this study, both social and scientific values are incorporated.

Multi-Criteria Analysis

Different restoration options exist (Van Andel and Aronson, 2012) as well as different opinions, and setting clear management goals is important because this will determine the restoration option chosen and can incorporate different stakeholder views. One can then plan management actions based on the predetermined goals and objectives set by stakeholders. Decisions concerning restoration and conservation actions are spatially orientated (Rouget et al., 2003) and Le Maître et al. (2011) proposes using spatial mapping for prioritizing areas for restoration, which will in turn motivate allocation of funding. This makes the identification of restoration priorities more credible and ensures that biodiversity benefits from these efforts (Rouget et al., 2003). The method chosen to incorporate the different goals and opinions in a clear and simple way in this thesis is called: Analytical hierarchical process (AHP), a multi-criteria approach (MCA) (Saaty, 1990).

It is imperative that science informs practice and this study aims to inform alien management practices by investigating the impact that alien invasions have on ecosystems and the potential for passive recovery, based on experiences and knowledge of experts in the field of restoration and invasion ecology. Records of success of management operation are usually not available, and managers often rely on personal knowledge and experience (Parker-Allie et al., 2004). The information on restoration attempts is scarce due to the lack of clear criteria to judge successes and no monitoring to produce quantitative data (although there are limited recent efforts to collate restoration data) (Suding, 2011). The MCA approach was chosen, to capitalize on personal information, not necessarily captured on record (Parker-Allie et al., 2004).

The process starts by setting out the problem and then stating a goal and dividing the problem into different levels of criteria and sub-criteria to meet the goal- thus constructing the framework (Arroyo et al., 2015). Criteria are the main factors of the AHP framework to consider and indicators (in the form of spatial data) can be used as a parameter of the criteria (Orsi et al., 2011). Pairwise comparisons are then done in each level of criteria to establish relative importance or priorities among criteria (Arroyo et al., 2015). Consistency of pairwise comparisons is checked by doing a consistency test (Ishizaka and Labib, 2009), by calculating the consistency ratio (Arroyo et al., 2015). After pairwise comparisons are made and consistency of the judgements checked, weights are derived by using the eigenvalue method (Ishizaka and Labib, 2009) to calculate and eigenvalue vector. This is in turn used to derive a weight for each criteria, indicating a criteria's relative importance (Arroyo et al., 2015). Criteria are weighted according to their relative importance by stakeholders through the pairwise comparison process (Mollot and Bilby, 2008) and weights are based on restoration goals set out initially (Crossman and Bryan, 2006). Software such as Expert Choice Software and Super Decisions Software can be used to facilitate the ranking and pairwise comparison process (Forsyth and Le Maitre, 2011; Forsyth et al., 2012). Robustness of the model can be tested by performing sensitivity analysis. Sensitivity analysis changes the model input to observe how the results change (Ishizaka and Labib, 2009).

The AHP can effectively incorporate different stakeholder views and support a large number of alternative options to compare options during decision making (Malczewski, 1999; Forsyth et al., 2011; Orsi et al., 2011). A multi-criteria approach can be used in conjunction with geographic information system (GIS) and georeferenced data, making spatial decisions possible (Orsi and Geneletti, 2010). Indicators for criteria or sub-criteria can be mapped and combined using GIS, usually illustrated as a prioritization map. The use of GIS in restoration planning is much more efficient than manual mapping and can combine data at a landscape scale, using many, big data sets from many sources (Lee et al., 2002).

A limitation to this approach is that results are only as good as the quality of data (Forsyth, 2013). Quality of data is important to make distinctions between alternative options (Forsyth, 2013). Data

quality is especially important for criteria with highest weights (Forsyth, 2013), playing the biggest role to determine which areas are selected and prioritized for restoration. An advantage is, that as new data are made available and understanding improves, rankings and weights can be adjusted and criteria can be added or removed. Following this approach can make the prioritization process defensible in that the method of deriving priorities is transparent (Forsyth, 2013). The process is participatory and transparent where decisions are discussed until consensus is reached, and results debated and discussed to everyone's understanding. Stakeholders involved in the implementation of alien control are mostly in agreement and get to be part of decisions (Forsyth, 2013). It has also been found to be a flexible way to prioritize areas for invasive species management (Nielsen and Fei, 2015)

2.3 Study Area

Over the recent years, there has been a shift in how people view nature in urban environments. Nature was thought to be separate from the urban environment but now there is a realization that natural open spaces can provide valuable services to people (Handel et al., 2013). Only recently has attention been given to the species composition and quality of these areas (Handel et al., 2013). Deciding where to restore ecosystems invaded by IAP in an ever-changing urban environment is difficult. In Cape Town a shift in paradigm is occurring: invasive species control and restoration are perceived as vital to ensure the sustainable provision of ecosystem services and conservation of biodiversity in this unique area of the Cape Floristic Region (CFR) (Crossman and Bryan, 2006; van Wilgen et al., 2012; Ma et al., 2013). Restoring green areas will benefit the inhabitants by providing them with ecosystem goods and services (Tongway and Ludwig, 2012). Valuable services from healthy ecosystems in the city include water provision, filtering the air, reducing noise, draining rain and attenuating overland flow, regulating the micro-climate, coastal protection, increasing property values and a suite of cultural services, including recreation (Bolund and Hunhammar, 1999; Costanza et al., 2006).

The study encompassed terrestrial areas within the borders of the City of Cape Town, an area covering 2,460 km² of urban and rural land, and the adjacent Stellenbosch and Drakenstein Municipality in the Western Cape, South Africa. The fynbos vegetation in this area is not only of high biodiversity importance but also of high economic value (Forsyth et al., 2012). For example, fynbos catchments provide clean water, rangelands for livestock production (in the renosterveld (Kemper et al., 1999)), food and income from cut wildflowers and tourism opportunities (Hassan, 2003; Turpie et al., 2003). Natural fynbos areas are also important in terms of the infiltration, quality-and provision of groundwater (O'Farrell et al., 2012). The economic benefit from the environment in the City of Cape Town ranges between R2-6 billion annually (De Wit et al., 2009).

The area has a Mediterranean-type climate and the vegetation is prone to fire. Vegetation is fire-dependent for regeneration and maintaining vegetation structure and biodiversity (Luger and Moll, 1993; Ruwanza, 2009). Vegetation in the CFR is primarily shrubland, with fynbos vegetation

occurring on nutrient poor soils and renosterveld on soils with higher nutrient availability (Specht et al., 1983; van Wilgen et al., 2012). Fynbos is renowned for having high levels of endemism and diversity (van Wilgen et al., 2012). Dominant growth forms include proteoids, ericoids, restioids and geophytes (Cowling et al., 1996a). Fynbos vegetation has a relatively low biomass and water requirements (Le Maitre et al., 2009), which is in contrast to invasive alien trees that have larger biomass and higher evapotranspiration rates (Chamier et al., 2012). Fynbos is mostly invaded by trees and shrubs with the most dominant genera being *Pinus* (pines), *Acacia* (wattles) and *Hakea* (shrubs in the family Proteaceae) (Forsyth et al., 2012). This study will focus on the dominant invader shrubs and trees from the genera *Pinus* (pines), and *Acacia* (wattles) and to a lesser extent *Hakea* (shrubs in the family Proteaceae) and *Eucalyptus* (gums).

2.4 Study Organisms

Invasive alien trees in South Africa are pre-adapted to the climatic conditions, are competitive with native vegetation (Le Maitre et al., 2000) and are especially a problem in riparian areas, where they use excessive amounts of water compared to native vegetation, like fynbos (Moran et al., 1999).

2.4.1 *Acacia*

Australian acacias are leguminous species that fix atmospheric nitrogen which can lead to a change in soil N-cycling (Yelenik et al., 2004). Even the clearing of these invasive alien trees can cause disturbances leading to changes in nutrient cycling (Vitousek and Melillo, 1979; Jovanovic et al., 2008) due to changes in rates of mineralization, soil microorganisms, microclimate, soil-chemistry, -processes and -properties. Plant available N is added to the system through microbial-assisted fixation and is then cycled in the system through plant uptake, litter production, mineralization, adsorption and desorption (Jovanovic et al., 2008). Nitrogen can be lost or reduced in the system through volatilization of ammonium, runoff and leaching, removing plant biomass and denitrification (Jovanovic et al., 2008). Nitrogen can also be leached into groundwater, negatively influencing water quality (Jovanovic et al., 2008). For example, Australian acacias can fix N, releasing up to 2.5-7.4 kg of N per 0.1 hectare/year. The biggest challenge of acacias is that the increase in soil fertility leads to a positive feedback loop, further facilitating acacia establishment, increase in abundance and dominance (Gaertner et al., 2012a). This promotes the out competition of native species (Marchante et al., 2008; van der Putten et al., 2013).

Even after alien clearing, the effects of increased soil fertility may remain as a legacy effect (Yelenik et al., 2004). When the acacia overstorey cover is cleared, increasing radiant energy reaches the soil and increases soil moisture due to less water uptake by acacias (Yelenik et al., 2004). These factors can contribute to increased rates of N mineralization (Yelenik et al., 2004). Increased mineralization decreases nutrient competition for decomposers, meaning rates of decomposing and mineralization of input litter can increase after clearing (Jovanovic et al., 2008). Mineralized N will then be abundantly

available for removal from the system through e.g. either leaching out (i.e. during the rainy season) or volatilization by fire (Jovanovic et al., 2008). Temperature, soil moisture and litter vary seasonally, meaning N concentrations in the soil are also seasonal but N will decrease in the soil in the absence of N fixing acacias with the main leaching agent being rainfall (Jovanovic et al., 2008). The precise residence time of N has yet to be determined. Using fire as a control method is popular to control acacia populations and deplete the acacia seed bank (Holmes, 1989; Pieterse and Boucher, 1997). Burning results in some aliens reprofiting from their stumps and mass seedling germination from the alien seed bank (Holmes, 1989; Pieterse and Boucher, 1997). Resprouting trees and mass regeneration can be more difficult and eventually more resource intensive to control during follow up (Pieterse and Boucher, 1997).

2.4.2 *Pinus*

Pine species have been extensively planted in the southern hemisphere for the past 300 years and plantations are a source of seed and spread for species becoming invasive. Control of pines outside plantations is a problem (Richardson, 1998). *Pinus radiata* can and has invaded nutrient poor environments and has been a problematic tree spreading in the fynbos (Richardson, 1998). Invasive pine species have large canopy-held seed banks and the seedlings can be highly competitive following a fire (Moran et al., 1999). Pine canopy cover can close as early as 5 years in some cases (Bekunda et al., 1990). In contrast, acacia canopy can close within a year post-fire (Gaertner et al., 2012a). Pines also increase soil nutrients but the availability in the soil depends on the initial nutrient concentration in litter and also litter quantity; the slash and litter left after clear felling is an important source of P (Bekunda et al., 1990). The rate of organic matter decomposition increases after clear felling, similarly to acacia felling and clearing, (Gadgil & Gadgil 1978) and other nutrients can be mineralized faster after clear-felling, releasing them from the litter into the soil (Bekunda et al., 1990). Soils under pine plantations have been observed to have increased acidity, electronic conductivity and soil organic matter (Jaiyeoba, 1998; Scholes and Nowicki, 2000; Mills and Fey, 2003). Increased soil acidity could increase available P supply by stimulating P release from microorganisms (Seeling and Zasoski, 1993).

2.5 Invasion and restoration in the fynbos

2.5.1 Threat of invasion

Indigenous vegetation is threatened by the loss of habitats and fragmentation due to land cover changes caused by urbanization and agricultural expansion (Seto et al., 2012; Bellard et al., 2014). The fragments are further threatened and degraded by IAP colonization (Seto et al., 2012). So great is the impact of IAP, that they are considered one of the major threats to biodiversity loss worldwide (Bellard et al., 2014). One way to use restricted resources efficiently is to limit and reduce the impact of IAP in areas that are the most valuable in terms of biodiversity, have high levels of endemism, but

also have the highest threat and vulnerability, such as those areas delineated as biodiversity hotspots (Mittermeier et al., 2011). Biodiversity hotspots, such as the CFR, are already subjected to disturbance and land use change and threatened by habitat loss and climate change, making them even more vulnerable to the impacts of IAP (Bellard et al., 2014).

2.5.2 Impact of invasion on fynbos species richness

The same processes thought to govern fynbos species richness, are also impacted by IAP and we can intuitively hypothesise that IAP must affect ecosystems at an important structural and functional level. Important processes include the 1) abiotic conditions of the ecosystem such as the climate and soils/geology 2) interspecific species competition and 3) the disturbance factors playing a dominant role in the ecosystem (Tilman and Pacala, 1993; Vlok, 1996). Fynbos is known for its large turnover in species composition over a short distance. In the fynbos, climate and geology (Cowling and Holmes, 1992; Cowling et al., 1996b), fire disturbance (Kruger, 1983; Cowling et al., 1992) and certain species competitive interactions (Yeaton and Bond, 1991; Vlok, 1996) determine the speciation and co-existence of a large number of species. Understorey richness and competitive outcomes depend on the pre-fire overstorey, species life-history traits, and also the fire characteristics (Yeaton and Bond, 1991). The understorey fynbos persistence and richness depends on the overstorey cover. Dominance of IAP in the overstorey leads to reduced indigenous understorey richness (van Wilgen and Richardson, 1985). An exclusion of the characteristic overstorey proteas can be facilitated by alien invasions and inappropriate disturbance regimes (such as short fire cycles caused by increased dry material by IAP). After IAP removal, the overstorey does often not return to facilitate and maintain understorey richness. Thus, changes in guild representation or the absence of guilds can alter ecosystem functioning, e.g. an increased proportion of sprouters to seeders can alter water yield in mountain fynbos (Bosch et al., 1986). Native species abundance, richness and diversity is often decreased beneath closed IAP cover, as a result of reduced seed input and the gradual reduction in soil stored seed bank (Holmes and Cowling, 1997a, 1997b).

2.5.3 Restoration and fynbos dynamics

Many species in the fynbos use passive- and wind dispersal for their small seeds, and these are deposited close to the soil surface (Parker-Allie et al., 2004). Small seeded species include long-lived seeders and shrubs. Fires of high intensity (as a result of large invader biomass) can damage and kill small seeds close to the soil surface, removing these guilds from the vegetation (Parker-Allie et al., 2004). Seeds buried deeper by ants (i.e. myrmecochory) have been observed to recover well after such fires (Holmes et al., 2000). Serotinous species, with canopy stored seed banks, such as Proteaceae, long-lived seeders and shrubs are usually the most impacted by alien invasions and clearing treatments, warranting their re-introduction to facilitate vegetation recovery. In most cases active reintroduction of these groups needs to be done since natural recolonization is slow in the fynbos, and an adjacent seed source will mostly not be present (closer than 1 km) (Parker-Allie et al., 2004).

Dormant seed banks and introduced seeds need to be cued for germination by pre-treating them with smoke and or heat (as appropriate to the species) or burning the areas post-clearing (Parker-Allie et al., 2004). Seed mixed for sowing can include fast growing fynbos species to protect soil surfaces, grasses, forbs and overstorey shrubs (Holmes and Richardson, 1999; Holmes et al., 2000; Parker-Allie et al., 2004).

2.5.4 Reducing impacts: IAP removal

We have accumulated a great deal of knowledge of plant invasion ecology and alien control programme implementation, additionally emphasis is placed on research involving the management of invasive alien species in the fynbos, e.g. clearing practises (Holmes and Marais, 2000) and post-vegetation recovery (Parker-Allie et al., 2004). Clearing usually involves initial mechanical clearing with treatment of chemical herbicide and fire (Parker-Allie et al., 2004). Follow up by hand pulling new seedlings and applying selective herbicide is required to sustain the benefits of clearing (Van Wilgen et al., 2000). Disturbance caused by restoration and IAP management activities can unfortunately in some instances actually favour invasions, causing more harm to ecosystems, rather than alleviate the situation (Richardson and Van Wilgen, 1986; Holmes et al., 2000; Holmes, 2001a; D'Antonio and Meyerson, 2002). Since control measures can affect the ecosystem's ability to self-repair after IAP removal, information on control measures impact is crucial. After this is established, one can consider if active restoration is required (Hobbs and Mooney, 1993; Holmes and Richardson, 1999; Holmes, 2001b), e.g. when plant richness is decreased and areas are invaded by alien herbaceous species (secondary invaders) (Parker-Allie et al., 2004). This can include assigning a proportion of the budget to introduce certain key species and guilds to increase the rate of vegetation recovery (Parker-Allie et al., 2004).

2.6 Conclusion

Management intervention such as vegetation clearing (passive restoration) can alleviate some of the negative effects of IAP on ecosystems (Mills and Fey, 2003). Since resources in conservation are scarce, one should manage invasions strategically and effectively, by identifying areas that would need active restoration and prioritizing active restoration to provide the most benefit both ecologically and socio-economically.

2.7 References

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Chapter 3: Prioritizing areas for active restoration in an urban setting

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3.1 Abstract

Background: Resources for conservation and invasive alien plant control are limited and restoring invaded vegetation is labour-intensive and expensive. It is therefore important to distinguish between areas that require only the removal of invasive alien plants (“passive restoration”) from those that require additional restoration measures (“active restoration”) and managers must prioritize their actions in order to achieve their goals most efficiently and effectively.

Aims: To develop, illustrate and test a framework to: (1) identify areas requiring active restoration and (2) prioritize areas for active restoration.

Methods: A multi-criteria approach- Analytical Hierarchical Process- was used for developing the frameworks.

Results: Framework criteria selected to determine the need for active restoration include: the dominant alien species invading the area, density of invasion, duration of invasion, how much indigenous vegetation is remaining, the adjacent land use, level of disturbance in an area, size of the area, the aspect the area is facing, soil texture, soil depth and erodibility, slope and the vegetation type considered for restoration. To decide which areas should be given priority for active restoration, areas were selected according to whether they improve the connectivity between natural areas, whether the area is part of a conservation plan or of biodiversity importance and how much of the native vegetation type is still left (how threatened the vegetation type is); other important factors included ecosystem functioning of an area in terms of the diversity of habitats and the importance of the areas in terms of soil conservation (e.g. soil erodibility and slope). After looking at ecological criteria, one should also take into consideration which area will provide society with ecosystem service benefits.

Conclusions: The frameworks provide a transparent and flexible method of decision-making. This method can serve as a tool for land managers to improve restoration efforts by identifying and prioritizing areas for active restoration.

Keywords: active restoration, analytical hierarchical process, ecosystem services, invasive alien plants, urban ecosystems

3.2 Introduction

Invasive alien plants (IAP) have negative impacts on ecosystems, affecting both biodiversity and ecosystem functioning (Mack et al., 2000). Managing IAP can ameliorate these impacts. There have been few cases where entire invasive populations have been eradicated (Simberloff et al., 2011; Vince, 2011), this is extremely costly and not always viable (Moore et al., 2011; Wilson et al., 2011). However, the clearing of invasive alien species in some areas has led to an increase in the delivery of ecosystem goods and services and an increase in native biodiversity (Van Wilgen et al., 1998; Wilson et al., 2013).

In many parts of the world, control of invasive species and restoration is seen as being essential for ensuring the sustainable provision of ecosystem services and the long-term conservation of biodiversity (Crossman and Bryan, 2006; van Wilgen et al., 2012a; Handel et al., 2013; Ma et al., 2013). In an increasingly urbanised world, urban biodiversity and ecosystem services are not only threatened by the expansion of urban areas and the proliferation of anthropogenic features such as land cover change, but also by IAP (Aronson et al., 2014; Zhou et al., 2014, 2015). Valuable services from healthy ecosystems in a city include filtering the air, reducing noise, draining rain and attenuating overland flow, flood protection, regulating the micro-climate, increasing property values and a suite of cultural services, including recreation (Bolund and Hunhammar, 1999; Costanza et al., 2006). Restoring invaded ecosystems in cities has the potential to benefit inhabitants by helping to ensure the sustained delivery of these ecosystem goods and services (Tongway and Ludwig, 2012).

Restoration is labour-intensive and expensive. Unsuccessful attempts to clear IAP wastes resources and often results in re-invasion of the same species or other weedy species (“secondary invasions”) (Hilderbrand et al., 2005; Holmes et al., 2008; Le Maitre et al., 2011). It is therefore important to distinguish between areas that require only the removal of IAP (“passive restoration”) from those that require additional restoration measures (“active restoration”). Selecting areas for restoration has for instance been done for reforestation (Kettle, 2012; Knowles, 2012), restoring species habitat (Beechie et al., 2008) and restoration after land transformation due to agriculture (Crossman and Bryan, 2006). There is, however, no protocol for distinguishing between areas needing passive or active restoration after IAP have been cleared.

In general, resources for conservation and IAP control are limited (Crossman and Bryan, 2006) and managers must prioritize their actions in order to achieve their goals most efficiently and effectively (Aronson et al., 2007; Rew et al., 2007; Skurski, 2012; van Wilgen et al., 2012a). Numerous studies have sought to prioritize areas and species for IAP management, but prioritization for restoration is typically not included (Holmes and Richardson, 1999; Van Wilgen et al., 2007; Roura-Pascual et al., 2009; Forsyth et al., 2011).

A common flaw in many restoration prioritization actions is the lack of clear goals (Beechie et al., 2008; Tongway and Ludwig, 2012; Richardson and Gaertner, 2013). Previous restoration prioritization exercises have usually focused on a single or a group of factors (Esler et al., 2008), for example on economic factors that determine restoration priorities. However, in many situations, the relative significance of biodiversity or ecosystem services of different areas should also be included, since benefits gained by restoration could justify expensive restoration costs (Gaertner et al., 2012b; Crookes et al., 2013).

Urban areas are complex environments, where perceptions on the value of particular land parcels typically needs to consider social equity, economic development and environmental conservation

(Campbell, 1996; Anderson and Elmqvist, 2012). Managing invasive alien species is often controversial in such settings (van Wilgen, 2012; Dickie et al., 2013). The challenge in prioritizing areas for active restoration is to weigh considerations relating to biodiversity conservation, social trade-offs and diverse “benefit to society” issues. Such decisions need to be transparent and must consider opinions of a wide range of stakeholders involved in urban land-use and ecosystem management decisions.

A multi-criteria approach using the Analytical Hierarchical Process (AHP; Saaty, 1990) method is appropriate for developing the required decision-making framework. The AHP structures a problem into a hierarchical structure, where criteria are ranked according to their relative importance in order to solve the problem. Analytical Hierarchical Process can incorporate different views and support a large number of alternatives to compare options (Forsyth et al., 2011; Orsi et al., 2011). It has been successfully used to prioritize species and quaternary catchments for IAP control (van Wilgen et al., 2008; Forsyth et al., 2009; Roura-Pascual et al., 2009; Roura-Pascual et al., 2010; Forsyth and Le Maitre, 2011; Forsyth et al., 2012). This process can also be utilized in a spatially-explicit manner during restoration planning (Cadenasso and Pickett, 2008) to incorporate expert opinions and knowledge, quantitative facts and integrate the objectives of the diverse group of stakeholders involved in invasive species management (Herath, 2004; Janssen et al., 2005).

The overall aim of this study was to develop, illustrate and test a tool to: (1) identify areas requiring active restoration and (2) prioritize areas for active restoration. General frameworks were developed using the AHP for evaluating restoration priorities in City of Cape Town, South Africa, as a case study.

Study area

The City of Cape Town is a good place to study the challenges of prioritizing areas for restoration in an urban context. The city is located in an extremely biodiverse area within a global biodiversity hotspot (the Cape Floristic Region). Many endemic and threatened species and vegetation types occur within the city borders. Vegetation in the Cape Floristic Region consists mostly of shrubland fynbos.

Fynbos is adapted to fire and many species require fire for regeneration. It is vital to maintain fire regimes for healthy ecological functioning and IAP management (van Wilgen et al., 2012b). Fires pose a risk to people and infrastructure in an urban environment making the use of prescribed fires a source of contention between nature conservationists and the public.

The area also contains a variety of landscapes and cultures, and a major economic centre in a developing country with a rapidly increasing human population (Holmes et al., 2008). Urban expansion, agriculture and IAP (Richardson et al., 1996) are key threats to the loss of habitat and native biodiversity, and have negative impacts on ecosystem services. Cape Town has a long history of alien introductions and management, but despite the negative impacts of invasive alien species,

some species provide a benefit to people (van Wilgen, 2012). Conflicts arise due to the different interests of stakeholders involved, adding complexity to invasive species management. The City has a fine-scale, systematic, spatial conservation plan, the Biodiversity Network (Holmes et al., 2012), which strives to meet national conservation targets for biodiversity pattern and process.

3.3 Methods

3.3.1 General approach of developing frameworks

Stakeholder workshops were held to develop two frameworks: one for the identification of active restoration sites and one for prioritizing sites for restoration. Stakeholders were chosen to be representatives of researchers in the field of restoration ecology informing practice and policy and managers from different conservation departments that are planning and implementing restoration.

Stakeholders were invited on recommendation of institutions responsible for alien restoration planning and implementation (both active and passive). Researchers in the fields of restoration ecology, conservation planning and invasion biology were invited. Institutions included: University of Stellenbosch, City of Cape Town, CSIR, SANParks, SANBI, Working for Water, Working on Fire, CapeNature and Western Cape Biosphere Reserves Forum. There were 11 workshop participants for each workshop, with 5 participants attending both workshops.

In both workshops, all stakeholders were involved in the setting of the goal, development of the overall frameworks and selection of criteria and sub-criteria. All stakeholders of each workshop did pairwise comparisons for the framework's criteria, sub-criteria and their categories. The only exceptions where experts that were not attending the workshops were asked to compare and rank criteria, were for criteria relating to landscape and soil (aspect, nutrient retention ability, soil depth, slope and soil erodibility) and ecosystem services. Two researchers in the field of restoration ecology, focussing on soil aspects and a soil scientist, ranked soil criteria. A researcher focussing on invasion ecology and ecosystem services and a top-level manager for the City of Cape Town's Invasive Species Unit ranked ecosystem services.

The general approach of AHP was followed where firstly, a goal was determined for active restoration *per se* and restoration prioritization. Stakeholders then identified criteria and sub-criteria required to achieve the goals. The overall framework criteria and their sub-criteria were then compared pairwise to each other through deliberation, facilitated in a workshop, to establish weightings. Weightings denote the relative importance of criteria and sub-criteria. Super Decisions Software (Adams, 2015, version 2.4.0) was used to facilitate pairwise comparisons by ranking and to assigning weights. Inconsistent judgements were checked for by using a consistency ratio given by the software: where the consistency ratio exceeded the, generally accepted, 0.1 limit, weights were re-evaluated by stakeholders and adjusted during the workshop until the ratio was below 0.1. Final weights developed

by stakeholders during the workshop were assigned to spatial data layers identified to represent criteria and sub-criteria.

'Need for active restoration' framework

The overall restoration goal and framework for identifying areas for active restoration were developed during the first workshop (see Fig 3.1). Ecological factors known to influence restoration potential for terrestrial sites were identified through stakeholder engagement during the workshop. Each ecological factor was discussed and suitable criteria and sub-criteria that would best represent ecological factors were decided upon. The numerical weightings assigned to criteria, sub-criteria and their respective categories indicate an area under these conditions' need for active restoration.

'Prioritizing' areas for active restoration framework

The second workshop developed an overall goal and a framework to prioritize areas for active restoration that had been identified in the first workshop (see Fig 3.1). Factors considered important when prioritizing and selecting areas for active restoration were identified through stakeholder engagement during the second workshop. Each factor was discussed and suitable criteria and sub-criteria to represent prioritization factors were decided upon. The numerical weights assigned to criteria, sub-criteria and their respective categories are based on the relative priority of an area for active restoration. The above mentioned framework considers the biophysical aspect of restoration prioritization. Two other prioritization aspects, ecosystem service provision and social considerations, were also decided upon at the workshop, and are discussed below.

Ecosystem service provision

Urban areas can be characterized by conflicting land use, more so in cases where urban areas overlap with regions of high biodiversity (O'Farrell et al., 2012). Natural vegetation is important for conserving biodiversity but they can also support functioning ecosystems with associated ecosystem services (O'Farrell et al., 2012). When vegetation can be restored to the benefit of society, projects are more likely to gain general support and be funded (Newman, 2008). An important assumption of this approach is that natural, non-invaded areas provide the best ecosystem service provision (Cadenasso and Pickett, 2008). However, it is recognized that invaded and other non-natural remnants could provide some form of ecosystem provisioning (O'Farrell et al., 2012). Ecosystem services were used as indicators for deciding on the benefit that a restored, functioning ecosystem could potentially provide. This in turn can be used to prioritize areas for active restoration, where areas providing a bundle of ecosystem services can receive preference for restoration above an area providing a single service or services to a lesser extent. Data on areas that are important for various ecosystem service provisioning were obtained from O'Farrell et al. (2012). Data was developed using a rapid ecosystem service assessment for the City of Cape Town to identify spatially which vegetation types and land uses are important in providing provisioning, regulatory and cultural ecosystem services.

Social considerations

The second workshop firstly discussed what ecological aspects would determine an area's priority for active restoration. Secondly, it was recognized that certain social aspects would need to be considered in restoration prioritization. Social criteria and sub-criteria were discussed, decided upon and weighed through pairwise comparison by stakeholders during the second workshop.

3.3.2 Analysis

The decision-making framework was applied to spatial data using Analysis Tools in ArcMap (ESRI, 2013, version 10.2). Each criterion and sub-criterion was assigned to the spatial data layer that best represents the criterion, e.g. vegetation type is represented by the map of remnants of indigenous vegetation within the boundaries of Cape Town (City of Cape Town, 2014) and the percentage of the vegetation type remaining by the Nation Ecosystem Threat Status map (Van Niekerk, 2012). Planning units were created by dividing areas within the municipal boundary area of City of Cape Town into sub-catchments as described and used in Maherry et al. (2013). Minimum catchment size was set to 5x5m, which was thought to be a practical unit to consider for restoration planning, i.e. to establish small nodes of restored vegetation to act as seed sources (P.M. Holmes, personal communications, 16 September 2015). Sub-catchments were then intersected with the vegetation indigenous remnant map of Cape Town (City of Cape Town, 2014), thereby creating polygons with relatively homogenous slopes of small enough size to be used for active restoration planning. This study used an area-based approach, which meant assigning the corresponding attribute value for each criterion and sub-criterion to planning units. Sub-criteria consisted of continuous or categorical data. Continuous data were multiplied by the weight of the sub-criterion while categories had to be further compared pairwise to assign relative weightings. Each category was then multiplied by the category's relative weight.

'Need for active restoration' framework

The attribute value of each criterion and sub-criterion was added to the attribute table of the corresponding planning units' map. Criteria, sub-criteria and the category values of planning units were then assigned weightings by experts during the workshop and via correspondence. All spatial layers were combined by summing the weights together and varied between 0-1. The score represents the likelihood that a unit requires active restoration. Higher values indicated a greater need for active restoration whereas lower values meant that passive restoration may still be possible or that very little active restoration is required. This resulted in a map indicating areas possibly requiring active restoration within the City of Cape Town (see Fig 3.1).

'Prioritizing' areas for active restoration

The same units as were identified from the 'Need for active restoration' framework were used to combine spatial layers of the 'Prioritizing' framework by adding the attribute value of each criterion and sub-criterion (as identified in the second workshop) to the corresponding planning unit's attribute

table. Ecological ‘Prioritizing’ criteria and sub-criteria weights were summed; values indicate the relative priority of an area for active restoration (range: 0-1, with 1 representing the highest priority). Two priority maps were produced. Firstly, a ‘Prioritizing’ map, considering only the ecological ‘Prioritizing’ framework criteria and sub-criteria (ranging between 0-1) was derived. The second map involved summing the ecological ‘Prioritizing’ scores with the ‘Need for active restoration’ scores (also ranging between 0-1). The sum of the two scores denotes the ‘Overall priority’ of areas for active restoration (see Fig 3.1).

Ecosystem service provision

‘Ecosystem service provision’ values were determined by assigning values for each ecosystem service to the planning units. ‘Ecosystem service provision’ criteria values were assigned their weights and summed together to provide a score indicating how important an area is in term of ‘Ecosystem service provision’ (ranging between 0-1). The ‘Ecosystem service provision’ score was then summed with the ‘Overall priority’ score to determine the rank of areas, considering the ‘Need for active restoration’ and the ecological ‘Prioritizing’ to restore these areas, along with the importance in terms of ‘Ecosystem service provision’ to society (see Fig 3.1).

Using this spatial approach, one can identify small patches with relative homogeneous characteristics. It should be noted that some of the currently available data are at a coarse, national resolution. Scores were averaged per protected area. This facilitates the compilation of a list of current protected areas with the highest priorities for active restoration and that contribute the most in terms of ecosystem service provision. Information presented in terms of protected areas are likely the most meaningful, since clearing and restoring areas that have legal protection status (managed and proclaimed as a protected area) will produce the highest benefit in terms of available resources (funding and labour and expertise); gains will also be maintained if the status of land is secured for conservation.

3.4 Results

3.4.1 Model development

‘Need for active restoration’ framework

Stakeholders agreed that the goal of the identification framework should be: *To identify characteristics of invaded natural sites that require active restoration to meet ecosystem biodiversity and/or ecosystem functioning targets.* Six criteria and nine sub-criteria were identified in the workshop to achieve this goal and are briefly discussed. Weightings for the ‘Need for active restoration’ framework are presented in Table 3.1. Table S1 in Appendix 3 gives weightings of criteria, sub-criteria and their units that were compared and weighed by experts.

Firstly, the invasive status was considered. This includes the dominant invasive species and the invasion history (see Table S1 for units of measurement). The type of invasive species (i.e. the species

that is currently dominating an area) was considered to be the most important criterion (**27%** weight; see Fig S1) for determining whether an area justifies active restoration. Since not all species will have the same effect on natural recovery of indigenous vegetation; areas dominated by species classified as a transformer species (*sensu* Richardson et al., 2000) will have a greater need for active restoration than those areas that are invaded by species that have less severe effects (Richardson and Rejmánek, 2011). Secondly the ‘Inherent need for active restoration’, disregarding current invasive status, was considered. All areas were given the same weight in terms of invasion history and species identity.

The invasion history of a site is the next most important criterion determining its restoration potential (**25%**). Invasion history is represented by two sub-criteria: the density of invasion (i.e. the density of stems per ha) (**55%**; Fig S2) and the duration of invasion (or in fire-prone ecosystems, the number of fire cycles since an area has been densely invaded) (**45%**). The number of fire cycles occurring in invaded stands or duration of invasion is associated with larger detrimental impacts to natural recovery (Holmes and Cowling, 1997a; Privett et al., 2001; Strayer et al., 2006; Le Maitre et al., 2011; Richardson and Gaertner, 2013). Fire events’ data does not span back to when alien species were first introduced and records only date as far back as 1960s. Even though it is an important factor, all areas were weighed equally for the duration of invasion or number of fire cycles since dense invasion.

Remaining native vegetation scored **20%** importance as a criterion for evaluating the ‘Need for restoration’, as native vegetation is needed to replenish seed banks and provide propagules for vegetation recovery and persistence beneath invasive canopies (see Fig S3).

Landscape criterion (**11%**) is further divided into soil depth, soil erodibility, aspect and nutrient retention ability of soil. Shallower soil was given a higher weight for active restoration need, since soil depth is related to water holding capacity and moisture available to plants (Sperry et al., 1998; Jackson et al., 2000; Schenk and Jackson, 2002). Deeper soils are also buffered against erosion relative to shallower soils (Fig S4). Erodibility of soil (**27%** weight) is further divided by sub-criteria of slope (Fig S5) and the soil’s erodibility factor (Fig S6). Slopes left bare after alien clearing are exposed to soil erosion, leading to potential loss of topsoil and increased sediment load in runoff (Chamier et al., 2012). Slope was given a higher weighting (**70%**) than soil’s inherent erodibility (**30%**) (Schulze and Horan, 2007). Aspect (**24%**) also relates to the soil moisture available to recovering vegetation. In the Southern Hemisphere warmer and drier north-facing slopes (Binkley and Fisher, 2012) would need more active restoration. The ability of fine textured soils to retain nutrients (Oades, 1988; Silver et al., 2000) were represented by weighing the percentage of clay in soils (**12%**, Fig S7).

Invasive alien plants have many types and levels of impacts on different vegetation types (Holmes, 2002) and will influence the amount of active restoration required and management options. According to vegetation type (Fig S8), the conditions of whether active and passive restoration is

needed might differ since some vegetation types (e.g. Sandstone Fynbos) are more resilient to invasion than others (e.g. Lowland Fynbos) (De Villiers et al., 2005; Le Maitre et al., 2011). Vegetation type was given a **10%** importance (vegetation type weightings are shown in Appendix 3 Table S1).

Local influences were given the lowest weighting of **7%** and did not contribute much to the final selection results. Disturbance was given the highest relative weighting of the sub-criteria (**78%**). Disturbances that could increase the likelihood of an area needing active restoration are those caused by grazing, trampling, granivorous and fossorial animals. All remnants were given an equal weight for disturbance. When considering the size of a remnant to be restored (**15%** weight), larger sizes are preferable. Even though restoring larger areas is preferable, dividing areas into smaller catchments meant that all but one remnant was larger than 600 ha. Adjacent land use was given a low relative weighting of **7%** and contributed very little to the final score but adjacent land use will determine the alien propagule threat following clearing and the ability to maintain areas according to restoration goals (Crossman and Bryan, 2006). Urban gardens and plantations are major sources of alien propagules and areas in close proximity to urban and agricultural areas, plantations and invaded areas will be under threat from alien reinvasion through dispersal (Rouget et al., 2003; Alston and Richardson, 2006; Roura-Pascual et al., 2009). Invaded areas that share a border with natural or low density invaded areas have a higher probability to passively restore by receiving propagules from adjacent native vegetation (K. A. Wilson et al., 2011) and was assigned a low likelihood of needing active restoration.

'Prioritizing' areas for active restoration

The goal for prioritizing areas for active restoration as identified in the second workshop is: *To improve resilience of the Biodiversity Network (ecologically and socially) by restoring ecosystem composition and biodiversity, ecosystem structure and functioning, ecosystem services and revegetating with indigenous species.* The criteria and sub-criteria that were identified to achieve the above-mentioned goal are presented in Table 3.2, along with their relative weights as decided upon by stakeholders. Table S2 in Appendix 3 gives the weightings of sub-criteria categories that were compared and weighed by experts.

The current conservation status of remnants was the most important criterion when prioritizing areas for active restoration (**48%**). Sub-criteria included the percentage of the vegetation type remaining (Fig S9) – the less of the original extent remained, the higher the weight given to a vegetation type. Critical biodiversity areas (CBA) rank (see Fig S10) was considered nearly as important as the former (**41% vs. 59%**).

Ecosystem functioning was considered an important part of achieving the restoration goal and was given a **38%** weight. Sub-criteria include soil protection (erosion) and habitat diversity. Habitat

diversity received the highest priority weight (64%). Areas with a higher number of habitat types should be prioritized in order to improve resilience. Erosion is further divided into level 3 sub-criteria slope and erodibility. To restore ecosystem function in order to improve resilience, soil should be preserved and areas at higher risk for erosion must be prioritized. Steep slopes are more prone to erosion, leading to the loss of topsoil and seedbanks which undermines ecosystem functioning. Steeper slopes were therefore given a higher weighting (65% weight). Soil was assigned an erodibility factor for each soil type, (k-value, see Schulze & Horan (2007)) where an increase in value indicating that soils are more erodible (Schulze & Horan, 2007). More erodible soil was given a higher weight (35% weight).

Physical attributes of remnants relating to their connectivity received the lowest weighting of **14%** and did not have a big influence on the overall score. It is preferable to restore wider habitat remnants (i.e. shortest distance between two vertices of the area) (36%), and wider areas were given a higher weight. If an area connects to a habitat of the same type (i.e. same vegetation type), it was deemed important to prioritize such sites for active restoration since this would allow for, among other things, natural dispersal of propagules between patches. The distance to natural uninvaded vegetation remnant received a 30% weight: Areas that can provide connectivity between natural areas are a higher priority to actively restore. Increase in natural areas and improved connectivity is vital to restore and improve resilience in ecosystems (Lindenmayer et al., 2006; Beaumont et al., 2007; Worboys et al., 2010; Keenelyside et al., 2012). Areas that are adjacent to natural areas should receive highest priority, followed by those not necessarily adjacent but closer to uninvaded areas (Fig S11).

Social criteria

As discussed in the second workshop (Table 3.4), social criteria that are important when prioritizing remnants for active restoration include: the legal status of remnants (i.e. publicly owned or privately owned; considered the most important, **83%**); and the ability to maintain the gains (i.e. the attitude of the community; secondary importance, **17%**). Whether areas are public or privately owned or under management by conservation authorities has major implications for restoration. Publicly owned and conserved areas are easier to manage and have the advantage of being easier to access for clearing and active restoration than privately owned land (Crossman and Bryan, 2006). Restoration in managed areas is more feasible since disturbances can be excluded to ensure successful restoration, whereas this is more difficult to control on private land (Bainbridge, 2012). Areas that are managed as identified in the Biodiversity Network were given higher weightings than areas that are not managed (Forsyth et al., 2012). The ability to maintain gains in urbanized areas will depend on the current level of community engagement (27%). If conservation departments have an established relationship with a community of a particular area, it is considered easier to sell them the benefits of actively restoring an invaded area. Where a community has an interest in biodiversity conservation the restoration effort will most likely receive support (e.g. volunteering and help with maintenance) (Newman, 2008). Even

if a community has been engaged with nature conservation departments, they could have a negative attitude towards them (and clearing/active restoration efforts). Therefore, areas where there is a positive attitude and support (and even possible positive attitudes in areas with no previous engagement) will receive highest priority for active restoration and received a higher relative weight (63%).

Ecosystem service provision

Ecosystem services and their weightings are listed in Table 3.3. The regulatory services were given the highest weighting (55%) since these services cannot be sourced from outside the city e.g. protection from flooding.

Regulating services: Critical infiltration areas (Fig S12) are those where intense rainfall can infiltrate through the soil (Schulze, 2006). Flood mitigation zones (Fig S13) were created by placing a buffer around rivers and wetlands that should remain undeveloped, for flood water to spread and infiltrate (O'Farrell et al., 2012). The coastal protection zone (Fig S14) is a buffer area around the coast that should be undeveloped and will protect the coast against storms and sea level rise (O'Farrell et al., 2012). Groundwater recharge (Fig S15) areas sustain water for river flow, certain vegetation and human use (O'Farrell et al., 2012). Groundwater yield (Fig S16) is measured in litres per second and is a proxy of available groundwater for abstraction and use (O'Farrell et al., 2012). Groundwater quality (Fig S17) uses groundwater conductivity (mS/m) as a proxy and is a measure of the amount of purification required before use; higher values indicate more treatment is required and thus lower water quality (O'Farrell et al., 2012).

Cultural services include heritage, tourism and education. These consist of the distances of natural remnants to heritage sites (Fig S18), popular tourism transport drop-off stations (Fig S19) and schools (Fig S20) (O'Farrell et al., 2012). Cultural ecosystem services were not given a much lower weighting (45%) than regulatory services since it is recognized that exposure to natural vegetation is of considerable importance in terms of education value, and is therefore important for both tourism and appreciation of our natural ecosystems and heritage (O'Farrell et al., 2012). The restoration of invaded vegetation to functioning and biodiverse ecosystems can lead to many benefits to humans, including improved health and well-being (Sandifer et al., 2015), providing sufficient motivation to restore remnants in close proximity to schools, areas with high tourist visitation rates and heritage sites.

3.4.2 Case study of model outputs: City of Cape Town

The developed frameworks were applied to the City of Cape Town and the outputs were illustrated in maps and are described below. The major woody invasive plants in Cape Town are species of *Eucalyptus* (gums), *Acacia* (wattles), *Pinus* (pines) and *Hakea* (hakeas) (Richardson et al., 1996). Gums were given the highest relative weight in terms of impacting ecosystems and reducing natural vegetation recovery (65%), although gums cover a small area (almost 3%) and are usually restricted

to riparian areas (Holmes et al., 2008; van Wilgen, 2012). Wattles carry the second largest weight in terms of species effects on ecosystem recovery (28%) and also cover the largest part of invaded areas in the Biodiversity Network (31% of the area). Pines and hakeas cover about 10% of invaded area in the Biodiversity Network and had the lowest relative weight (7%) among woody invasive species. Pine and hakea invasions are confined to the mountainous areas in the east of the city and some pine plantations occur in the lowlands close to the peninsula (see Fig S1). A mixture of species invades some areas. Areas containing mixtures of species were given the same weighting as the species with the highest score of the co-invading species. When considering the ‘Inherent need for active restoration’, disregarding current invasive status, areas invaded by gums had the highest need for active restoration, followed by areas currently invaded by wattles, pine and hakeas and lastly uninvaded areas. Areas invaded by gums and acacias will have the highest need for active restoration according to the framework. Areas invaded by gums will have the highest need for active restoration because the ecological characteristics of the areas (‘Inherent need for active restoration’) make them more vulnerable to poor vegetation recovery and because of the fact that gums are having the biggest impact on indigenous vegetation recovery.

Areas were additionally scored in terms of ‘Ecosystem service provision’, with areas invaded by wattles getting the lowest average ‘Ecosystem service provision’ score, followed by areas invaded by gums. Areas invaded by hakeas and pines are the most important in terms of providing ecosystem services. Wattle invasions cover the largest area and impact greatly on vegetation recovery but are less important in terms of providing ecosystem services. Areas invaded by wattles in general have lower ‘Ecosystem service provision’ scores but are very important in terms of conservation. Restoring gum, pine and hakea invaded areas on the other hand will have a higher benefit in terms of ecosystem service provisions as these species generally invade mountains and riparian areas, associated with the delivery of many ecosystem services in Cape Town. Even though gum, pine and hakea (but pines in particular) invasions threaten water-related ecosystem services, they also provide positive ecosystem services in some cases, such as where gums provide nectar for honey bees and provide shade. However, by law all listed invasive trees need to be cleared from waterways where they are most likely to have negative impacts on water resources (Allsopp and Cherry, 2004; National Environmental Management: Biodiversity Act (10),2004: Alien and Invasive Species List, 2014).

Density of invasion (Fig S2) varied between 0% (uninvaded) and 97% invasion. Densely invaded areas are few according to current data. Uninvaded areas (<25% cover and 10% weight), occupy about 72% of the Biodiversity Network area, and invaded areas 28%, of which 4% is densely invaded and the remainder a cover between 25-75%. The small 4% will mostly be targeted for active restoration and priority for restoration will depend on ecological ‘Prioritizing’ criteria.

The Biodiversity Network habitat condition map (Fig S3) was used as a proxy for the remaining native vegetation. Most remaining vegetation is classified as being high (11% weight) to medium

(23% weight) quality habitat, indicating good sources of propagules for vegetation recovery once alien invasive species have been cleared; these areas also correspond to protected areas. Poor habitat quality sites (66% weight) mostly are those isolated within an urban matrix, not formally protected or managed and will need the most active restoration (Fig S3).

Most soil in the lowland fynbos is deep and has a sandy texture (Fig S4), while mountainous areas have steep slopes and shallower soils (Fig S4 & S5) with the previously mentioned having the highest need for active restoration. The steep and shallow soils however do not coincide with the most erodible soil, based on their k-values (Fig S7). The most erodible soils are soils in the lower lying areas, having less need for active restoration based on soil depth and slope criteria.

The CBA rank (Fig S10) was developed as part of the original Biodiversity Network analysis. The categories are as follows in order of decreasing relative importance 1) Protected areas 2) CBA1a-c 3) CBA1d-e 4) CBA2 5) CESA & Other natural areas.

Vegetation remnants used in the maps were already classified into homogenous habitat types (in terms of vegetation). Habitat types including streams and wetlands could be included as additional habitat types and were represented by the Flood mitigation zone. All areas intersecting the flood mitigation layer were classified as having two habitat types and given a higher priority than those not intersecting with the flood mitigation zone.

Vegetation remnants with the highest 'Ecosystem service provision' scores (Fig 3.4) are situated around the mountainous areas of the Cape Peninsula and to the far east of the city boundaries within critical infiltration areas, flood mitigation zones and close to the city's heritage sites (criteria with highest weights). When looking at the distribution of scores across the 'Prioritizing'- (Fig 3.5), 'Prioritizing for active restoration'- (Fig 3.6) and with 'Ecosystem service provision'-map (Fig 3.7), they show the same pattern of highest scores being focussed in the periphery of the city where large conservation areas are situated, such as Table Mountain National Park in the South, Steenbras and Hottentots-Holland in the East.

The list of protected areas (Table S5) shows areas that are prioritized according to the 'Overall priority' and other associated scores used to calculate this. The list could be used to allocate budgets for active restoration, or to consider protected areas for more fine-scale screening such as field visits and site inspection to determine the need and extent of active restoration required.

3.5 Discussion

Areas in need of restoration were prioritized for management according to the restoration goals for Cape Town. The goals were firstly to: *Identify characteristics of invaded natural sites that would require active restoration to meet ecosystem biodiversity and/or ecosystem functioning targets* and secondly to: *Prioritize areas to improve resilience of the Biodiversity Network (ecologically and socially) by restoring ecosystem composition and biodiversity, ecosystem structure and functioning,*

ecosystem services and revegetating with indigenous species. Different areas were selected based on different combinations of goals (there may be some overlap among selected areas) (Egoh et al., 2011). As an example looking at the vegetation types: not considering the current status of invasive species and just simply the 'Inherent need for active restoration' of vegetation types with the average highest scores are Lowland fynbos, Mid-slope (both currently with the highest average density of invasion) and Renosterveld. Considering 'Need for active restoration' and the 'Prioritizing' factors, Lowland Fynbos, Renosterveld, Sandstone and Strandveld are ranked the highest but when also considering the 'Ecosystem service provision', Forest, Mid-slope- and Sandstone Fynbos are ranked highest.

When looking at the 'Need for active restoration' score (Fig 3.2), the maximum score reached was 0.66. In general it was expected for some areas to have a score close to one for 'Need for active restoration'. The low score is probably due to the overall low densities of invasive alien plants. Another reason could be that just over half of the City's natural areas are being managed (51%). Managed areas have alien species control plans, control implementation, and have a lower average density of transformer tree species than non-managed areas. Numerous clearing projects around the city could be responsible for the low density of transformer trees. Fine-scale data collected by managers were only available for formally protected areas (complete for 2013), while data on alien plant distribution for the rest of the City' had to be used from a national data set (Kotze et al., 2010) and a city scale assessment from 2009 (City of Cape Town, 2009). Species identity and invasion history-related aspects were given the highest weight in determining the likelihood that remnants need active restoration. More resources should be spent on developing spatially accurate data sets for these criteria in order for the method to be applied effectively and accurately. Even though processes might act on different scales (Kaplan et al., 2013), data collected at different scales are sufficient to use at a city landscape-scale (Laros and Benn, 2007; De Lange et al., 2012; O'Farrell et al., 2012). The most important criteria for each framework is also developed at a city scale (Laros and Benn, 2007; O'Farrell et al., 2012), and accurate for the areas of current interest for active restoration (e.g. species density and identity for protected areas).

Disturbance level information is not available spatially even though a decision rule could be developed to indicate areas at high risk of disturbance. However, this information would be of more value to consider at a site scale, when investigating which areas within a site to restore.

The 'Inherent need for active restoration' score (not considering current invasion status, Fig 3.3) is valuable for identifying ecologically vulnerable areas. Scores show similar spatial patterns to the score including invasion status, which suggests that the approach is robust, but values are elevated due to the equal maximum weight of invasion history and species weights. Areas most in need of active restoration are isolated patches through the centre of the urban matrix and to the north of Cape Town

where many high-priority areas surround protected areas but are not yet under formal protection and management.

The 'Ecosystem service provisioning' score provides further motivation to conserve natural vegetation remnants, and to restore invaded and degraded vegetation to an ecologically functional ecosystem. This will ensure that funds are applied efficiently, to provide the most benefit to society, but also contribute to securing natural resources for the future. Currently, regulatory and cultural services are mapped, but as future ecosystem services become important, they can be added to the framework. Weightings of services can be changed to reflect changing demands, making this a flexible approach. This approach adds together the score of multiple ecosystem services, motivating to spend resources on restoration not for a single service but to select areas that provide a 'bundle' of services or of high importance in providing one or a few services (Bennett and Balvanera, 2007; Trabucchi et al., 2012). Using this proposed method provides a holistic, multi-benefit approach. Restoration of remnants and their prioritization are supported based on providing ecosystem services, an area's conservation status and habitat condition.

High-priority areas occur in proclaimed and protected areas, highlighting the importance of currently protected areas and their future contribution to conservation priorities and ecosystem service delivery. The 'Need for active restoration', 'Prioritizing' and 'Ecosystem service provision' criteria are useful for making defensible decisions for allocating more funds towards restoration in these areas but can also identify new, valuable and priority areas to add to restoration projects. This will produce a list of areas, ranked according to their restoration priority and the benefit they can supply to society. This can produce an extensive list of areas. Some of the sites, such as the Lower Silvermine Wetlands, with the highest score of all protected areas (due to its overall priority, see Table S5 for list and scores), is currently managed as a conservation area but does not enjoy any formal conservation status. Using arguments such as its' importance in terms of meeting conservation targets at a national, provincial and local level could build a case to proclaim it as provincial nature reserve or secure long-term formal protection. A smaller subset would need to be chosen based on the available budget (Forsyth et al., 2012). Social criteria were not applied to the framework spatially, but can be applied to a final list of prioritized fragments or protected areas to rank them according to social criteria to refine the selection process. A subset can be chosen by applying social criteria, not because it is the least important to apply last, but because social criteria can be the most constraining factor. Both the protective status of a site and the level of community support towards a restoration project can determine the ultimate success and sustainability of outcomes.

Although use of the framework relies on available collected data, the framework is simple to implement and update (O'Farrell et al., 2012). It can be applied at different scales, including at the national level, using available national datasets and even for small sites, using simpler checklists and tables to compare and weigh localities. Model results can be confirmed by ground-truthing areas with

high priority for active restoration scores, to determine the degree of congruence between spatial data, model results and realities (Consorte Widis et al., 2015). Such ground-truthing was however beyond the scope of the study, due to severe time constraints. Ground-truthing results can lead to refinement of the model and also provide justification to adjust model weights (Consorte Widis et al., 2015).

The use of GIS in restoration planning is efficient at a city scale and can combine data at a landscape scale, combining data sets from many sources (Lee et al., 2002). Sources of data can be qualitative or quantitative, collected from different geographical scales and quality of data (Brown et al., 1998; Beechie et al., 2008; Consorte Widis et al., 2015). The MCA-AHP process is a transparent and flexible way to assemble and weigh criteria to reflect their importance. There is some level of subjectivity involved in the selection and weighing procedure (Arroyo et al., 2015) but the way that this it is done is set out clearly in the framework, making decisions defensible and justifiable (De Lange et al., 2012). Comparing criteria and sub-criteria enables relative comparison without considering the absolute different units criteria are measured in (Ishizaka and Labib, 2009). Dividing a problem into different components such as criteria, and doing pairwise comparisons is easy and come naturally to decision makers (Arroyo et al., 2015).

The AHP process involves the participation of stakeholders, and this process is important in an urban context, where multiple stakeholders are concerned in any land use decision. The weights derived from pairwise comparisons is subjective (Arroyo et al., 2015), depending on the preferences, knowledge and experience of stakeholders identifying and prioritizing areas needing active restoration. Traditional urban restoration planning focus on technical and scientific criteria but more recently the trend is to incorporate and encourage public participation (Newman, 2008). The AHP process employed in this study relies on experts, managers, planners and scientists to select and weigh criteria to identify and prioritize areas for restoration, as done in other studies (Newman, 2008; De Feo and De Gisi, 2010; Delgado-Galván et al., 2014). Due to the technical nature of deciding restoration need and priority (De Feo and De Gisi, 2010) it is common to use professionals and experts to develop and weigh model criteria (Consorte Widis et al., 2015).

Weights will differ depending on the stakeholder's chosen. This is why a team of researchers, experienced in the relevant field's and managers and decision makers planning and implementing restoration were invited. This is a technical framework, draws from the experiences of expert stakeholders, not necessarily captured in scientific literature. They are the most suited to weigh criteria concerning ecosystem recovery post alien clearing. Planners and managers implementing future active restoration are in the best position to rank priorities, according to their current knowledge (Suding, 2011) of planning and societal benefits of active restoration in an urban environment. The group all agreed on the goal and criteria and consensus was reached relatively easy on the relative importance of framework criteria, sub-criteria and their categories. If a more diverse stakeholder group was chosen, different criteria and weighting might have been chosen, and a

consensus might have taken more deliberation (Firouzabadi et al., 2008). Other studies have shown however that both technical and non-technical decision makers can place a similar level of importance to criteria relating to nature, biodiversity and natural resources (De Feo and De Gisi, 2010).

Robustness models can be tested by performing sensitivity analysis. Sensitivity analysis changes the model input to observe how the results change (Ishizaka and Labib, 2009). Sensitivity analysis can be useful but was not done in this study. It is acknowledged that changing weights will have effects on area's priority for active restoration score and change overall results (Consorte Widis et al., 2015). It should be noted that the weights will not be able to change without a proper justification, discussion and agreement among stakeholders (De Lange et al., 2012). Because of the technical and managerial nature of the frameworks, a more diverse stakeholder-opinion scenario is unlikely. The frameworks do explicitly take into account social criteria. The method encourages and facilitates active participation and discussion (De Lange et al., 2012). The method can easily accommodate and incorporate the views and needs of the public, should it be needed in the future, by including a stakeholder group from a wider selection of the general public. A diverse, multi-disciplinary stakeholder group is also likely to decrease subjectivity in selecting and weighing criteria (Ball, 2005). The important thing is that the method sets out the decision-making process in a clear and simple way. The choice of active restoration sites will also not generate the same level of controversy among urban residents, since these areas would have already been earmarked for alien clearing. The selection and prioritization of areas for passive restoration (clearing), is not the objective of this frameworks, only to select areas that would need active restoration and where to allocate resources to restore priority areas.

Universal application

The weights and rankings can have application in areas with a similar ecological and socio-economical characteristics (De Lange et al., 2012) but the framework and method is universally applicable to select and prioritize areas for active restoration. The framework can also be modified by adding or removing criteria depending on the nature and dynamics of environments that need restoration. As an example: in a nutrient poor environment such as fynbos, legacy effects from invasive alien plants in the form of increased nutrients would lead to poorer vegetation recovery (Yelenik et al., 2004; Marchante et al., 2008). The weighting might decrease or increase when applying this framework to other ecosystems, dependent on the relative importance of soil nutrients in vegetation recovery and competitive effects between indigenous and alien species. The frameworks can thus be applied to different ecosystems around the world; the importance of some criteria might be altered according to the ecosystem dynamics.

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Tables and figures:

Table 3.1 Framework of the model used to identify areas needing active restoration for the City of Cape Town, South Africa. Criteria and sub-criteria identified at a stakeholder workshop are listed. Level 1 criteria are in bold with the relative weight (%) indicating its importance compared to other level 1 criteria. Level 2 sub-criteria are sub-categories of level 1 and their relative weightings (%) indicate their relative importance compared to each other.

| <i>Criteria and sub-criteria</i> | <i>Relative weighting (%)</i> | |
|--|-------------------------------|-----------------------------|
| | <i>Level 1 criteria</i> | <i>Level 2 sub-criteria</i> |
| Invasive alien species | 27 | |
| Invasion History | 25 | |
| Density of invasion | | 55 |
| Duration of invasion/no. fire cycles | | 45 |
| Remaining indigenous vegetation | 20 | |
| Landscape | 11 | |
| Soil depth | | 37 |
| Erodibility | | 27 |
| Aspect | | 24 |
| Nutrient retention | | 12 |
| Vegetation type | 10 | |
| Local influences | 7 | |
| Disturbance | | 78 |
| Patch size | | 15 |
| Adjacent land use | | 7 |

Table 3.2 Framework of the model to prioritize areas for active restoration for the City of Cape Town, South Africa. Criteria and sub-criteria identified at an expert workshop are listed are listed. Level 1 criteria are in bold with the relative weight (%) indicating its importance compared to other level 1 criteria. Level 2 sub-criteria are sub-categories of level 1 and their relative weightings (%) indicate their relative importance compared to each other.

| <i>Criteria and sub-criteria</i> | <i>Relative weighting (%)</i> | | |
|--|-------------------------------|-----------------------------|-----------------------------|
| | <i>Level 1 criteria</i> | <i>Level 2 sub-criteria</i> | <i>Level 3 sub-criteria</i> |
| Conservation status | 48 | | |
| % of vegetation type remaining | | 59 | |
| CBA rank | | 41 | |
| Ecosystem functioning | 38 | | |
| Habitat diversity | | 64 | |
| Erosion | | 36 | |
| Slope | | | 65 |
| Soil erodibility | | | 35 |
| Physical attributes of connectivity | 14 | | |
| Width | | 36 | |
| Adjacent habitat the same | | 34 | |
| Distance to uninvaded habitat | | 30 | |

Table 3.3 Results of ‘Ecosystem service provision’ framework and their relative weightings (%) as scored by experts during a workshop, which were used to develop a framework for prioritization of areas in need of active restoration for the city of Cape Town, South Africa. Level 1 criteria are in bold with the relative weight (%) indicating their relative importance compared to other level 1 criteria. Level 2 sub-criteria are sub-categories of level 1 and their relative weightings (%) indicate their relative importance compared to each other. Level 3 sub-criteria are sub-categories of level 2 sub-criteria and their relative weightings (%) indicate their relative importance at that level.

| <i>Criteria and sub-criteria</i> | <i>Relative weighting (%)</i> | | |
|----------------------------------|-------------------------------|-----------------------------|-----------------------------|
| | <i>Level 1 criteria</i> | <i>Level 2 sub-criteria</i> | <i>Level 3 sub-criteria</i> |
| Regulating | 55 | | |
| Critical infiltration | | 34 | |
| Flood mitigation | | 34 | |
| Coastal protection | | 23 | |
| Groundwater | | 10 | |
| <i>Groundwater quality</i> | | | 50 |
| <i>Groundwater recharge</i> | | | 28 |
| <i>Groundwater yield</i> | | | 22 |
| Cultural | 45 | | |
| Education | | 65 | |
| Culture | | 35 | |
| <i>Tourism</i> | | | 60 |
| <i>Heritage</i> | | | 40 |

Table 3.4 Social criteria and sub-criteria that are important to consider when selecting areas to actively restore. The Social framework and their relative weightings (%) as scored by experts during a workshop, which were used to develop a framework for prioritization of areas in need of active restoration for the city of Cape Town, South Africa. Level 1 criteria are in bold with the relative weight (%) indicating its importance compared to other level 1 criteria. Level 2 sub-criteria are sub-categories of level 1 and their relative weightings (%) indicate their relative importance compared to each other in level 1 criteria.

| <i>Criteria and sub-criteria</i> | <i>Relative weighting (%)</i> | |
|---------------------------------------|-------------------------------|-----------------------------|
| | <i>Level 1 criteria</i> | <i>Level 2 sub-criteria</i> |
| Legal status | 83 | |
| Protected: In perpetuity | | 72 |
| Protected: Not in perpetuity | | 17 |
| Conservation area | | 11 |
| Ability to maintain gain | 17 | |
| Community attitude | | 63 |
| Current level of community engagement | | 37 |

Figure 3.1: Logical work sequence illustrating the framework development process from the input of two workshops and spatial analysis to produce an overall product for prioritizing areas for active restoration as outcome.

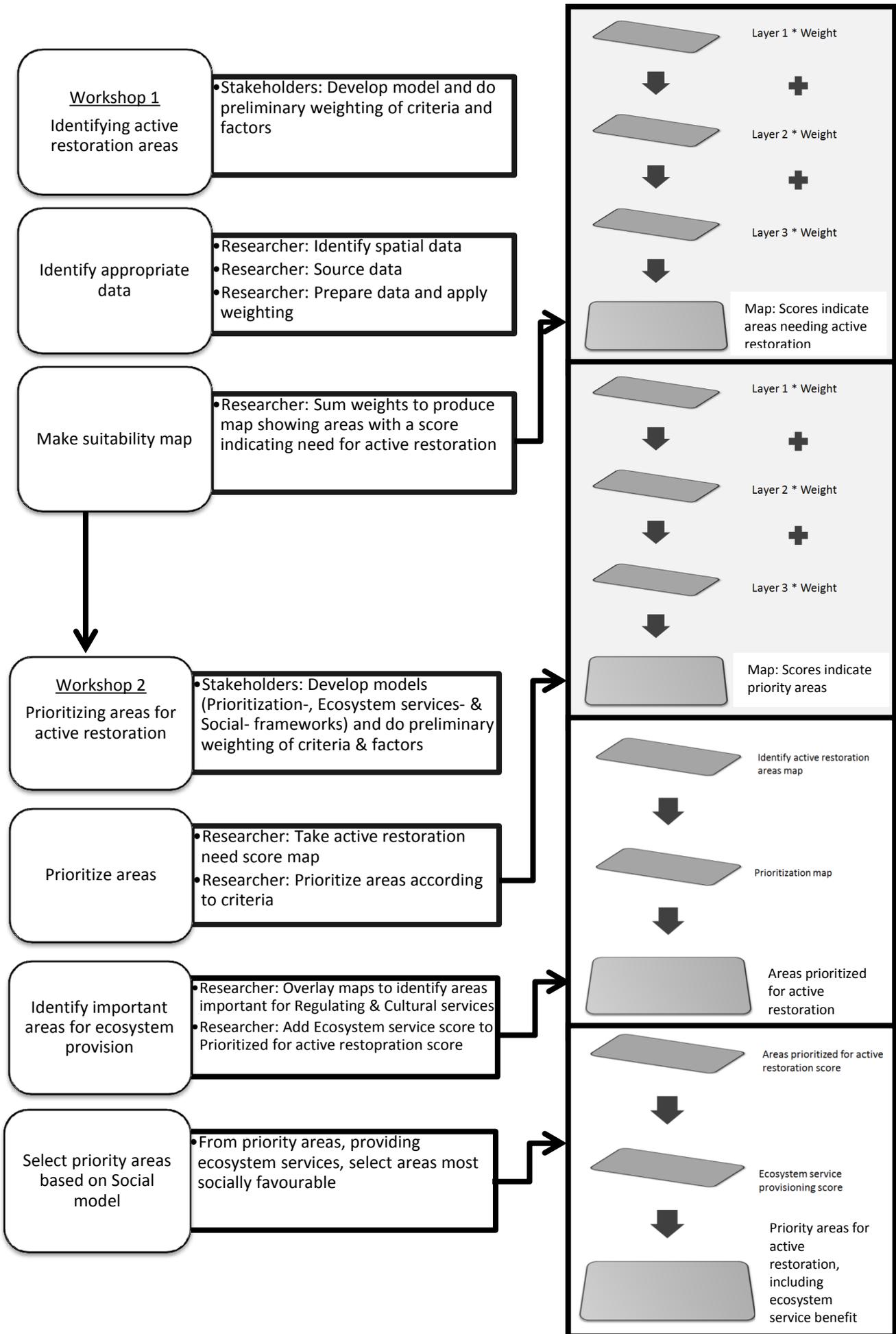


Figure 3.2-3.5. 3.2) ‘Need for active restoration’ score in City of Cape Town, based on criteria and sub-criteria, combined by their relative weights. Higher values indicate higher need for active restoration 3.3) ‘Inherent need for active restoration’; does not consider the current invasive status (dominant invasive species, density of invasion and duration of invasion/no. fire cycles) 3.4) Score of natural remnants, according to their importance in providing ecosystem services (ecosystem services weights combined for remnants) 3.5) ‘Prioritizing’ score of remnants, calculated by ‘Prioritizing’ criteria, not considering active restoration need

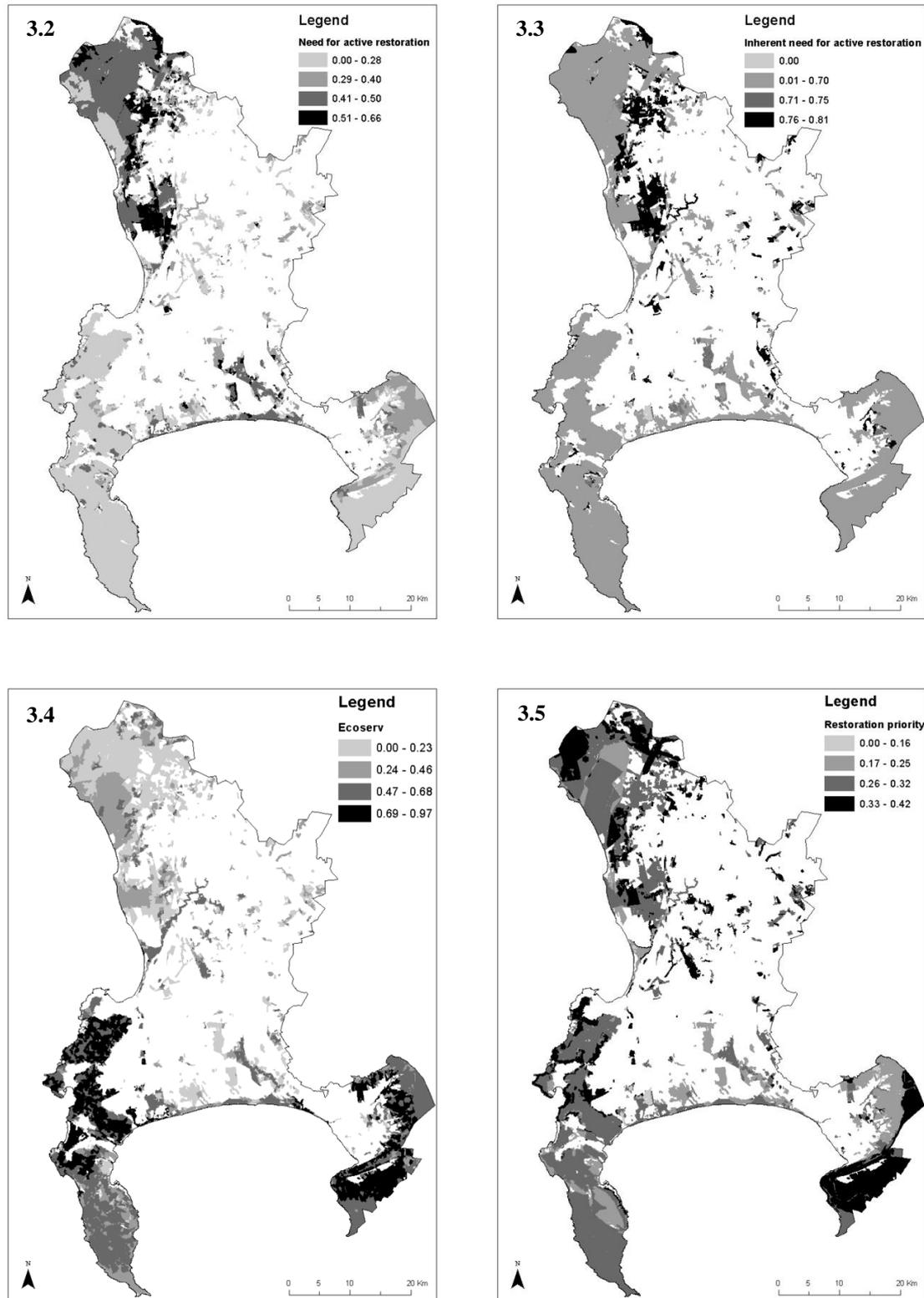
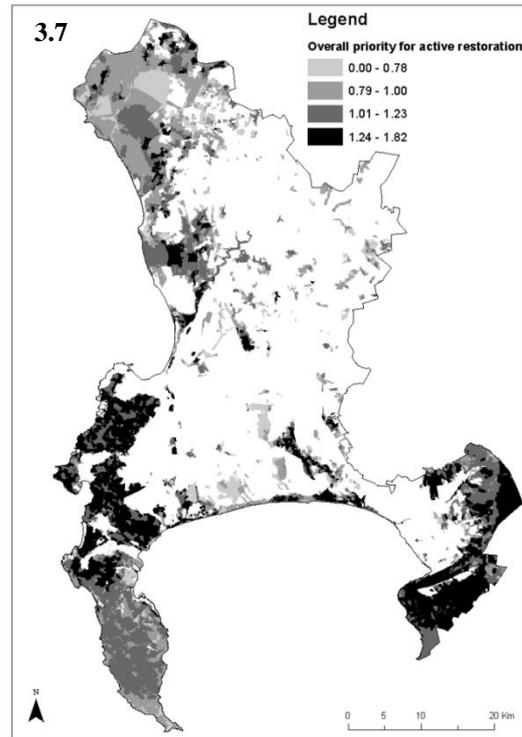
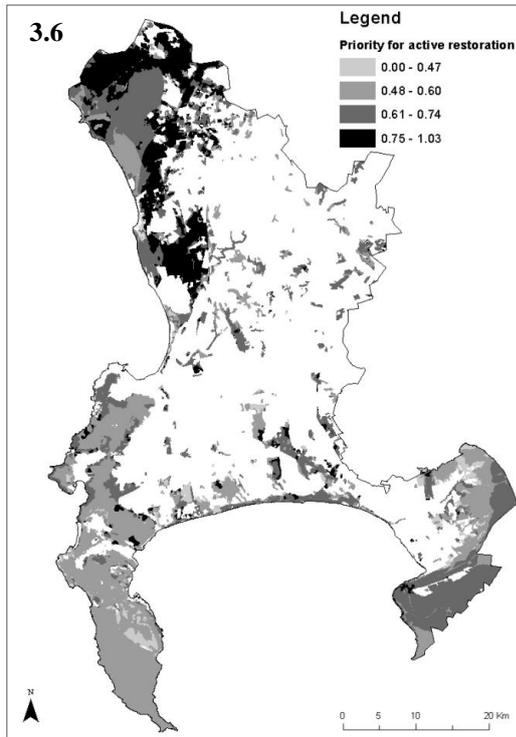


Figure 3.6-3.7. 3.6) ‘Active restoration priority’ score calculated by summing the ‘Need for active restoration’- and ‘Prioritizing’-score **3.7)** ‘Overall priority’- sum of ‘Ecosystems service provision’-, ‘Prioritizing’- and ‘Need for active restoration’-score (includes current invasion status)



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Chapter 4: Comparing impacts of different invasive alien trees on highly threatened lowland vegetation types in the Cape Floristic Region, South Africa

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4.1 Abstract

Invasive alien plants have negative impacts on biodiversity, ecosystem functioning and the delivery of ecosystem services. Management of invasive alien plants can potentially alleviate these negative impacts. This study investigated the autogenic recovery potential of native vegetation after clearing of dense invasive alien vegetation in two critically endangered vegetation types in South Africa's Cape Floristic Region, the Cape Flats Lowland- and Swartland Alluvium Fynbos. Sampling was done in areas previously occupied by either invasive *Acacia saligna* or plantations of *Pinus radiata*, and in an uninvaded fynbos reference site. Control treatments varied in terms of the length of invasion and management histories with the following variables accounted for: number of fire cycles since canopy closure or rotations of planting (in case of *P. radiata*) and number of follow-up treatments. Vegetation sampling included functional guild representation to investigate structural and functional recovery post-clearing. In terms of overall vegetation structure, uninvaded areas were dominated by perennial indigenous species. Pine areas recovered well in terms of indigenous perennial richness, but indigenous cover decreased with increasing number of planting rotations (growing cycle). Areas affected by acacias recovered poorly in terms of indigenous cover and indigenous richness exhibited a declining trend with increasing cycles of invasion. The characteristic proteoid overstorey of fynbos was lost in all invaded/planted sites and this element will need to be re-introduced to areas after one cycle of invasion regardless of the invasive species. Acacias changed some abiotic variables after two cycles of invasion, and in the case of indigenous cover already after one cycle, while lowland fynbos is resilient up to three rotations of pine planting in most cases. In terms of vegetation structure, perennial species and guild richness: acacias more negatively impacted invaded sites, whereas pine plantations recovered better compared to the reference site. Follow-up clearing generally promoted better ecosystem recovery in terms of overall species richness and structure but care should be taken not to damage indigenous shrubs. Overall, acacia invasion caused a greater change in biodiversity, and ecosystem structure and functioning compared to pine invasion.

Keywords: Active restoration, biological invasions, invasive alien plants, impacts, lowland fynbos, passive restoration, transformer species, tree invasions.

4.2 Introduction

Invasive alien plants can transform ecosystems by changing species composition, ecosystem structure and ecosystem functioning, and by fragmenting natural areas, driving degradation and negatively impacting biodiversity and the delivery of ecosystem goods and services (Van Wilgen et al., 1998; Richardson et al., 2000b; Mooney, 2005; Brownlie and Botha, 2009; Pejchar and Mooney, 2009; Vilà et al., 2009; Gaertner et al., 2012a; Handel et al., 2013). The range and impacts of invasive alien species is predicted to increase around the world (Walther et al., 2009; Sorte, 2014) including South Africa (Van Wilgen et al., 1996, 2008). This drives the investment of resources to prevent invasions and restore ecosystems degraded by invasive alien species (Pyšek and Richardson, 2010), including

research on alien species' impacts (Strayer, 2010; Vilà et al., 2011), cost-benefit analysis, effectiveness of control operations (Marais et al., 2004; Pretorius et al., 2008) and restoration strategies (Holmes and Richardson, 1999; Holmes et al., 2000).

Ecological restoration aims to speed up ecosystem recovery in terms of community composition, vegetation structure and ecosystem functioning (D'Antonio and Meyerson, 2002; Trabucchi et al., 2012). Restoration actions can include the control of invasive alien species and re-introduction of native vegetation (Holmes et al., 2008; Gaertner et al., 2012b). Clearing of invasive alien plants is sometimes not sufficient to allow ecosystems to recover adequately, and additional restoration interventions may be needed (Holmes and Cowling, 1997a; Crossman and Bryan, 2006; Esler et al., 2008; Reid et al., 2009; Gaertner et al., 2012b). Restoration efforts can be classified as either **passive** (involving the removal of the cause of habitat degradation, in this case invasive alien vegetation and leaving the ecosystem to self-repair) or **active** (involving additional measures, such as re-introducing native species by seed or propagated material, and in extreme cases soil stabilization, landscaping and engineering) (Allen, 1995).

Removal of invasive alien species that change the original properties of the ecosystems they occupy (i.e. transformer species *sensu* (Richardson et al., 2000b) can have unexpected results (Richardson et al., 2000b; Hobbs et al., 2006). The resources needed to restore native vegetation generally increase with the degree, magnitude or duration of invasion. Once the system has changed to an alternative ecosystem state, costs required to achieve restoration may be prohibitive (Holmes and Richardson, 1999; Gaertner et al., 2012a). Failing to restore ecosystems to their historical state (Whisenant, 1999; Hobbs and Harris, 2001; Suding et al., 2004) can often be attributed to ignoring the biotic and abiotic changes, and their interactions, that have occurred during invasions (Bakker and Berendse, 1999; Zedler, 2000; Suding et al., 2004). Transformer species often leave legacy effects, such as increased nitrogen levels in the soil (Yelenik et al., 2004). These can lead to secondary invasions that capitalize on the increased soil nutrient availability left by the aliens (Loo et al., 2009). If the maximum level of ecosystem resilience is exceeded, a threshold is crossed which can eventually lead to a change to an alternative ecosystem state (Suding et al., 2004).

The threshold model has been developed to explain the different stable states of ecosystems under different levels of invasions and the barriers separating these levels (Stringham et al., 2003). There are two general types of ecosystem thresholds, structural thresholds and functional thresholds (Beisner et al., 2003). Structural thresholds refer to ecosystem composition and structure. The crossing of a structural threshold can be initiated by changes to biotic and abiotic variables, e.g. a decrease in species richness and unnatural changes in nutrient availability, respectively (Stringham et al., 2003; Briske et al., 2005; Gaertner et al., 2012a). Functional thresholds represent changes in ecological processes (i.e. ecosystem function), e.g. greater fire intensity and increased resource competition due

to changes in nutrient cycling, lowered water tables and loss of top soil (Van de Koppel et al., 2001; Briske et al., 2005).

During alien plant invasions, structural biotic changes usually occur first (Gaertner et al., 2012a), followed by abiotic changes. However, abiotic structural changes can also occur alongside biotic structural changes. In recently invaded areas some ecosystem functions might still operate similarly to those of uninvaded sites; in such cases the system may recover without any further post-clearing interventions (Whisenant, 1999; Archer et al., 2001; Stringham et al., 2003; Gaertner et al., 2012a). Once the invasion is dense, changes in re-enforcing ecosystem feedbacks (e.g. higher nutrient levels will lead to more invader biomass) will result in altered ecosystem functioning, facilitating further dominance of invasive alien species (Gaertner et al., 2012a). These changes will result in decreased ecosystem resilience and eventually abiotic functional thresholds will be crossed. In such instances, restoration interventions will have to aim at restoring ecosystem functions and processes. In such extreme cases, active interventions (such as alleviating high soil nutrient levels) might be necessary (Holmes and Richardson, 1999; Stringham et al., 2003; Marchante et al., 2009; Gaertner et al., 2012a). Restoration thresholds have been documented in different ecosystems (Nyström et al., 2000; Van Auken, 2000); these highlight the importance of identifying functional and structural ecosystem changes (Suding et al., 2004).

In a biodiversity hotspot such as the Cape Floristic Region (encompassing the fynbos biome), it is crucial to consider what happens after clearing invasive species and to identify possible barriers to restoration. The fynbos biome is one of the most invaded biomes in South Africa (Richardson et al., 1997). Especially in the lowlands, a high proportion of vegetation is transformed or threatened by agricultural and urban developments, and invasion by alien plants (Rouget et al., 2003). Pines (*Pinus* spp.) and acacias (*Acacia* spp.) are two of the main woody transformer invaders of fynbos (Richardson et al., 1992; Wilson et al., 2014) with *Pinus radiata* D. Don (Monterey pine) plantations and invasions and widespread *Acacia saligna* (Labill.) H.L. Wendl. (Port Jackson Willow) invasions threatening lowland fynbos vegetation types (Rebelo et al., 2006). Invasive trees have different traits and can impact communities and ecosystems differently. *Acacia saligna* has higher growth rates and attains a greater height compared to native fynbos shrubs, resprouts after fire and cutting, can fix soil nitrogen and maintains large and persistent dormant seed banks (Witkowski, 1991a; Yelenik et al., 2004; Richardson and Kluge, 2008). These features mean that *A. saligna* has a greater and longer-lasting impact on fynbos ecosystems than some other invasive trees, such as the serotinous tree *P. radiata* which does not resprout, have a long-lived soil seed bank, or fix soil nitrogen (Richardson and Van Wilgen, 1986; Holmes et al., 2000; Holmes and Foden, 2001).

A conceptual approach, classifying categories of acacia and pine invasion in fynbos ecosystems and determining potential thresholds to native ecosystem recovery, has been developed but the conceptual predictions of different thresholds for pines *versus* acacias have not been empirically tested (Gaertner

et al., 2012a). By identifying measurable indicators of invasion stages and related ecosystem changes, one can identify the risks and benefits of certain management actions but also estimate the restoration potential (Stringham et al., 2003; Briske et al., 2005).

Previous research on the impacts of alien plants and restoration potential has mostly focused on riparian and mountain fynbos ecosystems (Musil, 1993; Blanchard and Holmes, 2008; Holmes, 2008; Pretorius et al., 2008; Vosse et al., 2008) and has generally focused only on one dominant alien species per study (Le Maitre et al., 2011; Ruwanza and Gaertner, 2013). This study concentrated on lowland fynbos, where restoration of highly threatened vegetation appears to be most challenging (Holmes, 2002, 2008) and focused on two invasive taxa, *A. saligna* and *P. radiata*. The two species seldomly co-invade, as pines are mainly invasive in mountain vegetation whereas *A. saligna* is most invasive in the lowlands (Richardson et al., 1992). However, the lowlands have been afforested with pines.

The aims of this study were: (1) to compare ecosystem impacts of acacia and pine invasion on lowland fynbos (2) to identify the most important management and invasion-history variables that influence vegetation recovery and abiotic variables, and (3) to assess the association between biotic and abiotic variables.

We examined the following hypotheses: (i) a greater change in biodiversity, and ecosystem structure and functioning (including guild composition and soil attributes) will occur in acacia-invaded than pine plantation areas; (ii) management and invasion-history (including number of follow-up treatments and whether an area has been burned after clearing, number of fire cycles since invasion or rotations in pine plantation), will affect the ability for autogenetic recovery of cleared areas in terms of biodiversity, and ecosystem- structure and functioning; and (iii) changes in abiotic variables will affect biodiversity, and ecosystem- structure and functioning i.e. influence ecosystem feedbacks.

If the invasion history is important in explaining biodiversity and differences in ecosystem structure and functioning among invaded sites, it could indicate that some thresholds have been crossed and active restoration measures could be required. Such insights are crucial for planning effective restoration efforts.

4.2. Materials and methods

4.2.1 Study sites

The study was conducted in two critically endangered vegetation types within the Cape Town, Stellenbosch and Drakenstein municipal areas, South Africa. Cape Flats Sand Fynbos (CFSF) is situated in a winter rainfall region (mean annual temperature, MAT, of 16.2 °C and mean annual rainfall, MAR, of 576 mm) and the landscape consists of predominantly flat plains with acidic, sandy soils. More than 85% of the vegetation is transformed (Rebelo et al., 2006). Main threats to this

vegetation type are urban sprawl and alien infestation, with many remaining areas being small patches, surrounded by urban areas. Cape Flats Sand Fynbos is prone to invasion by *Acacia cyclops* A. Cunn. ex G. Don (*rooikrans*) and *A. saligna*, *Pinus* spp., *Eucalyptus* spp. (gums), *Hakea* (hakeas), *Leptospermum laevigatum* (Gaertn.) F. Muell. (Australian myrtle) and to secondary invasion by alien annual grasses (Richardson et al., 2000a). The following study sites were situated within this vegetation type: Tokai Park, Youngsfield Military Base, Blaauwberg Nature Reserve, Penhill, Haasendal Conservation Area and a reference site 7km from the Blaauwberg site (Bas Ariesfontein) (Table 4.1).

The second vegetation type is Swartland Alluvium Fynbos (SAF) with a seasonal, winter-rainfall regime (Mean annual rainfall, 656 mm). It occurs next to mountains on slightly rolling plains with alluvial sands. Swartland Alluvium Fynbos forms dense closed stands close to water bodies. The main threats to this vegetation type are pine plantations, vineyards, orchards and alien plants such as *A. saligna* (Rebelo et al., 2006). The three study sites (Wemmershoek, Victor Verster and Safariland) within this vegetation type include seasonal wetland communities.

Study areas were chosen based on being previously invaded by *A. saligna* (>75% cover) or historical *P. radiata* plantations. Reference sites were used to provide goals for recovery (Buijse et al., 2002; Blanchard and Holmes, 2008) and to assess the degree of recovery success post-clearing. In this study, comparisons with a reference site (Bas Ariesfontein) were applied to indicate changes in ecosystem structure and function. Only one reference site could be sampled, since most remnants of these vegetation types around Cape Town are currently heavily invaded or have been previously heavily invaded by alien plants. The reference site was characterized by mature fynbos and was only sparsely invaded (<25% canopy cover) by *A. saligna*. Initial clearing of the reference site was done in 2011 and the reference site has had yearly follow-up treatments. All other study sites have been cleared of alien trees, with some areas being burned after clearing, at least more than a year prior to this study.

Historical and management information data were collected from managers and other knowledgeable stakeholders. Fire and invasion-history data were inferred from satellite images obtained from Google Earth (2005-2014) and the Department of Rural Development and Land Reform (1938-2005). Treatments varied over time scales and management histories with the following variables accounted for: number of fire cycles since canopy closure or rotations of planting, clearing method, time since initial clearing, time since last fire (vegetation age) and number of follow-up treatments. Areas that had not been burnt after the initial clearing treatment were classified as mature vegetation when fire data could not be inferred from satellite imagery. Table 4.1 gives a summary of management history and exact location information of study site.

4.2.2 Field sampling

Vegetation was sampled during September and October 2014. Three replicate 5 x 10m plots were set up in each treatment per study site (Cape Flat Sand Fynbos, n=33; Swartland Alluvium Fynbos, n=12), spaced out as far as possible (minimum of 50m apart in small areas but up to 200m where possible) to ensuring independence among sample plots. All species were identified either in the field or by collecting specimens for later identification and were categorized as indigenous or alien using published floras such as (Manning and Goldblatt, 2012) and (Bromilow, 2010). Total percentage canopy cover was estimated for each indigenous and alien species within the plot. Species richness was recorded for the whole plot.

Soil sampling was done after vegetation sampling in October. Elevation and GPS coordinates were taken at the South-East corner of each plot with a Garmin GPS. Three litter samples were taken within the plot, by randomly placing a 25 x 25 cm quadrat on the ground and collecting all litter in the quadrat. Litter was dried in an oven at 45 °C for 72 h and weighed. Three equal volume soil samples were taken per plot below soil litter, in the upper 10cm of soil and bulked. Samples were sent for analyses at Bemlab (Pty) Ltd. (Somerset West, South Africa) for soil texture analysis, available phosphorus (P, mg/kg, P Bray II), mineral nitrogen (ammonium, NH₄-N, mg/kg, and nitrate; NO₃-N, mg/kg, extracted from soil with 1N KCl and determined colorimetrically on a SEAL AutoAnalyzer 3 after reaction with a sodium salicylate), percentage carbon (%C) and nitrogen (%N). Electrical conductivity and pH were analysed at Stellenbosch University. The soil electrical conductivity (EC) was measured using a 5 g soil sample, mixed with deionized water (25mL) to form a 1:5 ratio, and the supernatant was measured with an EC meter. Soil pH was also measured using the 1:5 ratio, using a 0.01 M CaCl₂·2H₂O solution (25mL) and the pH of the supernatant was measured with a pH meter.

4.2.3 Analysis

Biotic and structural ecosystem components can be characterized by vegetation attributes such as indigenous species richness, abundance and changes in growth form composition (Eldridge et al., 2011; Gaertner et al., 2012a). In the Fynbos Biome, ecosystem functioning can be characterized using functional guild composition (Holmes and Richardson, 1999; Richardson et al., 2007). To determine whether native vegetation had recovered after alien plant clearing, invaded sites were compared to the uninvaded reference site.

Data were analysed using generalized linear models (GLM) in R statistical software (R Core Team, 2015). Models were tested for the following assumptions: residuals of response variable are normally distributed, homogeneity of residuals and collinearity of variables (Fox, 2008; Hothorn et al., 2014). Percentages of C and NO₃-N were correlated with NH₄-N (0.61 and 0.76 Pearson's correlation coefficient, respectively) and were therefore removed as explanatory variables. Percentage N was correlated with available P (0.62 Pearson's correlation coefficient) and removed. The assumption that

replicate plots are independent was tested by applying the Breusch-Godfrey test using 'lmtest'-package to models (Hothorn et al., 2014).

As indicators for abiotic functional recovery of the ecosystems, soil nutrients and litter biomass were analysed as response variables. Litter biomass could indicate structural and functional changes (i.e. changes in litter biomass and nutrient cycling process). Litter biomass was averaged and is expressed as grams of dry weight per m².

Richness of indigenous perennial plants was analysed as an indicator for the impact of invasion on recovery of biodiversity. The biotic structural recovery of ecosystems was investigated by using the relative cover of alien and indigenous species as response variables. The richness of functional guilds was used as a response variable indicating the post-clearing guild recovery. To categorize functional guilds, plant attributes such as growth form, longevity and leaf type (Holmes and Richardson, 1999; Holmes et al., 2000) were identified and assigned to species (see Table 4.2). Shrubs were subdivided into ericoid (fine-leaved shrubs) and non-ericoid shrubs. Cyperaceae were included with the graminoids (grasses) and restioids, and were placed as a separate category. To account for natural variation among sites, mean annual precipitation values (Schulze, 2006) or soil depth were included as environmental variables when spatial autocorrelation was detected. To reduce the number of explanatory variable, vegetation age was least informative during exploratory analysis and was therefore excluded from the model (Walker and Madden, 2008; Costello and Osborne, 2011). Species richness of guilds was used to assess guild recovery. The guilds analysed were the number of ericoid- and non-ericoid shrubs, indigenous perennial grasses and restioids since they are the main structural components in the two vegetation types.

Predictor variables included environmental, invasion history and management variables and were used to determine which invasion and management related variables are most important in determining vegetation and soil nutrient responses and recovery post-clearing. Variables included both continuous and categorical data. Predictor variables were standardized (the mean of each variable was subtracted from each data point and divided by twice the standard deviation of the variable; see Schielzeth, (2010) and (Grueber et al. (2011) for further explanation. This enables estimates of predictors to be comparable relative to one another (Schielzeth, 2010).

Response variables consisted of continuous variables (P, NH₄-N, Litter, EC, pH), count data (number of species of each guild: indigenous perennial species, restioids, indigenous perennial grasses, non-ericoid and ericoid shrubs) and percentage canopy cover data (relative cover of indigenous plants and relative alien cover). Appropriate error and link functions were chosen in models accordingly. For biotic ecosystem components (ecosystem structure, biodiversity and guild richness) two sets of models were run, one containing management and invasion-history variables as predictor variables and a second model was run using litter and soil variables as predictor variables.

If categorical variables were significant at $p < 0.1$, they were further analysed post-hoc to determine differences. Analyses were performed in R using ‘userfriendlyscience’ package (Peters, 2015). The Games-Howell test was used and is a multiple comparison test that takes into account heterogeneity of variances and unequal sample sizes (Games and Howell, 1976; Kromrey and La Rocca, 1995).

4.3 Results

Lower and upper confidence interval levels (CI) for the estimates are included, where small differences between the CI indicate precise estimates while large intervals show less precision. Full output and results from GLM analysis are shown in **Appendix 4A**. Results from post-hoc analyses and pairwise comparisons are presented in **Appendix 4B**. This includes the group sample sizes, means and variances, along with appropriate test statistics and significance levels.

Models showed that there was no significant autocorrelation among samples and that replicate plots can be considered independent ($P > 0.05$). The only model that showed signs of autocorrelation according to the Breusch-Godfrey test was the management model for non-ericoid shrub richness ($P < 0.05$). Other than the previously mentioned, no assumptions of models were violated. Swartland Alluvium Fynbos only harboured *P. radiata* plantations but no acacia-invaded sites. Significant differences between vegetation types occurred for indigenous and alien cover, ammonium and EC. Alien cover was significantly lower ($t = 4.4$, $df = 42$, $p < 0.001$) and indigenous cover was significantly higher ($t = 4.4$, $df = 42$, $P < 0.001$) in SAF sites than CFSF pine plantations. It is interesting to note, however, that in all cases, indigenous cover was significantly lower and alien cover significantly higher (all acacia-invaded and CFSF pine plantations) compared to uninvaded sites; only pine plantations in the SAF had recovered to a similar level of indigenous cover ($t = 2.3$, $df = 3.4$, $P = 0.253$) and alien cover ($t = 2.3$, $df = 3.3$, $P = 0.259$). Ammonium was significantly lower ($t = 3.11$, $df = 16.5$, $P = 0.03$) and soil EC was significantly higher ($t = 3.24$, $df = 15$, $P = 0.026$) in SAF compared to CFSF pine plantations. In terms of pH, CFSF pine plantations had significantly higher pH but SAF pine plantations had a similar pH to the uninvaded site ($t = 6.5$, $df = 14$, $P < 0.001$ and $t = 2.4$, $df = 12$, $P = 0.140$ respectively). Overall all sites had a sandy soil texture and were thus comparable in this regard.

Ecosystem impacts of acacia versus pine invasion on lowland fynbos vegetation types

Both pine plantations ($t = 3.9$, $df = 3.6$, $P = 0.046$) and acacia-invaded sites ($t = 6.1$, $df = 8.9$, $P < 0.001$) had significantly lower indigenous cover than the uninvaded site and acacia had significantly lower indigenous cover than pine plantation sites ($t = 3.8$, $df = 21.1$, $P = 0.003$) (Fig 4.1). Acacia-invaded sites ($t = 6.1$, $df = 8.7$, $P < 0.001$) and pine plantations ($t = 3.9$, $df = 3.5$, $P = 0.049$) had significantly higher alien cover than the uninvaded site, with acacia-invaded sites also having significantly more alien cover than pine areas ($t = 3.8$, $df = 21.0$, $P = 0.003$) (Fig 4.2). When separating alien cover into woody (Fig 4.3) and herbaceous cover (Fig 4.4), there was overall very low cover of woody aliens, with acacia-invaded areas having significantly higher woody alien cover than pine plantations ($t = 3.42$, $df = 14.9$,

$P=0.01$) and the uninvaded site ($t=3.37$, $df=15.9$, $P=0.01$) (both having a mean relative alien woody cover close to zero; $t=0.18$, $df=3.4$, $P=0.98$). The majority of alien cover consisted of herbaceous alien cover, with acacia-invaded areas having the highest cover but not significantly more than pine plantations ($t=2.1$, $df=20$, $P=0.125$). Both had significantly more herbaceous alien cover than the uninvaded site (acacia: $t=4.0$, $df=14$, $P=0.003$; pine: $t=3.7$, $df=20$, $P=0.004$) (Fig 4.4).

Species richness of indigenous perennial plants was the highest in uninvaded sites. Acacia-invaded sites had significantly lower indigenous perennial species richness compared to pine plantations ($t=3.7$, $df=21.5$, $P=0.003$), while pine plantations and acacia-invaded sites recovered to a similar level of richness than the uninvaded site (pine: $t=0.2$, $df=2.2$, $P=0.978$; acacia: $t=2.0$, $df=3.0$, $P=0.260$) (Fig 4.5). The uninvaded site had the highest number of ericoid species (Fig 4.6) while acacia-invaded and pine plantation sites were associated with a significantly lower ericoid shrub richness ($z=-4.147$, $P<0.001$, 95% CI=-4.392 to -1.619 and $z=-3.268$, $P=0.001$, 95% CI=-1.319 to -0.320, respectively), with the number of ericoid species being significantly lower in acacia than pine plantation sites ($t=3.3$, $df=30.9$, $P=0.007$). Non-ericoid shrub richness did not differ significantly among dominant invasive species treatments (acacia: $z=-0.933$, $P=0.351$, 95% CI=-2.435-0.889; pine: $z=0.455$, $P=0.649$, 95% CI=-0.730-1.493). Pine plantations had the highest richness of non-ericoid shrubs, with acacia-invaded sites having a lower number of non-ericoid species than the uninvaded site, although sites had an overall low richness of non-ericoid shrubs (maximum of two species for uninvaded site and four species for acacia- and pine-invaded sites) (Fig 4.7).

There was higher mean litter biomass in acacia-invaded sites ($z=2.181$, $P=0.036$, 95% CI=5.218-458.008; $t=0.74$, $df=13.2$, $P=0.75$) than uninvaded and pine sites ($t=1.76$, $df=23.8$, $P=0.21$) (Fig 4.8). In pine sites, there was less litter than in the uninvaded site ($t=1.37$, $df=6.8$, $P=0.41$). Ammonium levels in the soil did not differ significantly between the dominant invasive species and the uninvaded site (acacia: $t=2.3$, $df=14.9$, $P=0.091$; pine: $t=1.2$, $df=6.4$, $P=0.496$) (Fig 4.9), even though the results from GLM indicated a species effect (acacia: $z=2.086$, $P=0.044$, 95% CI=0.019-9.472; pine: $z=2.749$, $P=0.009$, 95% CI= 2.056-12.426). Sites invaded by acacia had the highest mean level of ammonium, with pine plantation sites having lower mean ammonium levels than the uninvaded site. Soil was more basic in acacia-invaded sites (Fig 4.10) in relation to the uninvaded site ($t=2.4$, $df=16$, $P=0.072$). Pine plantation sites had significantly more acidic soils than the uninvaded ($t=5.3$, $df=22$, $P<0.001$) and acacia-invaded sites ($t=5.6$, $df=29$, $P<0.001$). There was no significant difference in EC among treatments (Appendix 4B iii3), but the uninvaded site had the highest and acacia-invaded sites the lowest EC (Fig 4.11). Available phosphorus was elevated in both invaded sites compared to the uninvaded site (acacia: $t=3.06$, $df=8.1$, $P=0.037$; pine: $t=2.86$, $df=8.2$, $P=0.049$) (Fig 4.12).

The response of biotic and soil-nutrient factors to abiotic variables

The number of restioid species was correlated with the amount of available phosphorus, where available phosphorus levels were negatively associated with the number of restioid species ($z=-1.661$, $P=0.097$, 95% CI=-3.452-0.004). The number of indigenous perennial grass- and non-ericoid species was associated with ammonium, where grass ($z=-1.734$, $P=0.083$, 95% CI=-1.220-0.047) and non-ericoid richness ($z=-1.735$, $P=0.083$, 95% CI=-1.586-0.054) increased with lower levels of ammonium in the soil and indigenous perennial species richness was significantly lower with increasing ammonium ($z=-4.798$, $P<0.001$, 95% CI=-1.066 to-0.451). Non-ericoid richness significantly decreased with increasing soil EC ($z=-2.281$, $P=0.023$, 95% CI=-1.804 to -0.168). An increase in litter had a negative association with ammonium in the soil ($z=-1.872$, $P=0.070$, 95% CI= -2.944-0.134).

Associations between management and invasion-history and vegetation recovery and abiotic variables

Areas that were burned had significantly more indigenous cover ($z=-3.34$, $P=0.002$, 95% CI=0.289 to-0.076; $t=1.7$, $df=43$, $P=0.093$) (Fig S11i) and better guild recovery than those left unburned. Increased richness was observed for indigenous perennial species ($z=-2.515$, $P=0.012$, 95% CI= -0.401to-0.049, $t=1.9$, $df=32$, $P=0.067$) (Fig S10i), restioids ($z=-1.630$, $P=0.103$, 95% CI=-1.888-0.135; $t=0.83$, $df=29$, $P=0.41$), ericoid shrubs ($z=-1.835$, $P=0.066$, 95% CI= -0.732-0.024; $t=0.97$, $df=42$, $P=0.34$) and indigenous perennial grasses ($z=-1.692$, $P=0.091$, 95% CI=-0.733-0.054; $t=1.7$, $df=36$, $P=0.1$) (Fig S8i). Sites left unburned after clearing had significantly higher alien cover ($z=3.409$, $P=0.002$, 95% CI= 0.079-0.292; $t=1.7$, $df=43$, $P=0.09$).

There were larger amounts of litter in unburned areas (Fig S5i). Unburned sites had more acidic soils than those burned after initial clearing (Fig S2i) and a higher mean of available phosphorus ($z=2.990$, $P=0.005$, 95% CI= 0.003- 0.689; $t=1$, $df=32$, $P=0.32$) (Fig S4i).

Effect sizes show that the number of follow-up treatments received after clearing had a positive association with the richness of ericoids ($z=0.997$, $P=0.319$, 95% CI=-0.176-0.546) and a negative association with the richness of non-ericoid shrubs ($z=-0.051$, $P=0.959$, 95% CI=-0.555-0.517), even though non-significant. The number of follow-ups a site had received, was associated with significantly higher richness of indigenous perennial species ($z=3.436$, $P<0.001$, 95% CI=0.130-0.472) and higher litter biomass ($z=2.426$, $P=0.020$, 95% CI=15.143-124.069). Increasing follow-up treatments was associated with an increase in EC ($z=2.321$, $P=0.026$, 95% CI=1.106-9.909).

For cycles of invasion, acacias and pines were separated for visualisation and analysis when a cycle of invasion was indicated as significant during GLM analysis. Increasing cycles of invasion was associated with poor indigenous cover recovery. After one and two cycles of acacia invasion, indigenous cover was significantly lower than the uninvaded site ($t=14.3$, $df=2.9$, $P=0.002$ and $t=5.5$,

$P=0.002$ respectively). After one and two pine rotations, indigenous cover recovered to a similar level to the uninvaded site ($t=1.74$, $df=4.5$, $P=0.404$ and $t=2.49$, $df=3.6$, $P=0.214$ respectively). After three rotations of pine rotations, indigenous cover was significantly lower compared to the uninvaded site ($t=4.24$, $df=4.6$, $P=0.034$). The inverse trend was shown for alien cover. Acacia- invaded sites exhibited an unusual result, where after one cycle of invasion, indigenous cover was lower and alien cover higher when compared to two cycles of invasion ($t=7.0$, $df=12.9$, $P=0.001$ and $t=6.9$, $df=12.9$, $P<0.001$ respectively). Both one and two cycles of acacia invasion resulted in a lower richness of ericoid shrubs compared to the uninvaded site ($t=4.92$, $df=2.2$, $P=0.059$ and $t=4.36$, $df=2.7$, $P=0.054$ respectively). In pine plantations, two cycles of rotations had lower restioid richness than one cycle of rotation and significantly lower restioid richness than three cycles of rotation ($t=3.16$, $df=5.0$, $P=0.086$ and $t=5.00$, $df=17.0$, $P<0.005$, respectively).

After *A. saligna* invasion, pH was significantly higher (more basic) after two cycles of invasion than after one cycle of invasion ($t=3.8$, $df=7.6$, $P=0.014$) or the uninvaded site ($t=3.3$, $df=12.9$, $P=0.014$). Litter biomass did not differ significantly between the uninvaded site and the cycles of acacia invasion. Available phosphorus did not show a clear pattern in terms of cycles of invasion: after one cycle of acacia invasion, it had higher levels of available phosphorus than the uninvaded site ($t=2.7$, $df=13.0$, $P=0.046$), but two cycles of invasion did not increase significantly ($t=0.5$, $df=4.7$, $P=0.875$). Soil pH for pine plantation areas did not differ significantly among the uninvaded site and after one and two rotations of planting (see Appendix 4B iv2 pine). After three cycles of pine rotations, pH was significantly lowered (more acidic) compared to the uninvaded site ($t=7.09$, $df=17.4$, $P<0.001$), one cycle of rotation ($t=3.62$, $df=9.2$, $P=0.023$) and two cycles of rotation ($t=5.24$, $df=15.5$, $P<0.001$). Electrical conductivity did not differ significantly between different pine rotations and the uninvaded site. Litter biomass was lower after one pine rotation ($t=2.55$, $df=6.6$, $P=0.140$) and significantly lower after two rotations ($t=4.78$, $df=4.0$, $P=0.030$) in comparison to the uninvaded site, while after three rotations, litter was similar to the uninvaded site ($t=0.23$, $df=9.5$, $P=0.996$).

4.4 Discussion

The main aim of this study was to compare ecosystem impacts of acacia and pine invasion on lowland fynbos. The hypothesis that acacia will cause a greater change in biodiversity, and ecosystem structure and functioning was supported. The study also attempted to identify the most important management and invasion-history variables that influence vegetation recovery and abiotic variables. Some variables had much larger effects on biodiversity, and ecosystem structure and functioning and each variable differed in frequency of selection as the most important variable. The study further aimed to assess feedback processes between biotic and abiotic variables. It was found that changes in abiotic variables affected biodiversity, and ecosystem structure and functioning.

Ecosystem impacts of acacia versus pine invasion on lowland fynbos vegetation types

The hypothesis that a greater change in biodiversity, and ecosystem structure and functioning (including guild composition and soil attributes) will occur in acacia-invaded than pine plantation areas was supported in that acacias had a greater impact on indigenous vegetation recovery and ecosystem functioning than pines. Areas dominated by either acacias or pines did not recover structurally (in terms of indigenous cover) to the level of uninvaded vegetation with acacia areas having the least recovery. A lack of post-clearing recovery in terms of indigenous vegetation cover has been found in other studies in the fynbos (Holmes and Marais, 2000; Blanchard, 2008). Other studies also have found good persistence of indigenous seeds beneath an invasive pine canopy (Moles and Drake, 1999; Heelemann et al., 2013).

Acacia sites had the highest overall cover of aliens post-clearing, showing that the species had a negative impact on vegetation recovery. The fact that acacias persisted following clearing is indicative of the vigorous resprouting ability of cut stumps and germination from the large persistent seed bank (Holmes et al., 2005). Woody alien cover only consisted of acacia seedlings and resprouts, highlighting the importance of effective and thorough follow-up clearing by herbicide application and hand pulling of seedlings during initial clearing treatments and subsequent follow-up treatments.

Both species pose a challenge to remove from sites because of their high propagule pressure. Acacia seeds can germinate after a fire, but germination can also take place between fires (Holmes et al., 1987; Tozer and Ooi, 2014), making them persistent and effective competitors and ecosystem transformers (Moll et al., 1980; Pieterse and Boucher, 1997; Foxcroft et al., 2013). Monterey pine on the other hand does not resprout after fire and seed release from serotinous cones is only stimulated by fire, and seeds are either consumed by predators or rot, and do not form seed bank in the soil (Reyes and Casal, 2002).

The fact that alien herbaceous species dominated alien cover indicates a serious problem of secondary invasions that follow initial woody alien species clearing (Richardson et al., 2000a; Yelenik et al., 2004; Blanchard and Holmes, 2008). Secondary invasions were a bigger problem in acacia-invaded than pine plantation areas. This is due to the legacy effects in the soil after acacia invasions, with high soil nutrients and altered soil chemistry promoting competitive herbaceous aliens and acting as a barrier to native species recovery, causing secondary changes in species composition (Yelenik et al., 2004). High nutrient levels are known to persist in the soil for several years after clearing and can favour competitive weedy species to the disadvantage of native fynbos seedlings (Yelenik et al., 2004; Marchante et al., 2008).

In terms of functional guilds, ericoid shrubs did not recover to the same level as uninvaded sites. Ericoid shrubs are a key guild in the lowland fynbos (Cowling and Holmes, 1992; Rebelo et al., 2006) and may need to be re-introduced in cleared sites. Richness of non-ericoid shrubs did not differ

significantly between acacia- and pine-invaded sites but it was interesting that pine plantations had a higher richness of non-ericoid shrubs. The non-ericoid shrubs found in pine plantations were widespread species, e.g. shrubs that could have spread from the surrounding vegetation. In all invaded areas, the protea overstorey was absent and would need to be re-introduced. The exclusion of ericoid and proteoid shrubs in pine plantation and acacia-invaded sites, and non-ericoid shrubs in the case of acacia-invaded sites, could be due to shrubs not having sufficient time to mature and set seed between fire events (Schwilk et al., 1997) or between rotations of planting. The loss of key structural components is a common impact of plant invasions in the fynbos (Holmes and Richardson, 1999; Blanchard, 2008), especially the loss of overstorey proteas (Van Wilgen, 1982; Holmes and Cowling, 1997b; Schwilk et al., 1997). If certain functional guilds do not recover or are underrepresented, it could lead to a loss of overall diversity and ecosystem functioning (Parker-Allie et al., 2004; King and Hobbs, 2006).

The successful recovery of indigenous guilds and overall indigenous perennial richness in pine plantations could be due to the persistence of the native seed bank beneath the canopies (Holmes and Richardson, 1999; Heelemann et al., 2013). Indigenous vegetation can persist beneath pine canopies for a long time since it can take up to 13 years for complete canopy closure, giving indigenous species a chance to establish and replenish seed banks (Cremer, 1992; Holmes and Marais, 2000). Similar changes in structure and richness have been found in invaded riparian areas in the fynbos (Holmes et al., 2005).

Surprisingly, one and two cycles of pine rotation had lower amounts of litter than the uninvaded areas, but this could be due to the fact that the uninvaded area is mature vegetation, having accumulated large amounts of litter and senescent plant material (Van Wilgen, 1982). This is why all cycles of acacia-invaded sites showed similar levels of litter to the mature uninvaded site. Producing large amounts of nutrient-rich litter is a known impact of acacias, and large amounts of litter can pose a threat to indigenous vegetation recovery (Witkowski, 1991a; Yelenik et al., 2004): where large amounts of litter burn, the time required for vegetation recovery could be longer (Holmes et al., 2000; Blanchard and Holmes, 2008). In this study, high amounts of litter could pose a threat to native vegetation recovery in both invaded sites and the native senescent fynbos.

It was expected that acacia-invaded sites would have larger amounts of mineral nitrogen but ammonium levels were not significantly higher than uninvaded sites; however, it should be noted that ammonium data was highly skewed: both invaded sites had a lower median level of ammonium compared to the uninvaded site. The lack of extreme changes in soil nutrients in invaded sites could be explained as follows: recently cleared sites contained the highest amount of ammonium due to a legacy effect of the acacias, and due to poor nutrient retention in sandy soils excess nutrients could have leached out with rain infiltration or volatilized during fires (Stock and Lewis, 1986; D'Antonio and Vitousek, 1992). A legacy effect in soil however is the change in acidity, towards more basic soil

after two cycles of invasion; this could indicate a change in soil chemistry. (Witkowski, 1991b) and Yelenik et al. (2004) similarly found no difference in ammonium in the soil between acacia-invaded and fynbos, and an increase in available phosphorus but no change in soil pH. A further anomaly was higher impact after one cycle of acacia invasion on ecosystem recovery; this could be due to high levels of human disturbance, which can promote alien invasions and prevent indigenous species recovery (Morgan, 1998; Milton, 2004).

In pine plantations, soil was significantly more acidic than uninvaded and acacia-invaded sites and had increased levels of available phosphorus compared to uninvaded sites, indicating a change in soil chemistry. Invasion and afforestation by pines have led to soil acidification (Scholes and Nowicki, 2000) and an increase in available phosphorus from nutrient rich litter (Heelemann et al., 2013). Other studies have similarly found good indigenous vegetation recovery after clearing invasive pines (Holmes et al., 2000; Reinecke, 2008).

Association between management and invasion-history and vegetation recovery and abiotic variables

Burning is a key driver of fynbos dynamics, and many indigenous species depend on fire for regeneration. Vegetation can become senescent if left unburned for too long (Van Wilgen, 1982; Kraaij et al., 2013). The disturbance and regeneration triggered by fire causes an increase in species richness and indigenous cover directly following the fire event, both in South-African fynbos (Kruger, 1983) and Californian chaparral (Keeley et al., 1981). No statistically significant results in terms of post-hoc comparisons supported the improved effects of burning, although trends of improvement after burning can be observed in GLMs. In other studies (e.g. Blanchard, 2008) burned sites had higher indigenous species richness and cover than unburned sites. Species richness usually peaks one year after a fire and then declines, making richness comparisons between differently aged stands difficult (Schwilk et al., 1997), but in this case, even though the reference site was mature, indigenous species richness was still higher than in the more recently disturbed (cleared) sites. If the reference had been younger, the difference in richness would probably have been more significant.

Thick litter layers can also prevent the germination of native seeds by insulating the soil from heat or acting as a physical obstruction to emerging seedlings (Friedman et al., 1996; Blanchard and Holmes, 2008). If biomass is present in large amounts, hot fires can damage indigenous seed banks and trigger the germination or resprouting of alien species (Holmes, 2001). This does not seem to be the case in our study. Native vegetation recovered well in burned areas compared to areas that have not been burned after initial clearing, but large litter biomass can potentially lead to very hot, damaging fires in the uninvaded site. This is in contrast to other studies that found no difference between areas that were burned or not after clearing (Fernández et al., 2015).

Nitrogen volatilizes during burning, and can be reduced by up to 50% (Stock and Lewis, 1986). There was a large variance in ammonium and soil EC readings leading to the median level of ammonium and EC to be lower at burned sites, as expected. This could be because some of the recently cleared sites had extremely high levels of ammonium and levels started to decrease through leaching out over time, especially in the sandy lowland soils (Stock and Lewis, 1986). Similar to this study, an increase in soil ammonium was found directly after burning (accounting for some skewed data): not all ammonium-containing compounds are released during combustion and can be transferred down the soil profile (DeBano et al., 1976, 1979). Transfer of soil ammonium after fire depends on soil temperature reached during fire (DeBano, 1991). Available phosphorus responds differently, where in this case available phosphorus was either volatilized or phosphorus-containing compounds did not move down the soil, profile but were concentrated on the soil surface (which was not sampled in this case) (Stock and Lewis, 1986; DeBano, 1991). Fire has been linked to changes in soil chemistry (Stock and Lewis, 1986; D'Antonio and Vitousek, 1992), especially leading to increased pH after burning in the fynbos (Parker-Allie et al., 2004), but no significant effects of fire on pH were found in this study.

Litter has been linked to increased nutrient levels in the soil, where litter with a high phosphorus and nitrogen content could increase phosphorus release into the soil (Stock and Lewis, 1986). This was not the case in our study sites, where litter had a negative association with soil nutrients and no statistically significant effect was observed; this could be due to the uninvaded site being mature and having large amounts of litter and low soil nutrient content, leading to a lack of expected pattern. Additionally, Fynbos litter biomass also decomposes slowly, taking a long time to release nutrients back into the ecosystem (Bengtsson et al., 2012; Witkowski, 1991b).

High levels of available phosphorus, ammonium and soil EC could limit native vegetation performance and recovery because of strong competition from secondary invaders under high soil-nutrient conditions. Considering that fynbos is adapted to moderate amounts of disturbance by fires and low resources in terms of nutrients and summer drought, competition is usually considered to be of less importance (Huston, 1979; Cowling, 1987; Richards, 1993) but as soon as the resources (increased nutrients and more water consumption by pines and acacias) and disturbance regimes change (increased biomass and altered fire regimes), competition with invaders and secondary invaders could become important mediators of fynbos recovery.

The number of follow-up treatments had several effects on biotic and abiotic variables. There is a concern that indigenous species, specifically woody species, can be damaged during follow-up, especially where herbicide is applied (Parker-Allie et al., 2004); this could be why a wide range of responses was observed in the relationship between number of follow-up treatments and the richness of ericoid shrubs. The number of follow-up treatments can also be used as a proxy for time since initial clearing as follow-ups are usually done annually. Even though guilds could be

underrepresented after invasion or damaged by clearing or follow-up operations, diligent follow-ups over time resulted in improved richness of indigenous species indicating recovery in terms of biodiversity.

Litter increased with the number of follow-up treatments applied, even though there are fewer alien plants to contribute to litter production; litter can remain after clearing if not removed or burned, and recovering native species also add to the litter over time. High levels of ammonium and available P never occurred at the same time, even though both occurred at low levels simultaneously, high levels of the one soil nutrient, usually coincide with low levels of the other. The soil pH and the type of invasive species could explain this relationship between available P and ammonium. High organic matter from litter content and high soil pH can favour soil nitrification in acacia-invaded areas, immobilizing available phosphorus (Witkowski and Mitchell, 1987; Seeling and Zasoski, 1993). On the other hand, high soil available phosphorus and low nitrogen can be attributed to continued phosphorus input from decomposing litter and also less available phosphorus uptake by pine trees, as reported on the sandy soils of southern Australia (Bekunda et al., 1990).

Impacts of acacias and pines on the soil became more apparent when separating cycles of invasion or rotations of planting. After two cycles of invasion, acacia-invaded sites had significantly more basic soil than uninvaded areas and sites with only one cycle of acacia invasion, indicating greater impacts after each cycle of invasion. After two cycles of acacia invasion, changes to soil properties were significant which could mean an abiotic structural or functional threshold is approaching or has been crossed. For pine plantations, rotations of planting are only important in terms of significantly lowered pH after three rotations after planting.

This study provides evidence that the impact of invasive species on abiotic and biotic variables increases with duration of invasion and is complementary to other studies that have found increased negative impact on indigenous species recovery with longer duration of pine and acacia invasion (Holmes and Cowling, 1997a; Privett et al., 2001; Le Maitre et al., 2011; Richardson and Gaertner, 2013).

Assess re-enforcing feedbacks between abiotic and biotic variables

Biotic variables and soil nutrients correlated to changes in abiotic variables, when comparing invaded sites to each other and to the uninvaded site. Functional guilds were associated with changes in soil nutrients. Restioid species richness responded negatively to an increase in available phosphorus in the soil and indigenous perennial species and grass and non-ericoid richness decreased with increasing ammonium (and soil EC in the case of non-ericoid shrubs). These results indicate that increases in soil nutrients were associated with poor indigenous species recovery and this could be indicative of a re-enforcing feedback loop between high nutrient levels and poor indigenous vegetation recovery, giving an opportunity for re-invasion or colonisation by secondary invaders (van der Putten et al., 2013). An

increase in soil nutrients has been linked to further changes in ecosystem functioning such as altered nutrient cycling and soil microbial processes (Marchante et al., 2008).

Comparisons between different vegetation types

Comparisons between the two different vegetation types are justified by the fact that they are similar in dynamics and structure. Both are dominated by proteoids and restioids and have ericaceous species common in wetter areas. An asteraceous component is dominant in SAF but only forms a major component of CFSF in drier areas (Rebelo et al., 2006). All sites had comparable sand soil texture.

Only after the sample size of SAF is increased and compared to an uninvaded reference site, can more generalizations be made applying to both vegetation types. Swartland Alluvium Fynbos does however seem to be more resistant in terms of overall vegetation structure, having significantly higher relative indigenous cover and lower relative alien cover than CFSF. This could also be due to a higher mean number of follow-ups or more diligent follow-ups being done in plantations of the SAF. Some of the soil nutrients are also different between vegetation types: ammonium was lower and soil EC was higher in SAF compared to CFSF pine plantations.

In summary, in terms of biotic and abiotic thresholds, acacias changed abiotic variables after two cycles of invasion, and after one cycle in the case of indigenous cover, while lowland fynbos is resilient up to three rotations of pine planting. In terms of vegetation structure, perennial species and guild richness: acacias more negatively impacted invaded sites, whereas pine plantations recovered better in comparison to the reference site. Follow-up clearing generally promoted better ecosystem recovery in terms of overall species richness and structure but care should be taken not to damage indigenous shrubs.

4.5 Management recommendations and future studies

Although the two vegetation types generally seem to have similar dynamics, making them suitable for comparison, future research should separate vegetation types and locate a reference site suitable for SAF. There were not enough species in each functional guild and growth form to allow for a quantitative analysis of effects on native species recovery in terms of regeneration mode, although this would be an important aspect to study. Future studies investigating the restoration of lowland fynbos should include measures of heterogeneity at different scales. Only alpha diversity was considered in this study, while gamma and beta diversity might show more pronounced or different patterns of richness and diversity caused by invasive alien species (Cowling, 1990; Richards, 1993).

Working for Water does not currently incorporate active restoration measures in their clearing and follow-up control, but this study shows that further interventions are required in some cases, especially where the aim is to restore the original structure of fynbos, e.g. when the proteoid overstorey has been reduced or eliminated. In terms of management, some measures should be taken to reduce soil nutrients or at least reduce alien cover and re-introduce indigenous species to assist

indigenous vegetation recovery. Secondary invasion is a growing concern in areas cleared of acacias, as is the case with some other invasive woody plants in the fynbos (Ruwanza et al., 2013). Supplying indigenous seed sources or propagules, to supplement depleted seed banks or diminished seed supply is a tractable way of setting ecosystems on a trajectory of recovery to a functioning ecosystem (Galatowitsch and Richardson, 2005; Blanchard and Holmes, 2008).

4.6 Acknowledgements

Funding for this work was provided by 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” and the National Research Foundation (grant 85417 to DMR). We thank the following organizations access to study sites and providing information: SANParks (permit no. 2015/CRC/2014—024), CapeNature (permit no. 0552-AAA008-00018) and Cape Pine. Gratitude is extended to the following people for their time and assistance during the study: Greg Wilmans (Silviculture forester; Wemmershoek), Deon Rossouw (Conservation Manager, Limietberg Nature Reserve), staff from Kenilworth- and Brackenfell Nature Reserve, Suzaan Kritzinger-Klopper (Senior Technical Officer at the C·I·B), Stuart Hall and Dr Shayne Jacobs and field assistants.

Tables and figures:

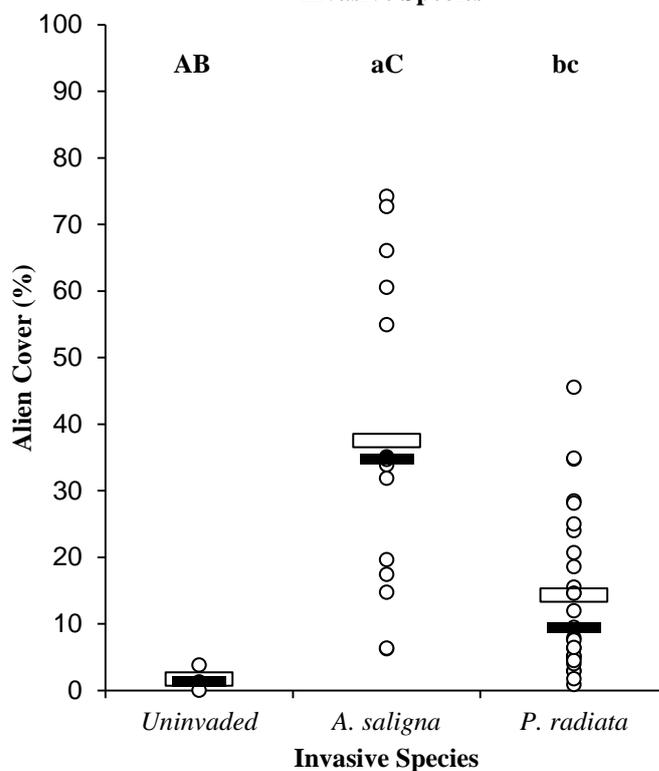
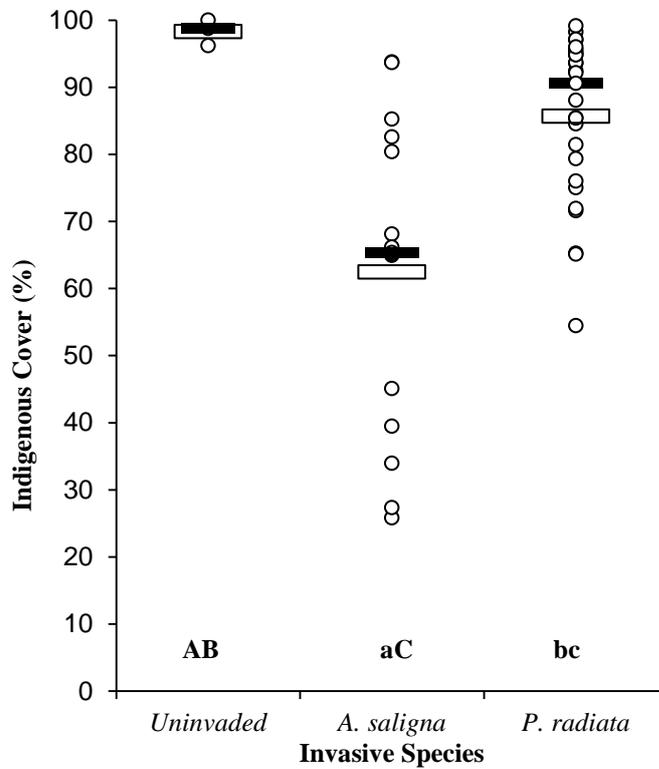
Table 4.1 Descriptive and management variables for study sites. Three different treatments were compared (an uninvaded reference site and sites cleared of dense (>75% cover) *Acacia saligna* and *Pinus radiata* stands) in terms of vegetation recovery. The extent of vegetation recovery takes into account the invasion history (no. cycles of invasion) and the management history (no. follow-up treatments received and whether a site has burned or not after initial clearing) and environmental variables (vegetation type and mean annual precipitation). The uninvaded reference site had a 25% canopy cover of acacia, but had been cleared and kept free of acacias since the initial clearing. UB= unburned; B= burned; CFSF= Cape Flat Sand Fynbos, SAF= Swartland Alluvium Fynbos.

| Site | Elevation (m) | Invasive species | Latitude (decimal degrees) | Longitude (decimal degrees) | Mean annual precipitation (mm) | No. cycles of invasion | Years since initial clearing | Initial clearing method | Post-clearing burn | Vegetation type | No. of follow-up treatments since initial clearing | Follow-up method |
|------------------|---------------|-------------------|----------------------------|-----------------------------|--------------------------------|------------------------|------------------------------|-------------------------|--------------------|-----------------|--|---|
| Bas Ariesfontein | 178 | Uninvaded | 33.719056 | 18.545167 | 422 | 0 | 3 | cut & herbicide | UB | CFSF | 3 | cut & herbicide; hand pulling |
| Blaauwberg A | 74 | <i>A. saligna</i> | 33.754444 | 18.486722 | 361 | 1 | 1 | Block burn | B | CFSF | 1 | cut below ground |
| Blaauwberg B | 72 | <i>A. saligna</i> | 33.756528 | 18.483944 | 361 | 2 | 1 | Stack burn | UB | CFSF | 1 | cut below ground |
| Haasendal | 85 | <i>A. saligna</i> | 33.919222 | 18.704417 | 580 | 2 | 4 | cut & herbicide | UB | CFSF | 3 | cut, herbicide, foliar spray |
| Penhill | 48 | <i>A. saligna</i> | 33.990333 | 18.727111 | 556 | 1 | 9 | cut & herbicide | B | CFSF | 7 | cut, herbicide, foliar spray |
| Safariland | 152 | <i>P. radiata</i> | 33.824667 | 18.999361 | 796 | 1 | 15 | clear felled | B | SAF | 1 | cut, herbicide, foliar spray |
| Tokai block 7 | 55 | <i>P. radiata</i> | 34.051361 | 18.421889 | 974 | 3 | 6 | clear felled | UB | CFSF | 1 | cut, herbicide, foliar spray |
| Tokai block 8 | 37 | <i>P. radiata</i> | 34.051333 | 18.424028 | 974 | 3 | 8 | clear felled | B | CFSF | 1 | cut, herbicide, foliar spray |
| Tokai block 14 | 29 | <i>P. radiata</i> | 34.055306 | 18.429611 | 967 | 3 | 10 | clear felled | UB | CFSF | 3 | hand pull (pine) & cut below ground (acacias) |
| Tokai block 17a | 26 | <i>P. radiata</i> | 34.054361 | 18.434861 | 967 | 3 | 9 | clear felled | UB | CFSF | 3 | hand pull (pine) & cut below ground (acacias) |
| Tokai block 17b | 20 | <i>P. radiata</i> | 34.053306 | 18.435444 | 967 | 3 | 9 | clear felled | B | CFSF | 3 | hand pull (pine) & cut below ground (acacias) |
| Victor Verster | 161 | <i>P. radiata</i> | 33.855694 | 19.004333 | 797 | 3 | 4 | clear felled | UB | SAF | 3 | cut, herbicide, foliar spray |
| Wemmershoek A | 182 | <i>P. radiata</i> | 33.877833 | 19.048972 | 886 | 2 | 6 | clear felled | UB | SAF | 4 | cut, herbicide, foliar spray |
| Wemmershoek B | 182 | <i>P. radiata</i> | 33.875806 | 19.04775 | 836 | 1 | 12 | clear felled | B | SAF | 8 | cut, herbicide, foliar spray |
| Youngsfield | 29 | <i>A. saligna</i> | 34.008417 | 18.487833 | 1018 | 1 | 5 | cut & herbicide | UB | CFSF | 4 | hand pulling |

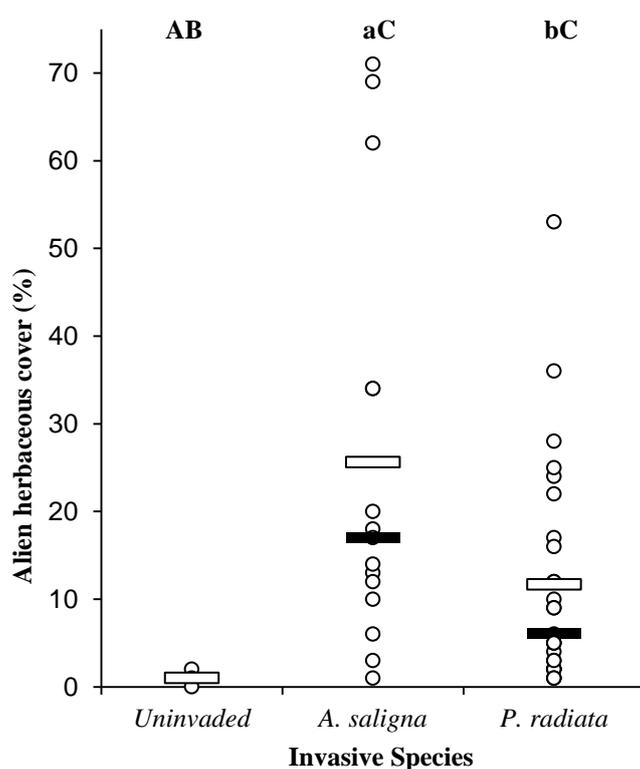
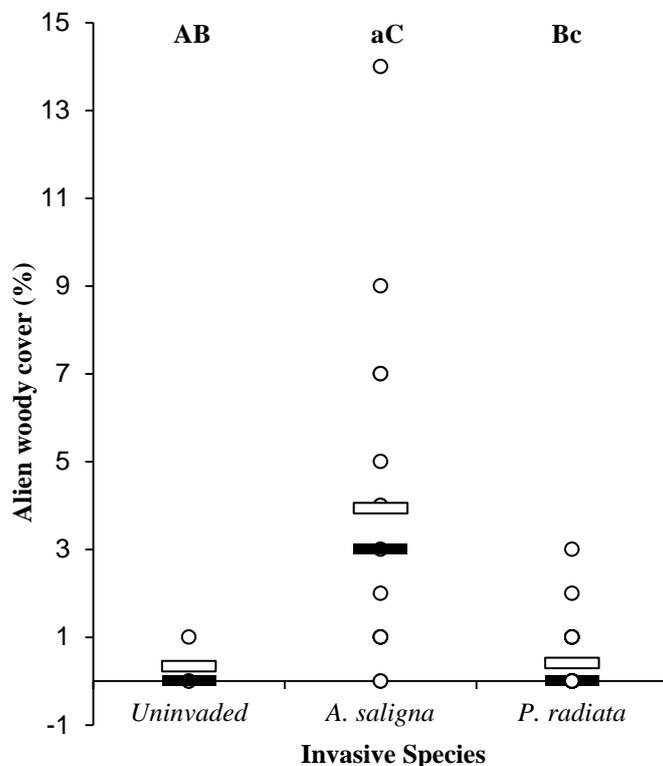
Table 4.2 Attributes used to classify species into functional guilds.

| <i>Plant species attribute</i> | <i>Range of possibilities</i> |
|--------------------------------|--|
| Origin | Indigenous or Alien species |
| Growth form | Shrub, Parasite, Graminoid, Geophyte, Forb, Restioid |
| Longevity | Annual or Perennial |
| Shrubs | Ericoid or Non-ericoid |

Figures 4.1-4.2: Vegetation recovery was compared across previously invaded and an uninvaded reference fynbos site. Relationship between biotic structural indicators as response variables **Figure 4.1** (top) Indigenous Cover and **Figure 4.2** (bottom) Alien Cover and the Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).



Figures 4.3-4.4: Vegetation recovery was compared across previously invaded and an uninvaded reference fynbos site. Relationship between biotic structural indicators as response variables **Figure 4.3** (top) Alien Woody Cover and **Figure 4.4** (bottom) Alien Herbaceous Cover and the Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).



Figures 4.5-4.6: Vegetation recovery was compared across previously invaded and an uninvaded reference fynbos site. Relationship between biotic functional indicators as response variables **Figure 4.5** (top) Indigenous Perennial Grass richness and **Figure 4.6** (bottom) Ericoid Shrub richness and Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).

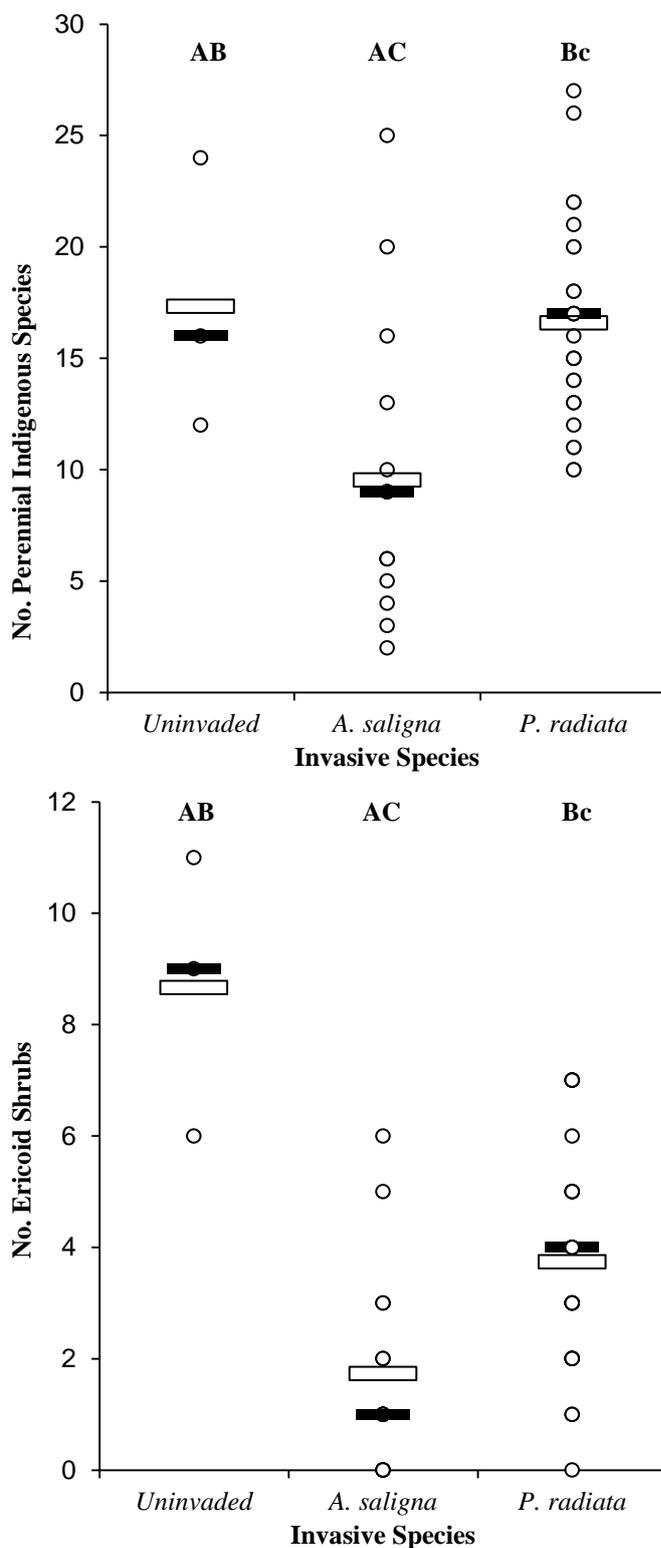
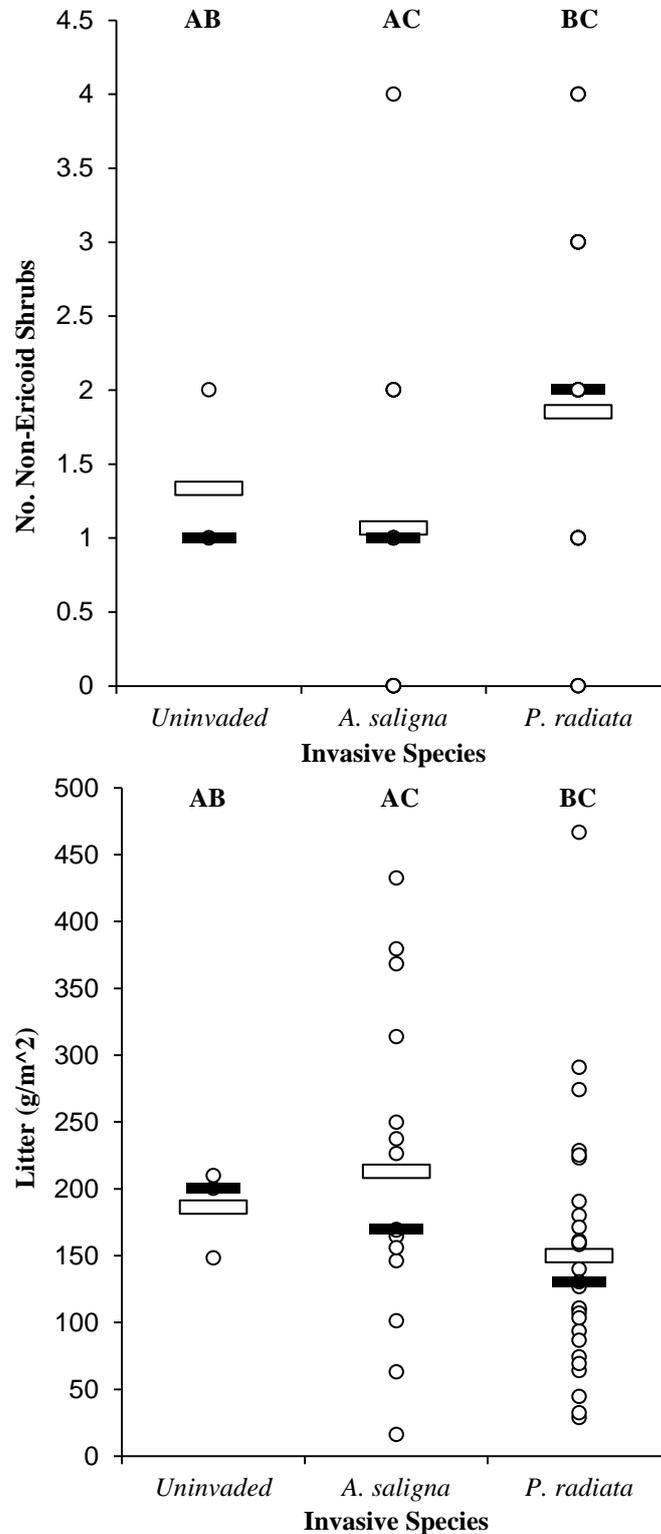
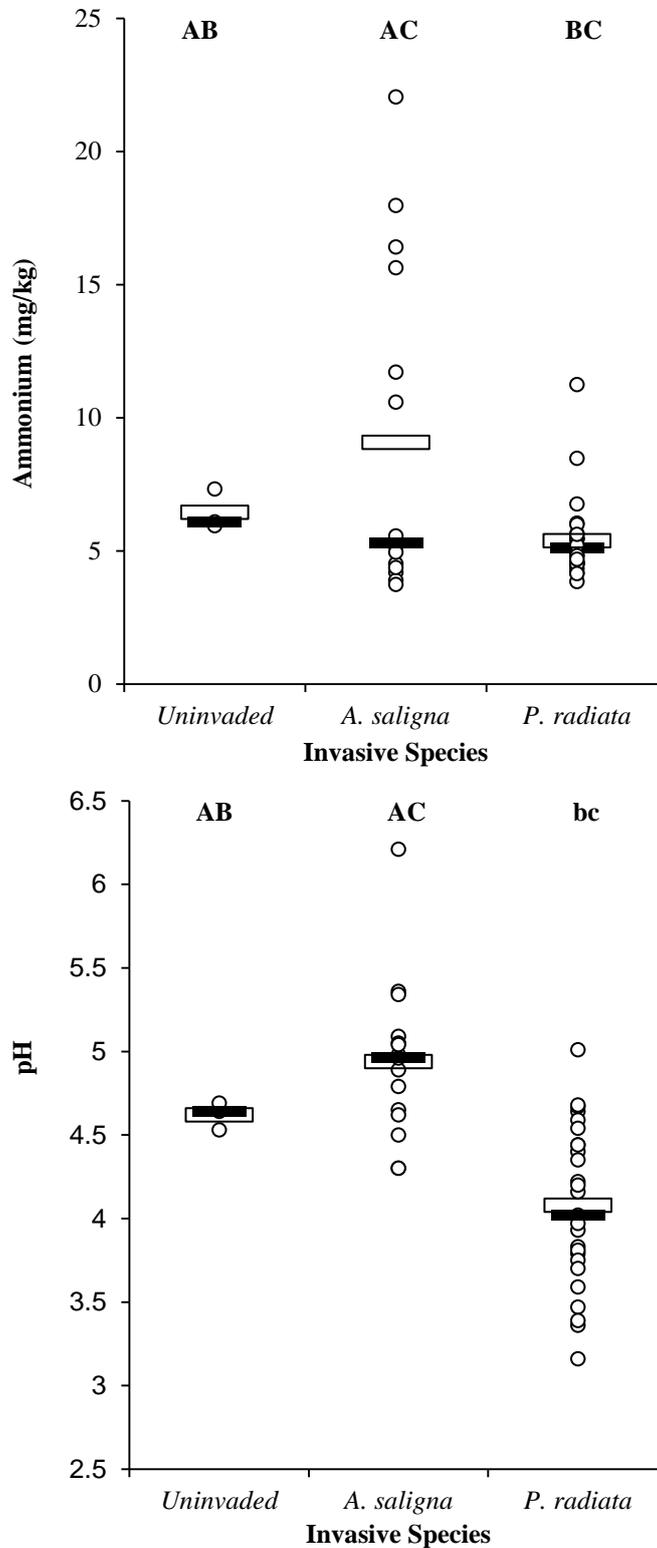


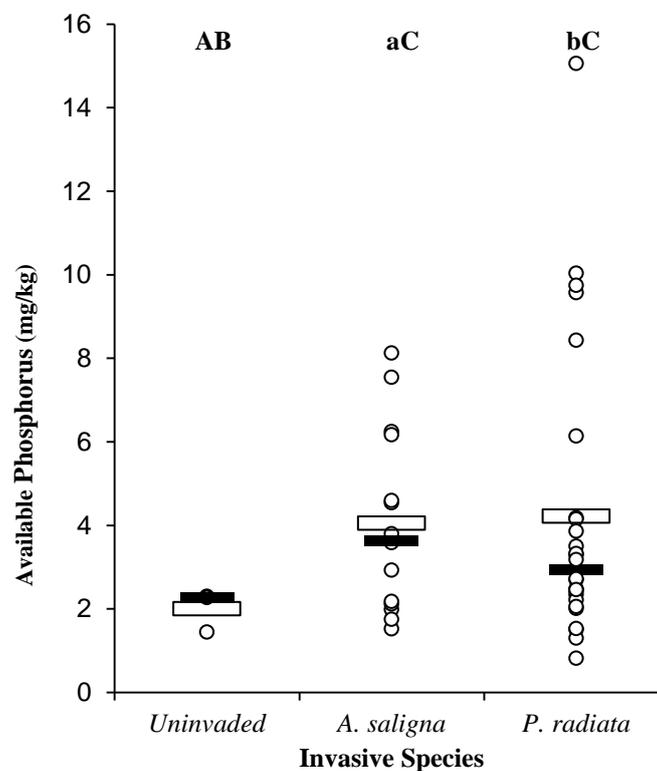
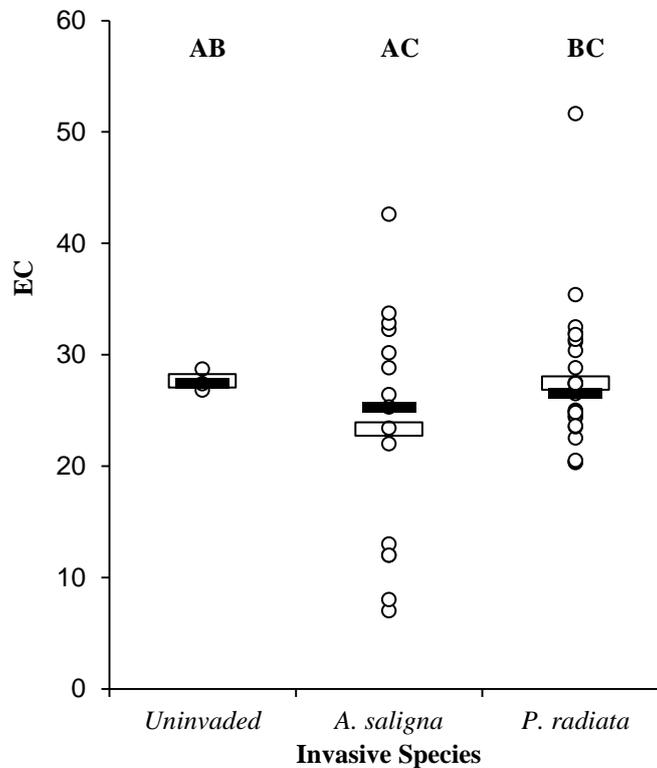
Figure 4.7-4.8: Vegetation recovery was compared across previously invaded and an uninvaded reference fynbos site. **Figure 4.7** (top) Relationship between biotic functional indicator as response variable, Non-Ericoid Shrub richness, and **Figure 4.8** (bottom) between abiotic functional indicator as response variables, Litter, and the Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*). Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$) and capital letters no significant differences.



Figures 4.9-4.10: Vegetation recovery was compared across previously invaded and an uninvaded reference fynbos site. Relationship between abiotic functional indicators as response variables **Figure 4.9** (top) Ammonium and **Figure 4.10** (bottom) pH and the Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).



Figures 4.11-4.12: Vegetation recovery was compared across previously invaded and an uninvaded reference fynbos site. Relationship between abiotic functional indicators as response variables **Figure 4.11** (top) EC and **Figure 4.12** (bottom) Available Phosphorus and the Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).



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Chapter 5: Summary of results

Invasions by transformer species, such as acacias and pines, pose a threat to natural vegetation that is providing us with the benefits of biodiversity, and the ecosystem services derived from functioning natural ecosystems. In many cases, restoration is required to alleviate the impacts of transformer species and the need for active restoration measures increases in areas with a longer history of invasion.

This study aimed to develop, illustrate and test a framework to distinguish areas in need of active restoration from those that do not, in the City of Cape Town, and to prioritize areas for restoration at a city scale. This study consists of three different parts: firstly, a literature review (chapter 2); secondly the development of two frameworks (chapter 3) (1) to identify areas needing active restoration and (2) to prioritize areas for active restoration; and thirdly an empirical site-scale study, to investigate native ecosystem recovery of lowland fynbos following clearing of invasive acacia species and removal of pine plantations (chapter 4).

5.1 Summary of research findings

Data for the framework to identify areas needing active restoration were collected during an expert workshop. The relative importance of certain factors in determining the likelihood of invaded areas needing active restoration following alien clearing was discussed. As an illustration of the framework, a map was produced indicating the ‘Need for active restoration’ for natural areas of Cape Town.

By using the above-mentioned framework, a second framework was developed to prioritize areas for active restoration in order to improve and optimize city-wide ecosystem functioning and ecosystem service delivery. During this second workshop, a framework was developed to prioritize areas for active restoration focusing on certain ecosystem services and the factors that can be used to prioritize areas for fynbos restoration. Both frameworks were built using an approach called Multi-Criteria Analysis, which is an easy, simple, transparent and flexible method to construct a goal, combine stakeholder opinions and facilitate spatial restoration planning

Many aspects such as ecological characteristics of an area, the ownership of the land (e.g. whether secured for conservation) and the benefit a restored area can contribute to society are considered when deciding on which alien-invaded areas would need active restoration and how it should be prioritized. According to a group of stakeholders the overall criteria that will be important are: the dominant alien species invading the area, density of invasion, duration of invasion, how much indigenous vegetation is remaining, the adjacent land use, level of disturbance in an area, size of the area, the aspect the area is facing, soil texture, soil depth and erodibility, slope and the vegetation type.

To decide which areas should be given priority for active restoration, areas can be selected according to whether they improve the connectivity between natural areas, whether the area is part of the Biodiversity Network (conservation plan) and how much of the vegetation type is still left (how threatened the vegetation type is); other important factors are ecosystem functioning of an area in terms of the diversity of habitats and the importance of the areas in terms of soil conservation (e.g. soil erodibility and slope). After looking at ecological criteria, one should also take into consideration which area will provide society with ecosystem services. Healthy ecosystems can provide valuable services to a city and invasive alien plants can have negative impacts on urban ecosystems, affecting both native biodiversity and ecosystem functioning. The clearing of invasive alien plants and restoration of areas can lead to a sustainable supply of ecosystem goods and services and an increase in native biodiversity in some cases. Whether an area already enjoys legal protected status or is under some form of conservation management is important, additionally the level of community engagement and their attitude towards restoration will be important in determining the success of restoration activities.

The traits of different invasive alien tree guilds exert different intensities of impacts at both community and ecosystem levels and consequently there will be differences in restoration potential of the ecosystem post-alien clearance. Chapter 4 compared the impacts of *A. saligna* and *P. radiata* on lowland fynbos restoration ability. The hypothesis that dense acacia stands impact restoration potential more than pine plantations was supported. A threshold of autogenic recovery likely was crossed, since acacia-invaded areas did not recover structurally to a level of dominance by indigenous species, but rather had a large component of herbaceous alien species. Pine-invaded areas generally had higher restoration potential than acacia-invaded areas. This threshold change was supported by changes in the soil nutrient and chemical variables and biotic structure, after two cycles of invasion for acacia areas and after three rotations of planting for pine areas. Management interventions can improve ecosystem recovery post-clearing: follow-up treatments were associated with improved vegetation recovery.

The aim of chapter 4 was not only to determine the degree of autogenic recovery of indigenous vegetation after dense invasions of acacia stands and pine plantations, but also to test some of the assumptions made in the 'Need for active restoration framework' in chapter 3 (table 3.1). The most important criteria (52% of weight) determining impact on indigenous vegetation recovery, according to stakeholders, were those factors relating to species characteristics (dominant invasive species) and invasion history (density and duration of invasion). These criteria had the biggest influence in the 'Need for active restoration' score (chapter 3, table 3.1). The impact of the invasive species (acacia vs pine), cycles of invasion/rotations of planting and the vegetation type was hence tested during the site scale study (Chapter 4). Density of invasion was not included since all invaded sites had a closed canopy cover (>75% cover) before initial clearing.

The site scale study revealed that biotic and abiotic variables were impacted by invasive species and the framework is correct in giving acacias a higher weighting than pines: acacias changed abiotic variables after two cycles of invasion while lowland fynbos is resilient up to three rotations of pine planting. In terms of vegetation structure, perennial species and guild richness: acacias more negatively affected recovery, whereas pine plantations recovered better, in comparisons to the uninvaded reference site. Site scale results confirm the importance of invasive identity and cycles of invasion, where the need for active restoration increases with time since dense invasion or cycles of invasion. Results however indicated a difference between vegetation types and the broad vegetation type categories used in the 'Need for active restoration framework' might not be homogenous. Both vegetation types had a sandy soil texture and have the same dominant structural elements. It was found that SAF had higher relative indigenous cover and lower relative alien cover than CFSF. Some of the soil nutrients are also different between vegetation types: ammonium was lower and soil EC was higher in SAF compared to CFSF pine plantations. Although the two vegetation types examined in Chapter 4 generally seem to have similar dynamics, making them suitable for comparison and could support the broad categories in the framework, future research should separate vegetation types and locate a reference site suitable for Alluvium Fynbos. Only after the sample size of Alluvium Fynbos is increased in future studies and compared to an uninvaded reference site, can more generalizations be made concerning both vegetation types. Weightings of vegetation types can be adjusted after further research comparing vegetation types or groups of vegetation types.

The 'Need for active restoration' framework is meant to be used with spatial data and the quality of the outcome will depend on the quality of the data. Especially the three criteria with the biggest weight require the most accurate data (species distribution, density and duration of invasion).

A discrepancy between the invasion history criteria, i.e. dominant invasive species and density classification of spatial data used in chapter 3 and data collected from study sites in Chapter 4 was found. Many study sites sampled in chapter 4 (cleared of dense invasions) had been classified as being uninvaded with 0% invasion density according to the spatial data used in chapter 3.

Four sources of data were consulted for dominant invasive species distribution and density in Chapter 3: a city scale map developed in 2009 for the city Biodiversity Network, 2013 alien clearing data as captured by Working for Water teams and assimilated by the Invasive Species Unit and the national invasive species distribution map (Kotze et al., 2010) and plantations, as indicated by the National Land Cover Map (2014). The misclassification of previously invaded areas as uninvaded could be because most areas were cleared of aliens prior to the development of any of these data layers, but also the majority of the data collection is confined to formally protected areas. In chapter 4 species identity, duration of invasion and fire history were clearly important in determining indigenous vegetation recovery, but accurate, complete and appropriate spatial data do not exist for these criteria.

More accurate and fine-scale mapping of invasive species and fire events are required for vegetation remnants across the City.

5.2 Recommendations

Determining the original density and identity of alien infestations before initial clearing is essential in conservation management. If one is not aware of historical conditions, one cannot monitor vegetation and determine if active restoration is needed. If no active restoration is done to restore missing structural elements, such as the proteoid overstorey, areas will simply be reinvaded by transformer species or overrun by secondary invaders: ultimately wasting resources if indigenous flora and fauna is not set on the trajectory of recovery. Many institutions are responsible for the management of Cape Town's natural resources and most keep good records of the management history such as alien clearing and density, fire records and follow-up treatments. These institutions include City of Cape Town's Environmental Resource Management Department (Biodiversity Management Branch: Invasive Species Unit that works closely with Working for Water), SanParks and Cape Nature. The City is unified by a systematic conservation plan, the Biodiversity Network, and I call on better information sharing and data accessibility by all stakeholders. By having a centralised data sharing and updating platform, accurate and fine-scale data can be made available. These data can be used for city planning and fund allocation in order to achieve the overall City and national conservation targets, to the benefit of all institutions and stakeholders.

Recommendations following dense invasion of acacia and pines are that the re-introduction of missing and under-represented guilds should follow clearing and burning of invaded areas. Burning generally improved ecosystem recovery, and should be included in management plans for natural areas. The overstorey, serotinous proteoid shrubs were missing in all invaded areas and after one cycle of invasion/rotation of planting, proteas should be re-introduced after clearing to set the ecosystem on the trajectory towards a structurally functional ecosystem. Ericoid shrubs, and non-ericoid shrubs in acacia areas, were also sensitive to dense invasion and should be re-introduced. Removal and control of alien herbaceous species is important, along with diligent annual follow-up clearing to remove any new alien woody recruitment.

5.3 Overall conclusions

The overall outcomes of this study will serve as a tool for the City of Cape Town and land managers to improve restoration effort by identifying and prioritizing areas for active restoration. Maps were produced as an illustration of the developed frameworks, indicating areas needing active restoration and indicating their priority, according to criteria including an areas' conservation and protected status and whether it is important in contributing to ecosystem services. Both frameworks can be updated with new data, additional criteria, factors and restoration goals as research continues and provides further insights in ecological restoration. Thus, the framework may be used in other areas of the CFR.

By applying these frameworks, resources can be used efficiently by either passively restoring areas having the lowest need for active restoration first, or areas with a high priority for active restoration could be restored concurrently, justified by their conservation status and/or ecosystem service provisioning.

This study has addressed the two main identified gaps in restoration, firstly by providing a framework for identifying and prioritizing areas for active restoration, to be used specifically in spatial planning of IAP management. The two frameworks set out a clear goal to follow and consider the multiple aspects involved in conservation and restoration, namely: biodiversity, ecosystem functioning and services, social and political aspects. Secondly, it is also a multi-species approach, considering the main woody transformers in the frameworks, testing the framework, and providing restoration recommendations for the two main lowland invaders: *Pinus radiata* and *Acacia saligna*.

The unique setting of Cape Town makes this biodiversity hotspot vulnerable to transformation by urbanization and urban sprawl, and the impacts of invasions in fragmented remnant vegetation patches. Future research should apply the developed frameworks, and monitor cleared areas in terms of vegetation recovery to confirm that the assumptions and predictions hold true. The framework can then be adjusted in terms of criteria and weightings to be more relevant with current data.

Appendices

Appendix 3

Table S1 ‘Need for active restoration’ framework, criteria and sub-criteria are listed with their weightings assigned. Categories are listed with the corresponding relative weights. Relative weights indicate a categories’ importance in each sub-criteria.

| Criteria | Sub-criteria | Categories | |
|-------------------------|-------------------------------|------------------------------------|----|
| Species 27 | Species | Wattle | 28 |
| | | Pine | 7 |
| | | Gums | 65 |
| Invasion History 25 | Density of Invasion 55 | <25% | 10 |
| | | 25-75% | 25 |
| | | >75% | 65 |
| | Duration/no fire cycles 45 | 1 fire/or <40yr invasion | 17 |
| | | 2 or more fires/or >40 yr invasion | 83 |
| Local influences 7 | Adjacent land use 7 | Natural vegetation, non-invaded | 7 |
| | | Vegetation, invaded | 32 |
| | | Urban | 31 |
| | | Agriculture | 30 |
| | Disturbance 78 | Low | 0 |
| | | Medium | 0 |
| | | High | 0 |
| | Patch size 15 | <5 ha | 16 |
| | | 5-600 ha | 27 |
| | | >600 ha | 57 |
| Native vegetation 20 | Remaining indigenous cover | Low | 66 |
| | | Medium | 23 |
| | | High | 11 |
| Landscape | Aspect | No slope | |

| | | | | | | |
|-----------------|--------------------|-----------------|------------------|----|---------|----|
| 11 | 24 | 25 | | | | |
| | | South facing | 25 | | | |
| | | North facing | 50 | | | |
| | Nutrient retention | 12 | Average % clay | 12 | | |
| | Erodibility | 27 | Soil erodibility | 30 | k-value | 30 |
| | | | Slope | 70 | <20% | 7 |
| | | | | | 20-33% | 14 |
| | | | | | 33-50% | 30 |
| | | | | | 50-100% | 49 |
| | Soil depth | 37 | <450 mm | 64 | | |
| 450-750 mm | | | 19 | | | |
| >750 mm | | | 17 | | | |
| Vegetation type | 10 | Vegetation type | Sandstone fynbos | 10 | | |
| | | | Mid-slope fynbos | 13 | | |
| | | | Lowland fynbos | 35 | | |
| | | | Renosterveld | 24 | | |
| | | | Strandveld | 6 | | |
| | | | Forest | 12 | | |

Table S2 ‘Prioritizing’ framework, criteria and sub-criteria are listed with their weightings assigned. Categories are listed with the corresponding relative weights

| | | | | |
|-----------------------------|--------------------------------------|--------------------------------------|---------------------------------|---------------|
| Physical attributes 14 | Connectivity 14 | Adjacent habitat the same 34 | Yes 72 | |
| | | | No 28 | |
| | | Distance to natural/reserve 30 | Width 36 | <100 11 |
| | | | | 100-300 38 |
| | | | | >300 51 |
| | | | | |
| Conservation status 48 | CBA rank 41 | CBA rank 41 | Protected areas 48 | |
| | | | CBA1a-c 24 | |
| | | | CBA1d-e 14 | |
| | | | CBA2 9 | |
| | | | CESA & other natural areas 5 | |
| | % remaining of vegetation type 59 | % remaining of vegetation type 59 | <30% 54.00 | |
| | | | 30-45% 23.00 | |
| | | | 45-60% 14.00 | |
| | | | >60% 9.00 | |
| | | | | |
| Ecosystem functioning 38 | Erosion 36 | Soil erodibility 35 | 35 | |
| | | | Slope 65 | <20% 7 |
| | | | | 20-33% 17 |
| | | | | 33-50% 35 |
| | | | | 5-100% 41 |
| | Habitat diversity 64 | No. habitats 64 | 1 6 | |
| | | | 2 12 | |
| | | | 3 27 | |
| | | | >3 55 | |
| | | | | |

Table S3 ‘Ecosystem service provisioning’, divided into regulating and cultural services. Each ecosystem service is listed with their sub-criteria and their relative weights

| Level 1 Criteria | Level 2 Sub-criteria | Level 3 Sub-criteria | |
|------------------|-----------------------------|----------------------|----------------------------|
| Regulating 55 | Critical infiltration 34 | | |
| | Flood mitigation 34 | | |
| | Coastal protection 23 | | |
| | Groundwater 10 | | Groundwater quality 50 |
| | | | Groundwater recharge 28 |
| | | | Groundwater yield 22 |
| Cultural 45 | Education 65 | | |
| | Culture 35 | Tourism 60 | |
| | | Heritage 40 | |

Table S4 Social criteria and sub-criteria along with weights assigned by experts

| | | |
|--------|--------------------------------|---|
| Social | Legal status 83 | Protected: In Perpetuity 72 |
| | | Protected: Not In Perpetuity 17 |
| | | Conservation Area 11 |
| | Ability to maintain gain 17 | Current level of community engagement 27 |
| | | Attitude of community 63 |

Table S5 List of top 25 protected areas, ranked by 'Overall priority', and the scores it was develop from: 'Need for active restoration', 'Prioritizing' and 'Ecosystem service provisioning' score

| Protected Area Name | Ecosystem services | Need for active restoration | Inherent restoration need | Prioritizing only | Need and priority | Overall priority |
|--|--------------------|-----------------------------|---------------------------|-------------------|-------------------|------------------|
| Blaauwberg | 0.36 | 0.45 | 0.66 | 0.32 | 0.77 | 1.13 |
| Driftsands | 0.46 | 0.38 | 0.66 | 0.29 | 0.67 | 1.13 |
| Uitkamp Wetland | 0.41 | 0.35 | 0.68 | 0.38 | 0.73 | 1.14 |
| Intaka Island | 0.48 | 0.34 | 0.67 | 0.33 | 0.67 | 1.15 |
| Hottentots-Holland | 0.54 | 0.29 | 0.66 | 0.32 | 0.61 | 1.16 |
| Glencairn Wetlands | 0.61 | 0.25 | 0.66 | 0.29 | 0.54 | 1.16 |
| Muizenberg East | 0.64 | 0.25 | 0.66 | 0.27 | 0.52 | 1.16 |
| Wolfgat | 0.54 | 0.35 | 0.63 | 0.29 | 0.63 | 1.17 |
| De Hel | 0.53 | 0.26 | 0.67 | 0.39 | 0.65 | 1.17 |
| Macassar Dunes | 0.48 | 0.42 | 0.63 | 0.29 | 0.70 | 1.18 |
| Helderberg-Silwerboomkloof section | 0.63 | 0.29 | 0.65 | 0.27 | 0.55 | 1.18 |
| Table Bay -Milnerton Race Course section | 0.39 | 0.42 | 0.70 | 0.38 | 0.80 | 1.19 |
| False Bay - Rondevlei section | 0.55 | 0.37 | 0.60 | 0.28 | 0.65 | 1.20 |
| Steenbras | 0.59 | 0.29 | 0.66 | 0.34 | 0.63 | 1.22 |
| Table Bay - Zoarvlei section | 0.50 | 0.39 | 0.70 | 0.35 | 0.73 | 1.23 |
| Zandvlei Estuary | 0.72 | 0.27 | 0.55 | 0.25 | 0.52 | 1.24 |
| Table Bay - Fynbos Corridor (Diep River-BCA) | 0.42 | 0.49 | 0.71 | 0.33 | 0.82 | 1.25 |
| False Bay - Capricorn Park section | 0.58 | 0.41 | 0.65 | 0.29 | 0.70 | 1.28 |
| Table Mountain - Tokai Park section | 0.66 | 0.25 | 0.66 | 0.37 | 0.63 | 1.29 |
| Rondebosch Common | 0.61 | 0.31 | 0.68 | 0.37 | 0.69 | 1.29 |
| Kirstenbosch Gardens | 0.62 | 0.33 | 0.67 | 0.34 | 0.67 | 1.30 |
| False Bay | 0.58 | 0.43 | 0.65 | 0.30 | 0.73 | 1.30 |
| Two Rivers Urban Park | 0.63 | 0.33 | 0.71 | 0.38 | 0.71 | 1.34 |

| | | | | | | |
|---------------------------|------|------|------|------|------|------|
| Helderberg | 0.66 | 0.39 | 0.66 | 0.29 | 0.68 | 1.34 |
| Lower Silvermine Wetlands | 0.74 | 0.38 | 0.68 | 0.29 | 0.67 | 1.41 |

Figure S1-S4 S1) Distribution of dominant invasive species in the Biodiversity Network S2) Average density of invasion S4) Habitat condition of vegetation, used as a proxy for the amount of remaining indigenous cover S4) Average soil depth in mm

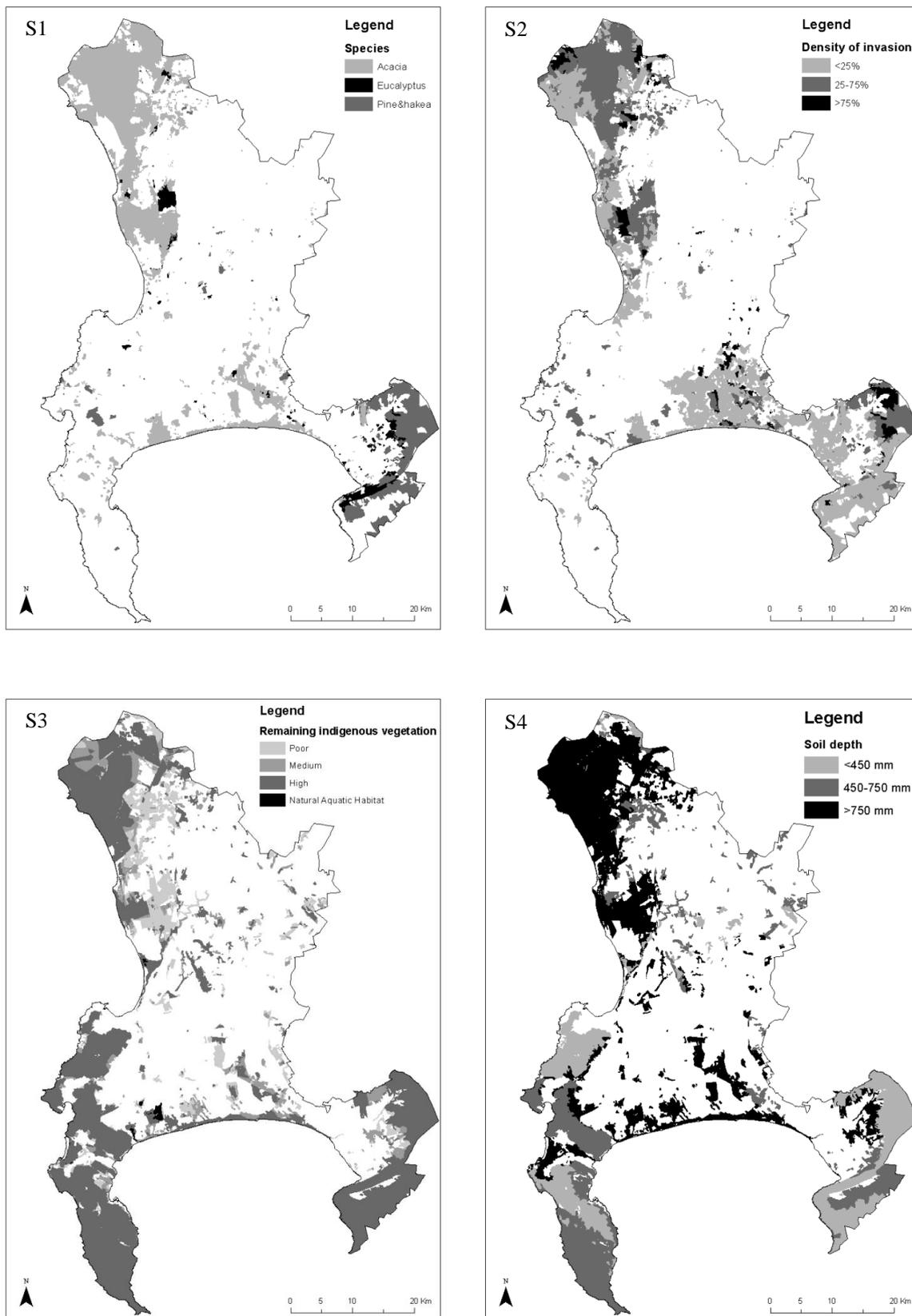


Figure S5-S8 S5) Average percentage slope of vegetation remnants S6) Soil erodibility factor, k-value S7) Average percentage clay in the soil S8) Broad vegetation type of the City of Cape Town

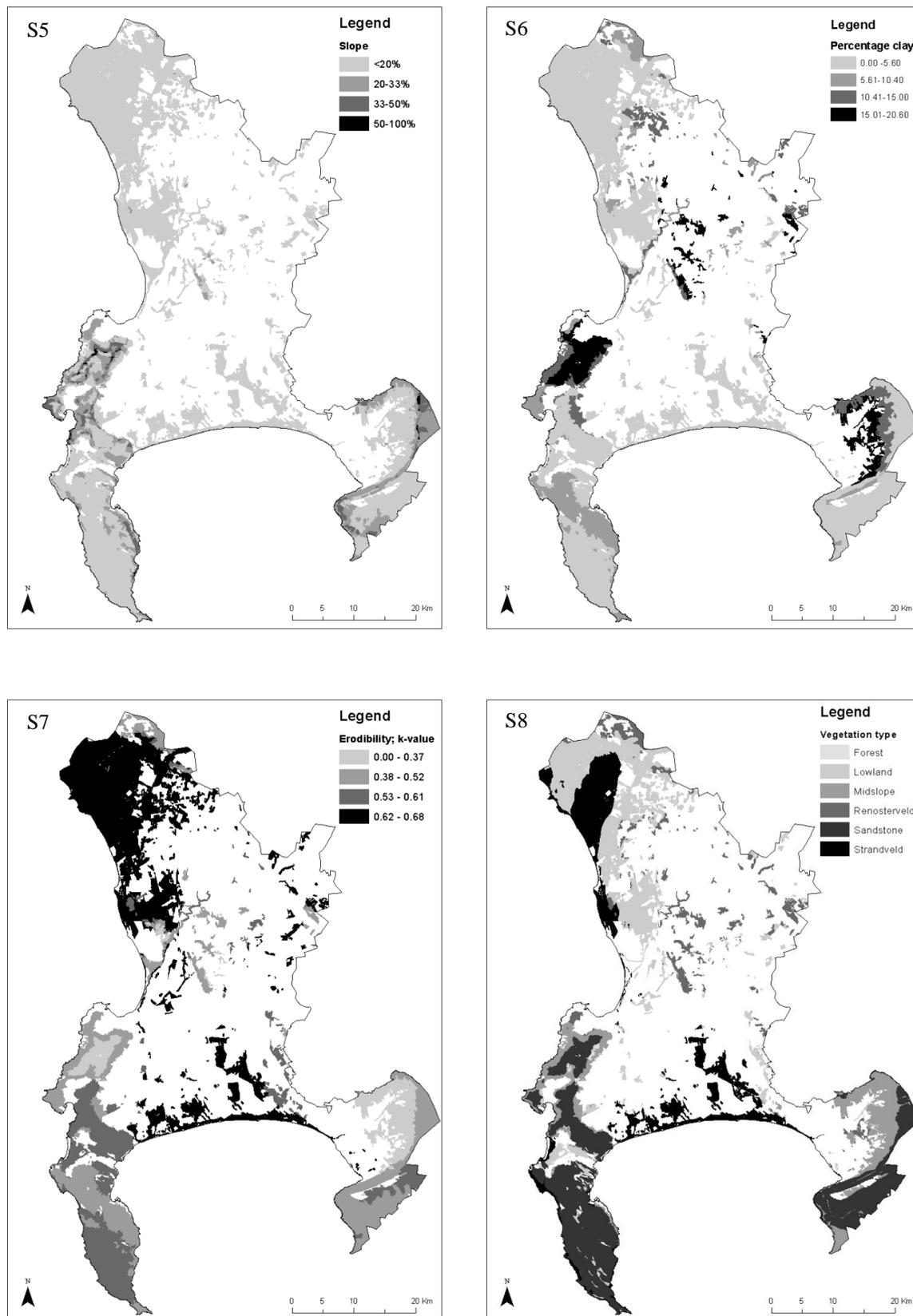


Figure S9-S12 S9) Remaining percentage of each vegetation type as represented by the conservation status of vegetation types S10) CBA category of vegetation remnants, taken from the Biodiversity Network S11) Distance to natural, uninvaded areas in meters (uninvaded is classified as having <25% invasive cover) S12) Areas important for groundwater infiltration

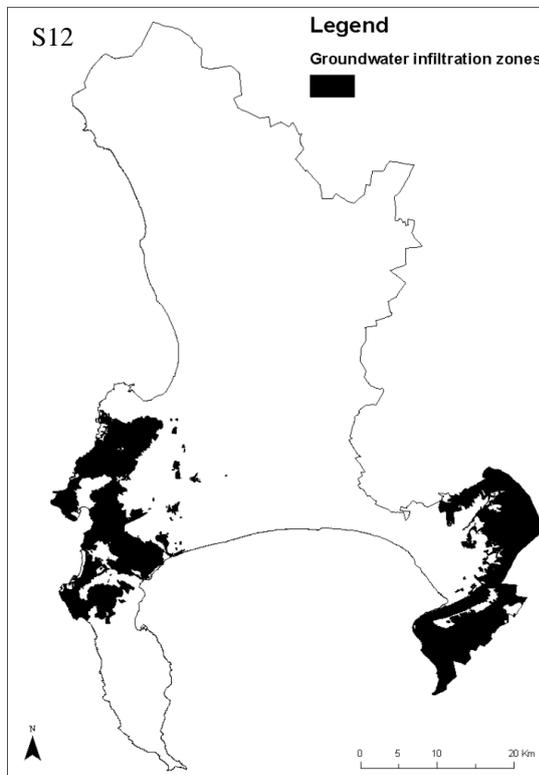
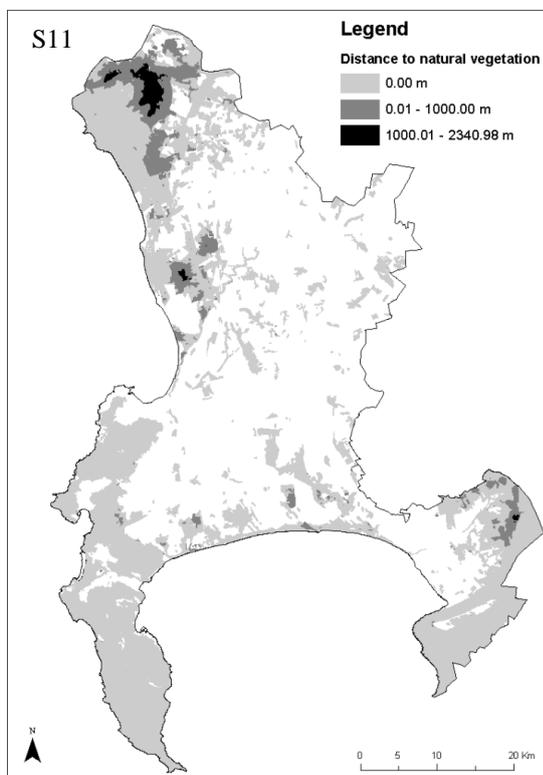
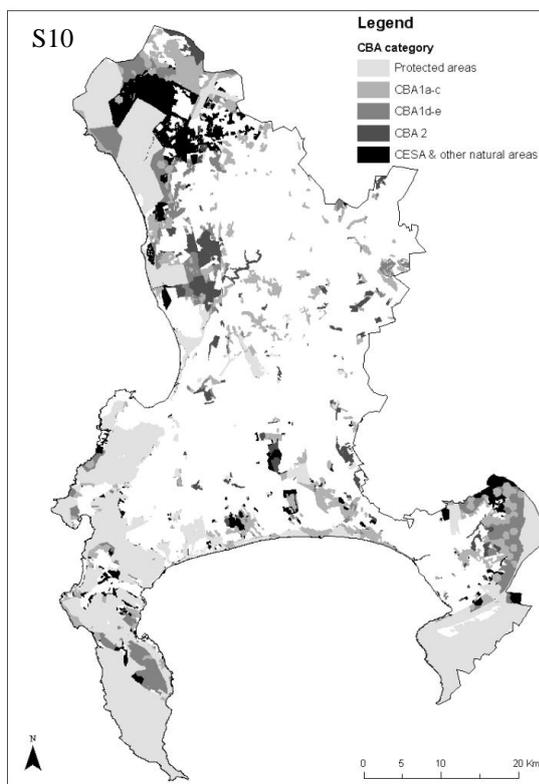
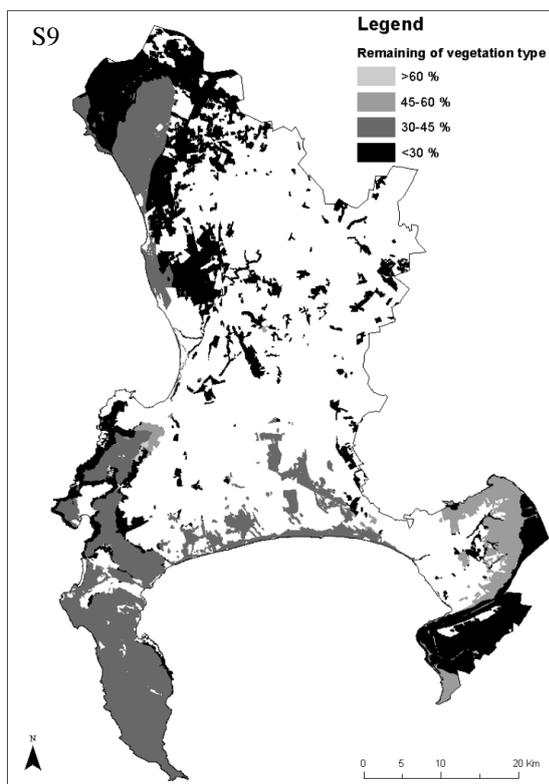


Figure S13-S16 S13) Areas important to flood mitigation S14) Natural remnants falling in the coastal protection zone S15) Groundwater recharge areas that sustain water for river flow, certain vegetation and human use S16) Groundwater yield in litres per second

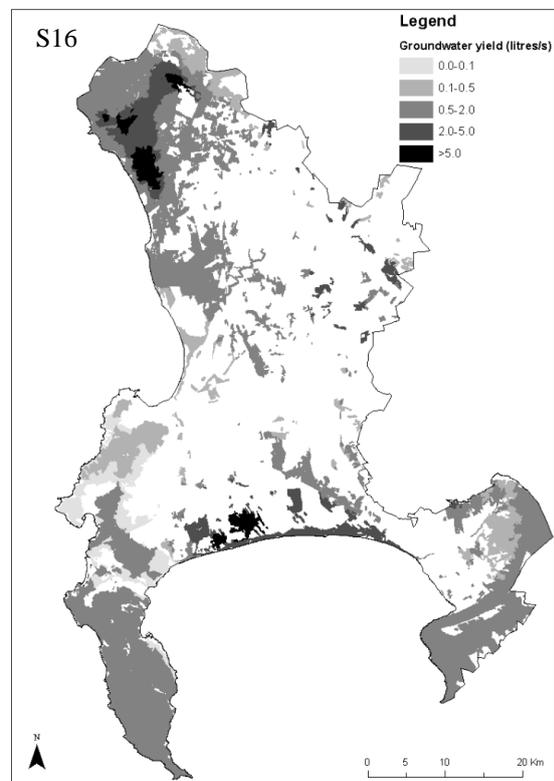
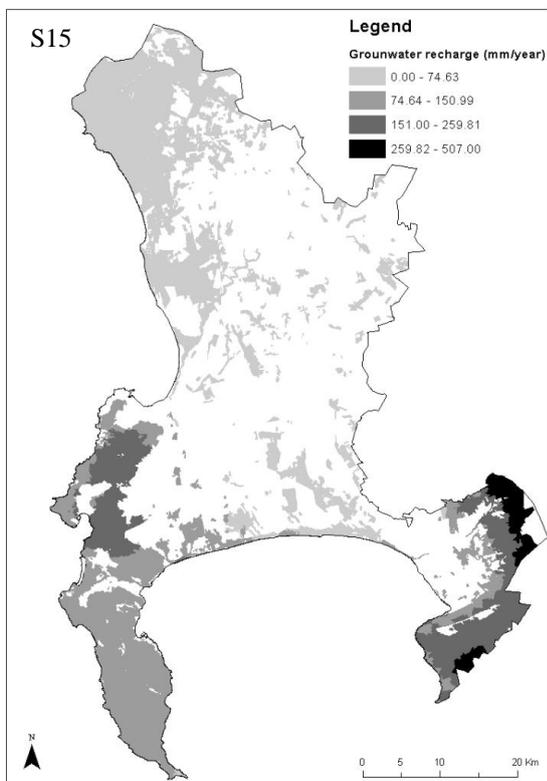
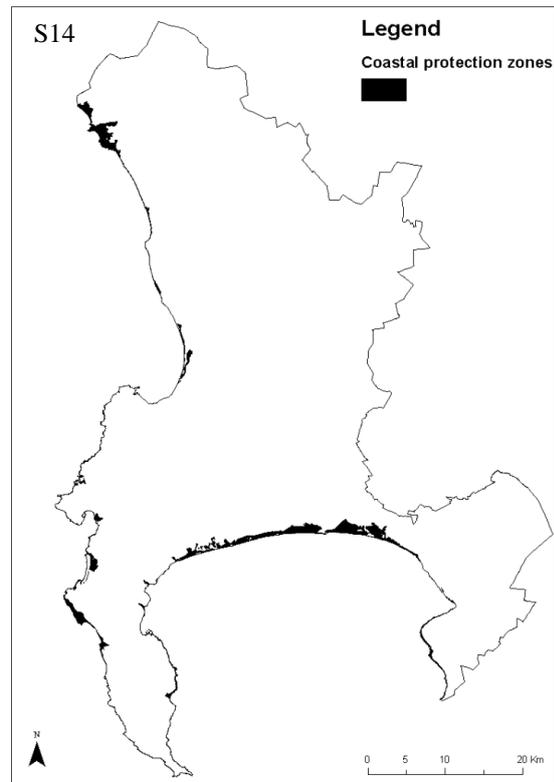
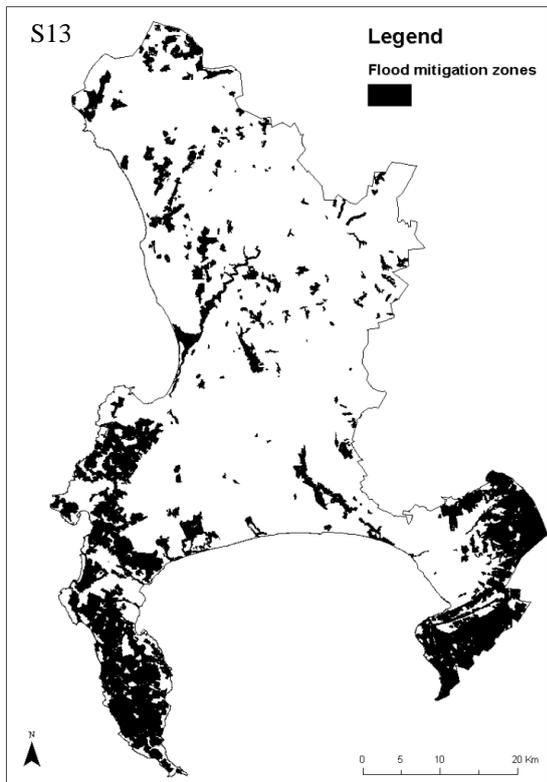
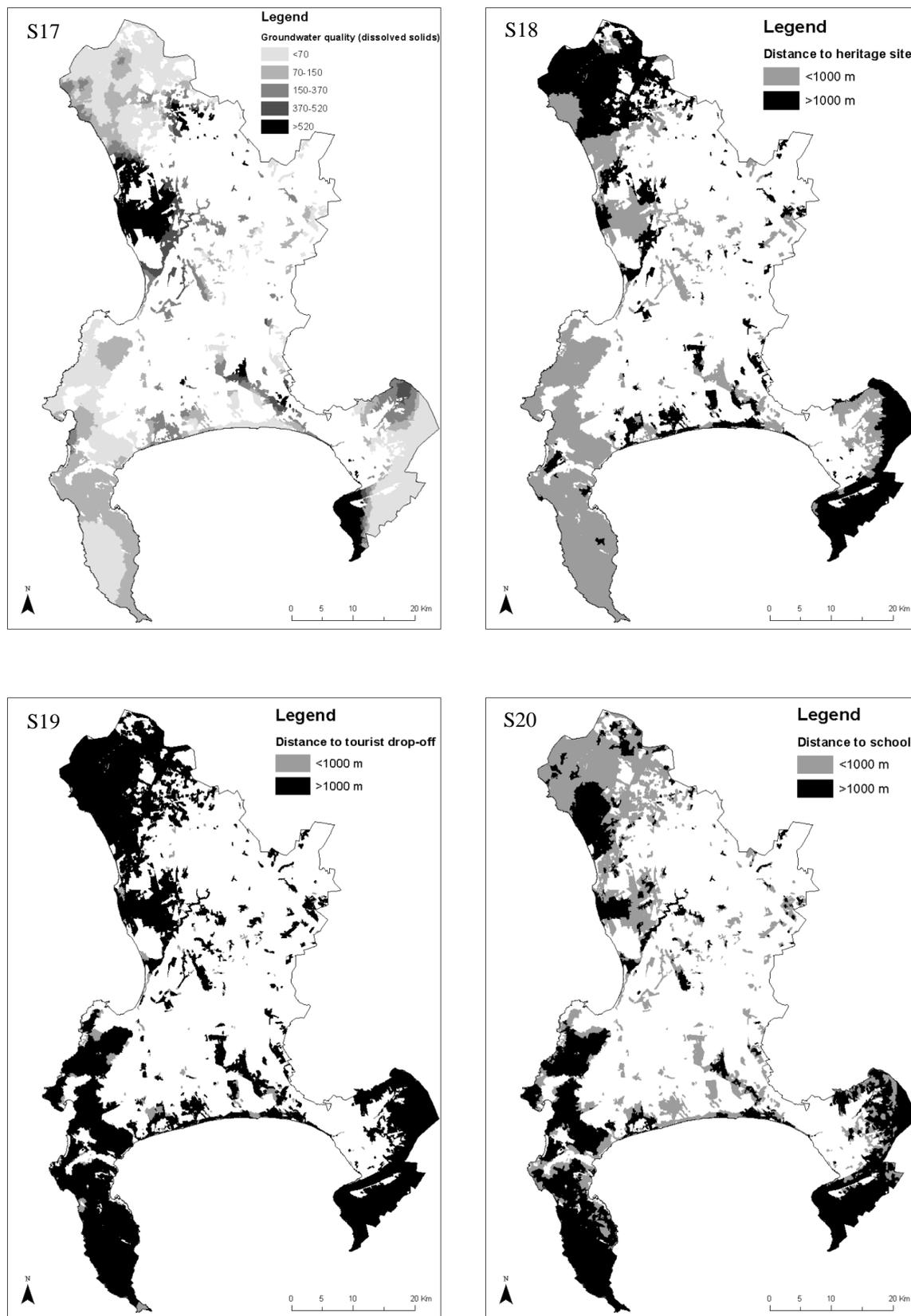


Figure S17-S20 S17) Groundwater quality, using the amount of dissolved solids in water as a proxy for groundwater quality S18) Natural remnants in close proximity to heritage areas S19) Remnants in proximity to popular tourist drop-off points S20) Natural remnants in close proximity to schools



Appendix 4A

Results from GLM analysis (R-output): S1) Ammonium S2) pH S3) EC S4) Available phosphorus and S5) Litter. The abiotic variables were related to variables of invasion history and management. InvasiveSp- Invasive species, *A. saligna* and *P. radiata* compared to the uninvaded reference site; BurnedUnburned- Burned after initial clearing, where unburned is compared to being burned; VegTypSAF- Vegetation type, Swartland Aluvium Fynbos is compared to Cape Flats Sand Fynbos; NrCycles- where one cycle of invasion (b), two cycles (c) and three cycles (d) are compared to no invasions (a); NrFU- No. of follow-up treatments a site has received; Litter- the biomass of litter in an area; MAP- Mean annual precipitation of an area.

S1. Ammonium

```
glm(formula = Ammonium ~ InvasiveSp + Burned + VegType + NrCycles + NrFU + Litter + MAP,
family = Gamma(link = "identity"))
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|----------|----------|----------|---------|---------|
| -0.56913 | -0.18594 | -0.06051 | 0.13325 | 0.71540 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | t value | Pr(> t) | |
|---------------------|----------|------------|---------|----------|-----|
| (Intercept) | 0.6945 | 2.2486 | 0.309 | 0.759275 | |
| InvasiveSpA.saligna | 4.7160 | 2.2605 | 2.086 | 0.044305 | * |
| InvasiveSpP.radiata | 7.2090 | 2.6220 | 2.749 | 0.009380 | ** |
| BurnedUnburned | 1.1832 | 0.8817 | 1.342 | 0.188264 | |
| VegTypeSAF | -3.1007 | 1.5067 | -2.058 | 0.047111 | * |
| NrCyclesb | 1.8813 | 1.7563 | 1.071 | 0.291419 | |
| NrCyclesc | -0.9011 | 1.5059 | -0.598 | 0.553435 | |
| NrCyclesd | NA | NA | NA | NA | |
| NrFU | -1.3017 | 0.7869 | -1.654 | 0.107001 | |
| Litter | -1.3717 | 0.7329 | -1.872 | 0.069649 | . |
| MAP | -6.3649 | 1.6479 | -3.863 | 0.000464 | *** |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.1150766)

Null deviance: 10.2603 on 44 degrees of freedom

Residual deviance: 3.7807 on 35 degrees of freedom
 AIC: 199.58

Number of Fisher Scoring iterations: 15

```
> coef(globalmodel)
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
      0.6944550      4.7159604      7.2090052      1.1832269      -3.1006760
      NrCyclesb      NrCyclesc      NrCyclesd      NrFU      Litter
      1.8813094      -0.9011187      NA      -1.3017353      -1.3717096
      MAP
      -6.3649449
> coef(globalmodel)
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
      0.6944550      4.7159604      7.2090052      1.1832269      -3.1006760
      NrCyclesb      NrCyclesc      NrCyclesd      NrFU      Litter
      1.8813094      -0.9011187      NA      -1.3017353      -1.3717096
      MAP
      -6.3649449
```

```
> confint(globalmodel)
              2.5 %      97.5 %
(Intercept) -3.67367774  5.3754985
InvasiveSpA.saligna  0.01878131  9.4722274
InvasiveSpP.radiata  2.05627044 12.4259681
BurnedUnburned     -0.67420425  3.0566437
VegTypeSAF         -6.13122023  0.0915479
NrCyclesb          -2.29203609  5.7723646
NrCyclesc          -4.48722825  2.0763335
NrCyclesd           NA          NA
NrFU               -3.41791122  0.6201628
Litter             -2.94447824  0.1338633
MAP               -9.52757739 -3.3443977
```

S2. pH

```
glm(formula = pH ~ InvasiveSp + Burned + VegType + NrCycles + NrFU + Litter + MAP)
```

```
Deviance Residuals:
      Min       1Q   Median       3Q      Max
```

-0.48857 -0.15826 0.01849 0.14026 0.99446

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | t value | Pr(> t) | |
|---------------------|----------|------------|---------|----------|-----|
| (Intercept) | 3.99128 | 0.33751 | 11.826 | 8.85e-14 | *** |
| InvasiveSpA.saligna | -0.70269 | 0.35676 | -1.970 | 0.056834 | . |
| InvasiveSpP.radiata | 0.24335 | 0.40087 | 0.607 | 0.547738 | |
| BurnedUnburned | 0.09328 | 0.13010 | 0.717 | 0.478152 | |
| VegTypeSAF | -0.98208 | 0.25303 | -3.881 | 0.000439 | *** |
| NrCyclesb | 1.40093 | 0.27871 | 5.026 | 1.48e-05 | *** |
| NrCyclesc | 1.27204 | 0.27296 | 4.660 | 4.46e-05 | *** |
| NrCyclesd | NA | NA | NA | NA | |
| NrFU | -0.06945 | 0.12739 | -0.545 | 0.589069 | |
| Litter | 0.02213 | 0.12002 | 0.184 | 0.854809 | |
| MAP | -0.73551 | 0.26004 | -2.828 | 0.007689 | ** |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.1077468)

Null deviance: 16.3237 on 44 degrees of freedom
 Residual deviance: 3.7711 on 35 degrees of freedom
 AIC: 38.137

> coef(globalmodel)

| (Intercept) | InvasiveSpA.saligna | InvasiveSpP.radiata | BurnedUnburned | VegTypeSAF |
|-------------|---------------------|---------------------|----------------|-------------|
| 3.99128120 | -0.70269421 | 0.24334587 | 0.09327741 | -0.98207971 |
| NrCyclesb | NrCyclesc | NrCyclesd | NrFU | Litter |
| 1.40092795 | 1.27203572 | NA | -0.06945330 | 0.02212569 |
| MAP | | | | |
| -0.73550866 | | | | |

> confint(globalmodel)

| | 2.5 % | 97.5 % |
|---------------------|------------|--------------|
| (Intercept) | 3.3297748 | 4.652787556 |
| InvasiveSpA.saligna | -1.4019351 | -0.003453311 |
| InvasiveSpP.radiata | -0.5423418 | 1.029033542 |
| BurnedUnburned | -0.1617140 | 0.348268778 |
| VegTypeSAF | -1.4780025 | -0.486156903 |
| NrCyclesb | 0.8546600 | 1.947195873 |
| NrCyclesc | 0.7370354 | 1.807036069 |

```

NrCyclesd           NA           NA
NrFU                -0.3191306  0.180223979
Litter              -0.2131187  0.257370128
MAP                 -1.2451764 -0.225840942

```

S3. EC

```

glm(formula = EC ~ InvasiveSp + Burned + VegType + NrCycles + NrFU + Litter + MAP,
family = Gamma(link = "identity"))

```

Deviance Residuals:

```

      Min       1Q   Median       3Q      Max
-0.49276 -0.10285 -0.00835  0.07150  0.57269

```

Coefficients: (1 not defined because of singularities)

```

              Estimate Std. Error t value Pr(>|t|)
(Intercept)    41.677      5.192    8.028 1.9e-09 ***
InvasiveSpA.saligna  -6.746      6.349   -1.063 0.295256
InvasiveSpP.radiata -21.616      6.603   -3.273 0.002396 **
BurnedUnburned    -2.304      1.675   -1.376 0.177686
VegTypeSAF        13.420      4.669    2.874 0.006844 **
NrCyclesb         -5.292      4.930   -1.073 0.290475
NrCyclesc         -4.384      5.212   -0.841 0.405963
NrCyclesd           NA           NA       NA       NA
NrFU              5.348      2.304    2.321 0.026226 *
Litter            2.603      1.746    1.490 0.145105
MAP               16.314      4.362    3.740 0.000658 ***

```

```

---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

(Dispersion parameter for Gamma family taken to be 0.04254575)

```

Null deviance: 5.2579 on 44 degrees of freedom
Residual deviance: 1.4298 on 35 degrees of freedom
AIC: 282.94

```

Number of Fisher Scoring iterations: 7

```

> coef(globalmodel)

```

```

(Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
  41.676589      -6.746327      -21.615783      -2.304133      13.419750
NrCyclesb      NrCyclesc      NrCyclesd      NrFU      Litter
 -5.291628      -4.384455      NA      5.348459      2.602528
MAP
16.313670
> confint(globalmodel)
              2.5 %      97.5 %
(Intercept)      31.6241914  52.441327
InvasiveSpA.saligna -19.5001459  6.109868
InvasiveSpP.radiata -35.0515279 -8.686994
BurnedUnburned      -5.6331663  1.036266
VegTypeSAF          4.8926707  23.608493
NrCyclesb          -15.8747624  3.978477
NrCyclesc          -15.4103420  5.833056
NrCyclesd          NA          NA
NrFU                1.1062655  9.908883
Litter             -0.9522874  6.416908
MAP                7.7014274  25.266860

```

S4. Available phosphorus

```
glm(formula = Plog10 ~ InvasiveSp + Burned + VegType + NrCycles + NrFU + Litter + MAP)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|----------|----------|----------|---------|---------|
| -0.29426 | -0.08020 | -0.02297 | 0.07060 | 0.35761 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | t value | Pr(> t) |
|---------------------|----------|------------|---------|------------|
| (Intercept) | 0.14246 | 0.18520 | 0.769 | 0.44690 |
| InvasiveSpA.saligna | -0.11187 | 0.19576 | -0.571 | 0.57135 |
| InvasiveSpP.radiata | 0.39606 | 0.21996 | 1.801 | 0.08039 . |
| BurnedUnburned | 0.21343 | 0.07139 | 2.990 | 0.00508 ** |
| VegTypeSAF | -0.26559 | 0.13884 | -1.913 | 0.06397 . |
| NrCyclesb | 0.49523 | 0.15293 | 3.238 | 0.00263 ** |
| NrCyclesc | 0.43598 | 0.14978 | 2.911 | 0.00623 ** |
| NrCyclesd | NA | NA | NA | NA |
| NrFU | 0.03717 | 0.06990 | 0.532 | 0.59827 |

```

Litter          -0.03532    0.06586   -0.536    0.59514
MAP             -0.16692    0.14269   -1.170    0.24997
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

(Dispersion parameter for gaussian family taken to be 0.03244137)

```

Null deviance: 1.9803 on 44 degrees of freedom
Residual deviance: 1.1354 on 35 degrees of freedom
AIC: -15.879

```

```

> coef(globalmodel)
(Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
-0.77740696 -0.48919312          0.50628498          0.34611839      -0.38793551
  NrCyclesb      NrCyclesc      NrCyclesd      NrFU      Litter
  0.89716139      1.05913953          NA          0.09943654      -0.09947430
      MAP
-0.13376540

```

```

> confint(globalmodel)
                2.5 %    97.5 %
(Intercept)    -1.666310391  0.1114965
InvasiveSpA.saligna -1.428802585  0.4504163
InvasiveSpP.radiata -0.549487902  1.5620579
BurnedUnburned    0.003472091  0.6887647
VegTypeSAF        -1.054334975  0.2784639
NrCyclesb         0.163110351  1.6312124
NrCyclesc         0.340229357  1.7780497
NrCyclesd         NA          NA
NrFU              -0.236068907  0.4349420
Litter           -0.415585532  0.2166369
MAP              -0.818634687  0.5511039

```

S5. Litter

```
glm(formula = Litter ~ InvasiveSp + Burned + VegType + NrCycles + NrFU, family = Gamma(link = "identity"))
```

```

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.63065 -0.48740 -0.06192  0.23247  0.88346

```

```

Coefficients: (1 not defined because of singularities)
              Estimate Std. Error t value Pr(>|t|)
(Intercept)   165.032    63.504   2.599  0.0134 *
InvasiveSpA.saligna 212.997    97.663   2.181  0.0356 *
InvasiveSpP.radiata  6.256    62.066   0.101  0.9203
BurnedUnburned   21.985    30.284   0.726  0.4724
VegTypeSAF      51.979    78.140   0.665  0.5100
NrCyclesb      -134.099    80.394  -1.668  0.1038
NrCyclesc      -198.966    75.543  -2.634  0.0123 *
NrCyclesd              NA         NA     NA     NA
NrFU           60.014    24.733   2.426  0.0202 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

(Dispersion parameter for Gamma family taken to be 0.2697923)

```

Null deviance: 18.264 on 44 degrees of freedom
Residual deviance: 11.644 on 37 degrees of freedom
AIC: 532.49

```

```

> coef(globalmodel)
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
      165.032288      212.996864          6.256444          21.984562          51.979111
      NrCyclesb      NrCyclesc      NrCyclesd
      -134.099309      -198.965536          NA
      NrFU
      60.014417

```

```

> confint(globalmodel)
              2.5 %      97.5 %
(Intercept)  50.154270 347.043854
InvasiveSpA.saligna  5.217773 458.007688
InvasiveSpP.radiata -172.476780 121.781366
BurnedUnburned     -55.425688  99.893426
VegTypeSAF        -81.321342 282.497142
NrCyclesb         -369.289205   9.659144
NrCyclesc        -425.466011 -82.233252
NrCyclesd              NA         NA
NrFU              15.143520 124.068868

```

Results from GLM analysis (R-output): S6) Ericoid shrub richness S7) Restioid richness S8) Indigenous perennial grass richness S9) Non-ericoid richness S10) Indigenous perennial species richness S11) Indigenous cover and S12) Alien Cover. The biotic variables were related to variables of invasion history and management (Management model). InvasiveSp- Invasive species, *A. saligna* and *P. radiata* compared to the uninvaded reference site; BurnedUnburned– Burned after initial clearing, where unburned is compared to being burned; VegTypSAF- Vegetation type, Swartland Aluvium Fynbos is compared to Cape Flats Sand Fynbos; NrCycles- where one cycle of invasion (b), two cycles (c) and three cycles (d) are compared to no invasions (a); NrFU- No. of follow-up treatments a site has received; Litter- the biomass of litter in an area; MAP- Mean annual precipitation of an area. The biotic variables were secondly related to soil variables: Litter- litter biomass; NH4N- soil ammonium; EC- soil electrical conductivity; pH- soil pH level; Pbray- soil available phosphorus.

S6. Ericoid shrub richness

Management model

```
glm(formula = Nr.Ericoid.Shrubs ~ Invasive.Sp + Burned + Vegetation_type + NrCycles + NrFU, family = poisson)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|----------|----------|----------|---------|---------|
| -1.96162 | -0.85375 | -0.04247 | 0.59704 | 1.86692 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | z value | Pr(> z) | |
|-----------------------|----------|------------|---------|----------|-----|
| (Intercept) | 2.5155 | 0.2746 | 9.161 | < 2e-16 | *** |
| Invasive.SpA. saligna | -2.8488 | 0.6870 | -4.147 | 3.37e-05 | *** |
| Invasive.SpP. radiata | -0.8295 | 0.2538 | -3.268 | 0.00108 | ** |
| BurnedUnburned | -0.3531 | 0.1924 | -1.835 | 0.06646 | . |
| Vegetation_typeSAF | -1.3300 | 0.5994 | -2.219 | 0.02650 | * |
| NrCyclesb | 0.9870 | 0.6342 | 1.556 | 0.11964 | |
| NrCyclesc | 1.0789 | 0.6500 | 1.660 | 0.09694 | . |
| NrCyclesd | NA | NA | NA | NA | |
| NrFU | 0.1828 | 0.1835 | 0.997 | 0.31900 | |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

Null deviance: 92.776 on 44 degrees of freedom
Residual deviance: 45.581 on 37 degrees of freedom
AIC: 183.06

Number of Fisher Scoring iterations: 5

```
> coef(EsRichnessManagment)
      (Intercept) Invasive.SpA. saligna Invasive.SpP. radiata      BurnedUnburned
      2.5155133      -2.8488157      -0.8294825      -0.3530869
Vegetation_typeSAF      NrCyclesb      NrCyclesc      NrCyclesd
      -1.3300018      0.9870091      1.0788991      NA
      NrFU
      0.1828370
> confint(EsRichnessManagment)
      (Intercept)      2.5 %      97.5 %
Invasive.SpA. saligna -4.39176528 -1.61886649
Invasive.SpP. radiata -1.31946353 -0.32007140
BurnedUnburned      -0.73235252  0.02402175
Vegetation_typeSAF -2.75040090 -0.31633671
NrCyclesb      -0.11729906  2.45433167
NrCyclesc      -0.07443618  2.56516872
NrCyclesd      NA      NA
NrFU      -0.17637265  0.54614990
```

Soil nutrients

```
glm(formula = Nr.Ericoid.Shrubs ~ Litter + NH4N + EC + pH + Pbray,
     family = quasipoisson)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|---------|---------|---------|--------|--------|
| -2.5412 | -1.1622 | -0.1189 | 0.5598 | 2.9985 |

Coefficients:

| | Estimate | Std. Error | t value | Pr(> t) |
|-------------|------------|------------|---------|--------------|
| (Intercept) | 1.182e+00 | 1.217e-01 | 9.710 | 5.86e-12 *** |
| Litter | 1.505e-02 | 2.425e-01 | 0.062 | 0.951 |
| NH4N | -6.919e-01 | 4.389e-01 | -1.577 | 0.123 |
| EC | -7.451e-05 | 3.420e-01 | 0.000 | 1.000 |
| pH | 2.144e-01 | 2.861e-01 | 0.749 | 0.458 |
| Pbray | -1.208e-01 | 2.919e-01 | -0.414 | 0.681 |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasipoisson family taken to be 2.051015)

Null deviance: 92.776 on 44 degrees of freedom

Residual deviance: 82.173 on 39 degrees of freedom

AIC: NA

Number of Fisher Scoring iterations: 6

```
> coef(EsRichnessSoilNutrients)
(Intercept)      Litter      NH4N      EC      pH      Pbray
1.181777e+00 1.504726e-02 -6.918931e-01 -7.451055e-05 2.144005e-01 -1.207791e-01
> confint(EsRichnessSoilNutrients)
                2.5 %    97.5 %
(Intercept) 0.9314300 1.4100565
Litter      -0.4748065 0.4772471
NH4N        -1.6111491 0.1214891
EC          -0.6993351 0.6459288
pH          -0.3435269 0.7813192
Pbray       -0.7362131 0.4132361
```

S7. Restioid richness**Management**

Call:

```
glm(formula = Nr_IPR ~ InvasiveSp + Burned + VegType + NrCycles +
     NrFU + SoilDepth, family = poisson, data = nr)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|---------|---------|---------|--------|--------|
| -1.6055 | -0.7663 | -0.2735 | 0.5208 | 1.7969 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | z value | Pr(> z) |
|---------------------|----------|------------|---------|----------|
| (Intercept) | 0.5780 | 0.9057 | 0.638 | 0.5234 |
| InvasiveSpA.saligna | -0.1004 | 1.2268 | -0.082 | 0.9348 |

```
InvasiveSpP.radiata -0.8579    0.6741   -1.273    0.2031
BurnedUnburned     -0.8239    0.5055   -1.630    0.1031
VegTypeSAF         0.8579    0.6741    1.273    0.2031
NrCyclesb          -1.9309    0.8928   -2.163    0.0306 *
NrCyclesc          -1.6292    1.1917   -1.367    0.1716
NrCyclesd           NA          NA        NA        NA
NrFU                0.4809    0.4920    0.977    0.3283
SoilDepth           2.6586    2.6062    1.020    0.3077
```

```
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

(Dispersion parameter for poisson family taken to be 1)

```
Null deviance: 45.267  on 44  degrees of freedom
Residual deviance: 28.102  on 36  degrees of freedom
AIC: 91.548
```

Number of Fisher Scoring iterations: 6

```
> coef(globalmodelnrRmanagement)
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
      1.23711174   -0.08102454      -0.97988860      -0.94097020      0.97988860
      NrCyclesb   NrCyclesc      NrCyclesd      NrFU
      -2.06278766   -2.14381220      NA      0.52570166
```

```
> confint(globalmodelnrRmanagement)
              2.5 %      97.5 %
(Intercept) -0.2481078  2.61166202
InvasiveSpA.saligna -2.5420877  2.43266035
InvasiveSpP.radiata -2.2970047  0.42765066
BurnedUnburned     -2.0086607  0.02694079
VegTypeSAF         -0.4276507  2.29700473
NrCyclesb          -3.8858909 -0.31552385
NrCyclesc          -4.8910770 -0.01888269
NrCyclesd           NA          NA
NrFU               -0.3985568  1.55830938
```

Soil nutrients

```
glm(formula = Nr_IPR ~ Litter + pH + Pbray + NH4N + EC, family = poisson)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|---------|---------|---------|--------|--------|
| -1.6184 | -0.9545 | -0.2621 | 0.3777 | 1.7395 |

Coefficients:

| | Estimate | Std. Error | z value | Pr(> z) |
|-------------|----------|------------|---------|------------|
| (Intercept) | -0.88337 | 0.29692 | -2.975 | 0.00293 ** |
| Litter | 0.19823 | 0.38451 | 0.516 | 0.60618 |
| pH | -0.37615 | 0.45079 | -0.834 | 0.40405 |
| Pbray | -1.46517 | 0.88214 | -1.661 | 0.09673 . |
| NH4N | -0.89717 | 1.06519 | -0.842 | 0.39964 |
| EC | -0.04776 | 0.68012 | -0.070 | 0.94401 |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

Null deviance: 45.267 on 44 degrees of freedom
 Residual deviance: 32.495 on 39 degrees of freedom
 AIC: 89.942

Number of Fisher Scoring iterations: 5

```
> coef(globalmodelnrSoilNutrients)
(Intercept)      Litter          pH          Pbray          NH4N          EC
-0.88337133  0.19822801 -0.37614543 -1.46517042 -0.89716860 -0.04776463
> confint(globalmodelnrSoilNutrients)
                2.5 %          97.5 %
(Intercept) -1.5851757 -0.382372732
Litter      -0.5912132  0.926328538
pH          -1.2845880  0.501944613
Pbray      -3.4517418  0.003654487
NH4N       -3.4940998  0.815543890
EC         -1.4228194  1.238080284
```

S8. Indigenous perennial grass richness**Management**

```
glm(formula = Nr_IPGr ~ InvasiveSp + Burned + VegType + NrFU + NrCycles, family = poisson)
```

```
Deviance Residuals:
```

```
      Min       1Q   Median       3Q      Max
-1.53305 -0.60709 -0.08429  0.55783  1.29015
```

```
Coefficients: (1 not defined because of singularities)
```

```
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    1.54255    0.37414   4.123 3.74e-05 ***
InvasiveSpA.saligna 0.26881    0.51259   0.524  0.6000
InvasiveSpP.radiata -0.45181    0.37199  -1.215  0.2245
BurnedUnburned  -0.33867    0.20022  -1.692  0.0907 .
VegTypeSAF      0.71417    0.33955   2.103  0.0354 *
NrFU            -0.00611    0.17817  -0.034  0.9726
NrCyclesb      -0.46728    0.37728  -1.239  0.2155
NrCyclesc      -0.59109    0.41936  -1.410  0.1587
NrCyclesd              NA           NA      NA      NA
```

```
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
(Dispersion parameter for poisson family taken to be 1)
```

```
Null deviance: 29.810 on 44 degrees of freedom
Residual deviance: 22.942 on 37 degrees of freedom
AIC: 168.19
```

```
Number of Fisher Scoring iterations: 4
```

```
> coef(globalmodelngmanagement)
```

```
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
      1.542547864      0.268811188      -0.451810172      -0.338673380      0.714174437
      NrFU      NrCyclesb      NrCyclesc      NrCyclesd
      -0.006109945      -0.467275741      -0.591088846      NA
```

```
> confint(globalmodelngmanagement)
```

```
              2.5 %      97.5 %
(Intercept)    0.75652217  2.23630188
InvasiveSpA.saligna -0.72913969  1.29415523
InvasiveSpP.radiata -1.14667408  0.32723129
BurnedUnburned  -0.73323459  0.05393524
VegTypeSAF      0.01567811  1.35779847
```

```

NrFU                -0.35807490 0.34365580
NrCyclesb          -1.19034596 0.29810643
NrCyclesc          -1.42203826 0.23576835
NrCyclesd                NA          NA

```

Soil nutrients

```
glm(formula = Nr_IPGr ~ Litter + Pbray + NH4N + pH + EC, family = poisson)
```

Deviance Residuals:

```

      Min       1Q   Median       3Q      Max
-1.2518 -0.5524 -0.1182  0.5453  2.0017

```

Coefficients:

```

              Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.04178    0.09091  11.460 <2e-16 ***
Litter       -0.04595    0.18306  -0.251  0.8018
Pbray        -0.31216    0.23439  -1.332  0.1829
NH4N         -0.55863    0.32218  -1.734  0.0829 .
pH           0.25887    0.21285   1.216  0.2239
EC           0.10151    0.25729   0.395  0.6932

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

```

Null deviance: 29.810 on 44 degrees of freedom
Residual deviance: 20.101 on 39 degrees of freedom
AIC: 161.35

```

Number of Fisher Scoring iterations: 4

> coef(globalmodelngsoilnutrients)

```

(Intercept)      Litter      Pbray      NH4N      pH      EC
1.04178118 -0.04595462 -0.31216356 -0.55862787 0.25887463 0.10150861

```

> confint(globalmodelngsoilnutrients)

```

              2.5 %      97.5 %
(Intercept)  0.8573303 1.21424082
Litter       -0.4129643 0.30522186

```

```
Pbray      -0.7980725 0.12244858
NH4N      -1.2203392 0.04743955
pH        -0.1564849 0.67924839
EC        -0.4174851 0.59307548
```

S9. Non-ericoid shrub richness

Managment

```
glm(formula = Nr_IPNes ~ InvasiveSp + Burned + VegType + NrFU +
     NrCycles, family = poisson)
```

Deviance Residuals:

```
   Min       1Q   Median       3Q      Max
-2.0543 -0.6001 -0.3022  0.4310  1.7594
```

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | z value | Pr(> z) |
|---------------------|----------|------------|---------|----------|
| (Intercept) | 0.69671 | 0.56891 | 1.225 | 0.221 |
| InvasiveSpA.saligna | -0.77390 | 0.82918 | -0.933 | 0.351 |
| InvasiveSpP.radiata | 0.25126 | 0.55209 | 0.455 | 0.649 |
| BurnedUnburned | -0.40925 | 0.27166 | -1.506 | 0.132 |
| VegTypeSAF | -0.25126 | 0.55209 | -0.455 | 0.649 |
| NrFU | -0.01377 | 0.27075 | -0.051 | 0.959 |
| NrCyclesb | -0.32390 | 0.64089 | -0.505 | 0.613 |
| NrCyclesc | 0.46233 | 0.62642 | 0.738 | 0.460 |
| NrCyclesd | NA | NA | NA | NA |

(Dispersion parameter for poisson family taken to be 1)

```
Null deviance: 48.734 on 44 degrees of freedom
Residual deviance: 39.532 on 37 degrees of freedom
AIC: 144.92
```

Number of Fisher Scoring iterations: 5

```
> coef(globalmodelnesManagment)
(Intercept) InvasiveSpA.saligna InvasiveSpP.radiata BurnedUnburned VegTypeSAF
0.6967098      -0.7738952      0.2512623      -0.4092494      -0.2512623
```

```

                NrFU                NrCyclesb                NrCyclesc                NrCyclesd
-0.0137747      -0.3239016      0.4623295                NA
> confint(globalmodelnesManagment)
                2.5 %      97.5 %
(Intercept)    -0.5718950  1.7122500
InvasiveSpA.saligna -2.4347280  0.8891764
InvasiveSpP.radiata -0.7296433  1.4929220
BurnedUnburned   -0.9500918  0.1214399
VegTypesSAF      -1.4929220  0.7296433
NrFU              -0.5546015  0.5170029
NrCyclesb        -1.5266414  1.0465410
NrCyclesc        -0.7203252  1.8049604
NrCyclesd                NA                NA

```

Soil Nutrients

```
glm(formula = Nr_IPNes ~ Litter + Pbray + NH4N + EC + pH, family = poisson)
```

Deviance Residuals:

```

    Min      1Q   Median      3Q      Max
-1.8785 -0.6862 -0.1396  0.6255  1.9452

```

Coefficients:

```

            Estimate Std. Error z value Pr(>|z|)
(Intercept)  0.386945  0.126773  3.052  0.00227 **
Litter       -0.009093  0.264575 -0.034  0.97258
Pbray        0.312050  0.274572  1.136  0.25575
NH4N        -0.722125  0.416284 -1.735  0.08280 .
EC          -0.952746  0.417764 -2.281  0.02257 *
pH          -0.277131  0.318758 -0.869  0.38462
---

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

```

Null deviance: 48.734 on 44 degrees of freedom
Residual deviance: 41.945 on 39 degrees of freedom
AIC: 143.33

```

Number of Fisher Scoring iterations: 5

```
> coef(globalmodelnesSoilNutrients)
(Intercept)      Litter      Pbray      NH4N      EC      pH
0.386944816 -0.009092513 0.312050226 -0.722125405 -0.952745873 -0.277131232
> confint(globalmodelnesSoilNutrients)
              2.5 %      97.5 %
(Intercept) 0.1261298 0.62445239
Litter      -0.5444980 0.49396593
Pbray       -0.2628938 0.82162082
NH4N        -1.5863571 0.05438293
EC          -1.8039292 -0.16829820
pH          -0.9101744 0.34469395
```

S10. Indigenous perennial species richness

Management

```
glm(formula = NrIPS ~ InvasiveSp + Burned + VegType + NrCycles + NrFU, family = poisson)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|----------|----------|----------|---------|---------|
| -2.79223 | -0.82844 | -0.09951 | 0.48363 | 2.73120 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | z value | Pr(> z) | |
|---------------------|-----------|------------|---------|----------|-----|
| (Intercept) | 3.082804 | 0.165018 | 18.682 | < 2e-16 | *** |
| InvasiveSpA.saligna | -0.717309 | 0.262798 | -2.730 | 0.00634 | ** |
| InvasiveSpP.radiata | 0.009205 | 0.157870 | 0.058 | 0.95351 | |
| BurnedUnburned | -0.225347 | 0.089609 | -2.515 | 0.01191 | * |
| VegTypeSAF | -0.434088 | 0.187361 | -2.317 | 0.02051 | * |
| NrCyclesb | 0.074520 | 0.210835 | 0.353 | 0.72375 | |
| NrCyclesc | -0.032163 | 0.225197 | -0.143 | 0.88643 | |
| NrCyclesd | NA | NA | NA | NA | |
| NrFU | 0.299877 | 0.087271 | 3.436 | 0.00059 | *** |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

Null deviance: 130.302 on 44 degrees of freedom
 Residual deviance: 60.891 on 37 degrees of freedom
 AIC: 274.28

Number of Fisher Scoring iterations: 4

```
> coef(globalmodelipManagement)
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata      BurnedUnburned      VegTypeSAF
      3.08280356      -0.71730923      0.00920474      -0.22534659      -0.43408793
      NrCyclesb      NrCyclesc      NrCyclesd      NA      NrFU
      0.07451963      -0.03216259      NA      0.29987664

> confint(globalmodelipManagement)
              2.5 %      97.5 %
(Intercept)      2.7500701  3.3980093
InvasiveSpA.saligna -1.2377751 -0.2054192
InvasiveSpP.radiata -0.2919406  0.3281804
BurnedUnburned      -0.4009515 -0.0494790
VegTypeSAF          -0.8178583 -0.0811094
NrCyclesb           -0.3282787  0.5003988
NrCyclesc           -0.4678510  0.4176763
NrCyclesd           NA          NA
NrFU                0.1295556  0.4719800
```

Soil nutrients

```
glm(formula = NrIPS ~ Litter + Pbray + NH4N + EC + pH, family = poisson)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|---------|---------|--------|--------|--------|
| -2.8521 | -0.9813 | 0.1321 | 0.7980 | 2.4500 |

Coefficients:

| | Estimate | Std. Error | z value | Pr(> z) |
|-------------|-----------|------------|---------|-------------|
| (Intercept) | 2.605599 | 0.042291 | 61.611 | < 2e-16 *** |
| Litter | 0.013477 | 0.083480 | 0.161 | 0.872 |
| Pbray | -0.003354 | 0.096562 | -0.035 | 0.972 |
| NH4N | -0.751484 | 0.156631 | -4.798 | 1.6e-06 *** |
| EC | -0.111108 | 0.120714 | -0.920 | 0.357 |

```

pH          -0.127061  0.097347  -1.305    0.192
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

(Dispersion parameter for poisson family taken to be 1)

```

Null deviance: 130.302 on 44 degrees of freedom
Residual deviance: 78.153 on 39 degrees of freedom
AIC: 287.54

```

Number of Fisher Scoring iterations: 4

```

> coef(globalmodelipSoilNutrients)
(Intercept)      Litter      Pbray      NH4N      EC      pH
2.605599286  0.013477038 -0.003354095 -0.751483835 -0.111108120 -0.127060811
> confint(globalmodelipSoilNutrients)
                2.5 %      97.5 %
(Intercept)  2.5212279  2.68709497
Litter       -0.1519721  0.17533549
Pbray        -0.1972091  0.18155994
NH4N         -1.0664717 -0.45185118
EC           -0.3512870  0.12201820
pH           -0.3179210  0.06382808

```

S11. Indigenous cover

Management

```
glm(formula = IndigenousCover ~ InvasiveSp + Burned + Vegetation_type + NrCycles + NrFU)
```

```

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.27302 -0.10216 -0.01508  0.08540  0.36895

```

```

Coefficients: (1 not defined because of singularities)
              Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.65134    0.10875  15.185 < 2e-16 ***
InvasiveSpA.saligna -0.52962    0.15477  -3.422  0.001532 **
InvasiveSpP.radiata -0.39839    0.10616  -3.753  0.000599 ***

```

```

BurnedUnburned    -0.18239    0.05450   -3.347  0.001887 **
Vegetation_typeSAF  0.28665    0.10616    2.700  0.010388 *
NrCyclesb         -0.27357    0.11966   -2.286  0.028062 *
NrCyclesc         -0.03915    0.12425   -0.315  0.754460
NrCyclesd         NA          NA         NA      NA
NrFU              0.06118    0.05368    1.140  0.261702

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.02659802)

Null deviance: 2.87258 on 44 degrees of freedom
Residual deviance: 0.98413 on 37 degrees of freedom
AIC: -26.315

Number of Fisher Scoring iterations: 2

```

> coef(globalmodelicManagement)
      (Intercept) InvasiveSpA.saligna InvasiveSpP.radiata  BurnedUnburned  Vegetation_typeSAF
      1.65134099   -0.52962108         -0.39838969         -0.18238630         0.28664515
      NrCyclesb   NrCyclesc         NrCyclesd         NrFU
      -0.27356568   -0.03915066             NA         0.06118481

```

```

> confint(globalmodelicManagement)
                2.5 %      97.5 %
(Intercept)    1.43819177  1.86449021
InvasiveSpA.saligna -0.83297075 -0.22627142
InvasiveSpP.radiata -0.60645179 -0.19032758
BurnedUnburned   -0.28919987 -0.07557274
Vegetation_typeSAF  0.07858305  0.49470726
NrCyclesb        -0.50809079 -0.03904056
NrCyclesc        -0.28267680  0.20437548
NrCyclesd         NA         NA
NrFU             -0.04402836  0.16639798

```

Soil nutrients

glm(formula = IndigenousCover ~ Pbray + NH4N + Litter + pH + EC)

Deviance Residuals:

```

      Min       1Q   Median       3Q      Max
-0.60061 -0.14208  0.00342  0.17725  0.45796

```

Coefficients:

```

      Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.13501    0.03901  29.098 <2e-16 ***
Pbray        0.01790    0.09520   0.188  0.852
NH4N       -0.12671    0.12168  -1.041  0.304
Litter     -0.04035    0.08455  -0.477  0.636
pH         -0.06694    0.09683  -0.691  0.493
EC         -0.06747    0.11453  -0.589  0.559
---

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.06846864)

```

Null deviance: 2.8726 on 44 degrees of freedom
Residual deviance: 2.6703 on 39 degrees of freedom
AIC: 14.603

```

Number of Fisher Scoring iterations: 2

```

> coef(globalmodelicSoilNutrients)
(Intercept)      Pbray      NH4N      Litter      pH      EC
 1.13501039  0.01789824 -0.12670846 -0.04035087 -0.06694476 -0.06747385
> confint(globalmodelicSoilNutrients)
      2.5 %      97.5 %
(Intercept)  1.0585586  1.2114622
Pbray       -0.1686996  0.2044961
NH4N       -0.3651967  0.1117798
Litter     -0.2060564  0.1253547
pH         -0.2567297  0.1228401
EC         -0.2919543  0.1570066

```

S12 Alien Cover

Management

```
glm(formula = AlienCover ~ InvasiveSp + Burned + VegType + NrCycles + NrFU)
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|----------|----------|---------|---------|---------|
| -0.36229 | -0.08262 | 0.00733 | 0.10555 | 0.27184 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | t value | Pr(> t) |
|---------------------|----------|------------|---------|--------------|
| (Intercept) | -0.08573 | 0.10843 | -0.791 | 0.434227 |
| InvasiveSpA.saligna | 0.52681 | 0.15432 | 3.414 | 0.001567 ** |
| InvasiveSpP.radiata | 0.40368 | 0.10585 | 3.814 | 0.000502 *** |
| BurnedUnburned | 0.18525 | 0.05434 | 3.409 | 0.001587 ** |
| VegTypeSAF | -0.29478 | 0.10585 | -2.785 | 0.008389 ** |
| NrCyclesb | 0.28161 | 0.11931 | 2.360 | 0.023642 * |
| NrCyclesc | 0.04546 | 0.12389 | 0.367 | 0.715779 |
| NrCyclesd | NA | NA | NA | NA |
| NrFU | -0.06102 | 0.05352 | -1.140 | 0.261605 |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.02644319)

Null deviance: 2.8915 on 44 degrees of freedom
 Residual deviance: 0.9784 on 37 degrees of freedom
 AIC: -26.578

Number of Fisher Scoring iterations: 2

> confint(globalmodelacManagement)

| | 2.5 % | 97.5 % |
|---------------------|-------------|-------------|
| (Intercept) | -0.29825426 | 0.12680158 |
| InvasiveSpA.saligna | 0.22434692 | 0.82927780 |
| InvasiveSpP.radiata | 0.19622691 | 0.61113817 |
| BurnedUnburned | 0.07875066 | 0.29175510 |
| VegTypeSAF | -0.50223687 | -0.08732561 |
| NrCyclesb | 0.04776545 | 0.51544846 |
| NrCyclesc | -0.19736091 | 0.28827168 |
| NrCyclesd | NA | NA |
| NrFU | -0.16592560 | 0.04388738 |

> coef(globalmodelacManagement)

| (Intercept) | InvasiveSpA.saligna | InvasiveSpP.radiata | BurnedUnburned | VegTypeSAF |
|-------------|---------------------|---------------------|----------------|------------|
|-------------|---------------------|---------------------|----------------|------------|

| | | | | |
|-------------|------------|------------|-------------|-------------|
| -0.08572634 | 0.52681236 | 0.40368254 | 0.18525288 | -0.29478124 |
| NrCyclesb | NrCyclesc | NrCyclesd | NrFU | |
| 0.28160695 | 0.04545538 | NA | -0.06101911 | |

Soil nutrients

glm(formula = AlienCover ~ Pbray + NH4N + Litter + pH + EC, data = ac)

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|---------|---------|---------|--------|--------|
| -0.4582 | -0.1724 | -0.0098 | 0.1429 | 0.5991 |

Coefficients:

| | Estimate | Std. Error | t value | Pr(> t) |
|-------------|----------|------------|---------|--------------|
| (Intercept) | 0.43610 | 0.03913 | 11.145 | 1.09e-13 *** |
| Pbray | -0.01606 | 0.09551 | -0.168 | 0.867 |
| NH4N | 0.12471 | 0.12207 | 1.022 | 0.313 |
| Litter | 0.04150 | 0.08481 | 0.489 | 0.627 |
| pH | 0.06805 | 0.09714 | 0.701 | 0.488 |
| EC | 0.06469 | 0.11490 | 0.563 | 0.577 |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.06890397)

Null deviance: 2.8915 on 44 degrees of freedom
Residual deviance: 2.6873 on 39 degrees of freedom
AIC: 14.888

Number of Fisher Scoring iterations: 2

> confint(globalmodelac2)

| | 2.5 % | 97.5 % |
|-------------|------------|-----------|
| (Intercept) | 0.3594094 | 0.5127983 |
| Pbray | -0.2032485 | 0.1711318 |
| NH4N | -0.1145380 | 0.3639525 |
| Litter | -0.1247359 | 0.2077271 |
| pH | -0.1223402 | 0.2584343 |
| EC | -0.1604988 | 0.2898872 |

Appendix 4B

Post-hoc test were done on response variables used in GLMs 1) Ammonium 2) pH 3) EC 4) Available phosphorus 5) Litter 6) Ericoid Shrub richness, 7) Restiod richness 8) Indigenous Perennial Grass richness 9) Non-Ericoid Shrub richness 10) Perennial Indigenous Species richness 11) Indigenous Cover 12) Alien Cover and categorical predictor variables i) Site treatment after initial clearing (Burned or Unburned) ii) Vegetation type (Cape Flat Sand Fynbos, CFSF, or Swartland Alluvium Fynbos, SAF) iii) Dominant Invasive species (Uninvaded, *A. saligna*, *P. radiata*) and the iv) Number of cycles of invasion (Uninvaded, One, Two or Three), separated by species (acacia or pine) and v) separated species and vegetation types. Numbers correspond to figure numbers as in **Appendix 4C**. Results give the group sample size (n) means and variances. Pairwise comparisons are indicated, along with appropriate test statistics (t-statistic, degrees of freedom (df) and significance level (p-value).

Ammonium**> i1**

| | n | means | variances |
|----------|----|-------|-----------|
| Burned | 18 | 8.7 | 31.5 |
| Unburned | 27 | 5.3 | 2.4 |

| | t | df | p |
|-----------------|-----|----|-------|
| Burned:Unburned | 2.5 | 19 | 0.021 |

> ii1

| | n | means | variances |
|------|----|-------|-----------|
| CFSF | 33 | 7.2 | 20.4 |
| SAF | 12 | 5.3 | 3.7 |

| | t | df | p |
|----------|-----|----|-------|
| CFSF:SAF | 1.9 | 42 | 0.058 |

> iii1

| | n | means | variances |
|-------------------|----|-------|-----------|
| Reference | 3 | 5.1 | 0.29 |
| <i>A. saligna</i> | 15 | 8.9 | 39.76 |
| <i>P. radiata</i> | 27 | 5.6 | 2.19 |

| | t | df | p |
|---------------------------------------|-----|------|-------|
| Reference: <i>A. saligna</i> | 2.3 | 14.9 | 0.091 |
| Reference: <i>P. radiata</i> | 1.2 | 6.4 | 0.496 |
| <i>A. saligna</i> : <i>P. radiata</i> | 2.0 | 14.9 | 0.153 |

> iv1 acacia

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 6.4 | 0.57 |
| b | 3 | 5.1 | 0.29 |
| c | 12 | 10.1 | 43.22 |

| | t | df | p |
|-----|-----|------|-------|
| a:b | 2.5 | 3.6 | 0.151 |
| a:c | 1.9 | 12.0 | 0.195 |
| b:c | 2.6 | 11.6 | 0.061 |

> iv1 pine

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 6.4 | 0.57 |
| b | 6 | 4.6 | 0.19 |
| c | 3 | 4.2 | 0.13 |
| d | 18 | 5.8 | 2.71 |

| | t | df | p |
|-----|-----|-----|-------|
| a:b | 3.9 | 2.7 | 0.102 |
| a:c | 4.5 | 2.9 | 0.063 |

```

a:d 1.1 6.0 0.720
b:c 1.4 4.9 0.570
b:d 2.8 21.6 0.046
c:d 3.6 16.4 0.012

```

```
> v1
```

| | n | means | variances |
|---------------|----|-------|-----------|
| A.salignaCFSF | 15 | 9.1 | 38.17 |
| P.radiataCFSF | 15 | 6.0 | 2.98 |
| P.radiataSAF | 12 | 4.6 | 0.22 |
| Uninvaded | 3 | 6.4 | 0.57 |

| | t | df | p |
|-----------------------------|------|------|------|
| A.salignaCFSF:P.radiataCFSF | 1.84 | 16.2 | 0.29 |
| A.salignaCFSF:P.radiataSAF | 2.81 | 14.2 | 0.06 |
| A.salignaCFSF:Uninvaded | 1.58 | 15.6 | 0.42 |
| P.radiataCFSF:P.radiataSAF | 3.11 | 16.5 | 0.03 |
| P.radiataCFSF:Uninvaded | 0.68 | 7.2 | 0.90 |
| P.radiataSAF:Uninvaded | 4.09 | 2.4 | 0.11 |

```
pH
```

```
> i2
```

| | n | means | variances |
|----------|----|-------|-----------|
| Burned | 18 | 4.5 | 0.49 |
| Unburned | 27 | 4.3 | 0.30 |

| | t | df | p |
|-----------------|------|----|------|
| Burned:Unburned | 0.83 | 30 | 0.41 |

```
> ii2
```

| | n | means | variances |
|------|----|-------|-----------|
| CFSF | 33 | 4.5 | 0.37 |
| SAF | 12 | 4.2 | 0.36 |

| | t | df | p |
|----------|-----|----|------|
| CFSF:SAF | 1.4 | 20 | 0.18 |

```
> iii2
```

| | n | means | variances |
|------------|----|-------|-----------|
| Reference | 3 | 4.6 | 0.0067 |
| A. saligna | 15 | 4.9 | 0.2300 |
| P. radiata | 27 | 4.1 | 0.2232 |

| | t | df | p |
|-----------------------|-----|----|---------|
| Reference:A. saligna | 2.4 | 16 | 7.0e-02 |
| Reference:P. radiata | 5.3 | 22 | 8.1e-05 |
| A. saligna:P. radiata | 5.6 | 29 | 1.5e-05 |

```
> iv2 acacia
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 4.6 | 0.0067 |
| b | 3 | 4.4 | 0.0408 |
| c | 12 | 5.1 | 0.1924 |

| | t | df | p |
|-----|-----|------|-------|
| a:b | 1.6 | 2.6 | 0.379 |
| a:c | 3.3 | 12.9 | 0.014 |
| b:c | 3.8 | 7.6 | 0.014 |

```
> iv2 pine
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 4.6 | 0.0067 |
| b | 6 | 4.5 | 0.1396 |
| c | 3 | 4.4 | 0.0090 |
| d | 18 | 3.9 | 0.1611 |

| | t | df | p |
|-----|------|-----|---------|
| a:b | 0.63 | 5.9 | 9.2e-01 |

```

a:c 2.44  3.9 2.1e-01
a:d 7.09 17.4 8.9e-06
b:c 0.47  6.1 9.6e-01
b:d 3.62  9.2 2.3e-02
c:d 5.24 15.5 4.7e-04
> v2
      n means variances
A.salignaCFSF 15  4.9  0.2300
P.radiataCFSF 15  4.0  0.1107
P.radiataSAF  12  4.2  0.3592
Uninvaded     3  4.6  0.0067

      t df      p
A.salignaCFSF:P.radiataCFSF 6.3 25 7.2e-06
A.salignaCFSF:P.radiataSAF  3.5 21 1.1e-02
A.salignaCFSF:Uninvaded     2.4 16 1.2e-01
P.radiataCFSF:P.radiataSAF  1.1 16 6.9e-01
P.radiataCFSF:Uninvaded     6.5 14 6.5e-05
P.radiataSAF:Uninvaded     2.4 12 1.4e-01

```

EC

```

> i3
      N means variances
Burned  18  26  84
Unburned 27  26  54

```

```

      t df      p
Burned:Unburned 0.27 31 0.79

```

> ii3

```

      n means variances
CFSF  33  24  56
SAF   12  31  51

```

```

      t df      p
CFSF:SAF 3 21 0.0069

```

> iii3

```

      n means variances
Reference  3  28  0.94
A. saligna 15  23 114.74
P. radiata 27  27  40.41

```

```

      t df      p
Reference:A. saligna 1.53 15 0.30
Reference:P. radiata 0.15 24 0.99
A. saligna:P. radiata 1.37 20 0.38

```

> iv3 acaia

```

      n means variances
a  3  28  0.94
b  3  36 33.87
c 12  20 85.74

```

```

      t df      p
a:b 2.4  2.1 0.228
a:c 2.7 11.9 0.044
b:c 3.7  5.0 0.033

```

> iv3 pine

```

      n means variances
a  3  28  0.94
b  6  32 104.72
c  3  30  3.99
d 18  26 20.67

```

```

      t df      p

```

```

a:b 0.92  5.2 0.80
a:c 1.56  2.9 0.51
a:d 1.59 16.8 0.41
b:c 0.43  5.7 0.97
b:d 1.34  5.7 0.57
c:d 2.49  6.4 0.15

```

```
> v3
```

| | n | means | variances |
|---------------|----|-------|-----------|
| A.salignaCFSF | 15 | 23 | 114.74 |
| P.radiataCFSF | 15 | 24 | 10.51 |
| P.radiataSAF | 12 | 31 | 50.73 |
| Uninvaded | 3 | 28 | 0.94 |

| | t | df | p |
|-----------------------------|------|----|-------|
| A.salignaCFSF:P.radiataCFSF | 0.32 | 17 | 0.988 |
| A.salignaCFSF:P.radiataSAF | 2.36 | 24 | 0.112 |
| A.salignaCFSF:Uninvaded | 1.53 | 15 | 0.443 |
| P.radiataCFSF:P.radiataSAF | 3.24 | 15 | 0.026 |
| P.radiataCFSF:Uninvaded | 3.37 | 12 | 0.024 |
| P.radiataSAF:Uninvaded | 1.78 | 12 | 0.326 |

Available phosphorus

```
> i4
```

| | n | means | variances |
|----------|----|-------|-----------|
| Burned | 18 | 0.60 | 0.055 |
| Unburned | 27 | 0.67 | 0.038 |

| | t | df | p |
|-----------------|---|----|------|
| Burned:Unburned | 1 | 32 | 0.32 |

```
> ii4
```

| | n | means | variances |
|------|----|-------|-----------|
| CFSF | 33 | 0.61 | 0.032 |
| SAF | 12 | 0.73 | 0.075 |

| | t | df | p |
|----------|-----|----|------|
| CFSF:SAF | 1.4 | 15 | 0.19 |

```
> iii4
```

| | n | means | variances |
|------------|----|-------|-----------|
| Reference | 3 | 0.47 | 0.0054 |
| A. saligna | 15 | 0.67 | 0.0331 |
| P. radiata | 27 | 0.65 | 0.0542 |

| | t | df | p |
|-----------------------|------|------|-------|
| Reference:A. saligna | 3.06 | 8.1 | 0.037 |
| Reference:P. radiata | 2.86 | 8.2 | 0.049 |
| A. saligna:P. radiata | 0.27 | 35.3 | 0.961 |

```
> iv4 acacia
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 2.0 | 0.23 |
| b | 3 | 4.5 | 2.32 |
| c | 12 | 3.9 | 5.30 |

| | t | df | p |
|-----|-----|------|-------|
| a:b | 2.7 | 2.4 | 0.174 |
| a:c | 2.7 | 13.0 | 0.046 |
| b:c | 0.5 | 4.7 | 0.875 |

```
> iv4 pine
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 2.0 | 0.23 |
| b | 6 | 5.2 | 13.40 |
| c | 3 | 9.6 | 29.59 |
| d | 18 | 3.0 | 3.28 |

| | t | df | p |
|--|---|----|---|
|--|---|----|---|

```

a:b 2.1  5.3 0.25
a:c 2.4  2.0 0.31
a:d 1.9 13.6 0.27
b:c 1.3  2.9 0.64
b:d 1.5  5.8 0.52
c:d 2.1  2.1 0.38
> v4
      n means variances
A.salignaCFSF 15 0.67 0.0331
P.radiataCFSF 15 0.59 0.0320
P.radiataSAF  12 0.73 0.0752
Uninvaded     3 0.47 0.0054

      t  df  p
A.salignaCFSF:P.radiataCFSF 1.22 28.0 0.619
A.salignaCFSF:P.radiataSAF  0.67 18.3 0.908
A.salignaCFSF:Uninvaded     3.06  8.1 0.060
P.radiataCFSF:P.radiataSAF  1.55 18.1 0.431
P.radiataCFSF:Uninvaded     1.80  7.9 0.338
P.radiataSAF:Uninvaded     2.84 12.5 0.061

```

Litter

```

> i5
      n means variances
Burned  18 155 11002
Unburned 27 185 10556

```

```

      t df  p
Burned:Unburned 0.95 36 0.35

```

> ii5

```

      n means variances
CFSF  33 189 9011
SAF   12 129 13760

```

```

      t df  p
CFSF:SAF 1.6 17 0.13

```

> iii5

```

      n means variances
Reference  3 186 1097
A. saligna 15 213 14274
P. radiata 27 150 8867

```

```

      t  df  p
Reference:A. saligna 0.74 13.2 0.75
Reference:P. radiata 1.37  6.8 0.41
A. saligna:P. radiata 1.76 23.8 0.21

```

> iv5 acacia

```

      n means variances
a  3 186 1097
b  3 187 1181
c 12 219 17722

```

```

      t df  p
a:b 0.026  4 1.00
a:c 0.775 13 0.72
b:c 0.752 13 0.74

```

> iv5 pine

```

      n means variances
a  3 186 1097
b  6 109 3291
c  3  56 1143
d 18 179 9380

```

```

      t  df  p

```

```

a:b 2.55 6.6 0.140
a:c 4.78 4.0 0.030
a:d 0.23 9.5 0.996
b:c 1.75 6.5 0.372
b:d 2.15 15.0 0.182
c:d 4.12 9.2 0.011
> v5
      n means variances
A.salignaCFSF 15 213 14274
P.radiataCFSF 15 166 5008
P.radiataSAF 12 129 13760
Uninvaded 3 186 1097

      t df p
A.salignaCFSF:P.radiataCFSF 1.30 22.7 0.57
A.salignaCFSF:P.radiataSAF 1.82 23.9 0.29
A.salignaCFSF:Uninvaded 0.74 13.2 0.88
P.radiataCFSF:P.radiataSAF 0.96 17.2 0.77
P.radiataCFSF:Uninvaded 0.75 6.5 0.88
P.radiataSAF:Uninvaded 1.46 12.3 0.49

```

Ericoid shrub richness

```

> i6
      n means variances
Burned 18 3.8 4.9
Unburned 27 3.1 7.7

```

```

      t df p
Burned:Unburned 0.97 42 0.34

```

```

> ii6
      n means variances
CFSF 33 3.5 7.8
SAF 12 3.1 3.5

```

```

      t df p
CFSF:SAF 0.59 29 0.56

```

```

> iii6
      n means variances
Reference 3 8.7 6.3
A. saligna 15 1.7 3.4
P. radiata 27 3.7 3.9

```

```

      t df p
Reference:A. saligna 4.5 2.4 0.0585
Reference:P. radiata 3.3 2.3 0.1255
A. saligna:P. radiata 3.3 30.9 0.0065

```

```

> iv6 acaia
      n means variances
a 3 8.7 6.33
b 3 1.3 0.33
c 12 1.8 4.15

```

```

      t df p
a:b 4.92 2.2 0.059
a:c 4.36 2.7 0.054
b:c 0.74 12.3 0.745

```

```

> iv6 pine
      n means variances
a 3 8.7 6.3
b 6 4.2 3.0
c 3 3.0 1.0
d 18 3.7 4.8

```

```

      t df p

```

```

a:b 2.79  3.0 0.19
a:c 3.62  2.6 0.12
a:d 3.21  2.5 0.16
b:c 1.28  6.6 0.60
b:d 0.51 10.9 0.96
c:d 0.93  6.0 0.79

```

```
>V6
```

| | n | means | variances |
|---------------|----|-------|-----------|
| A.salignaCFSF | 15 | 1.7 | 3.4 |
| P.radiataCFSF | 15 | 4.3 | 3.8 |
| P.radiataSAF | 12 | 3.1 | 3.5 |
| Uninvaded | 3 | 8.7 | 6.3 |

| | t | df | p |
|-----------------------------|-----|------|--------|
| A.salignaCFSF:P.radiataCFSF | 3.7 | 27.9 | 0.0052 |
| A.salignaCFSF:P.radiataSAF | 1.9 | 23.4 | 0.2655 |
| A.salignaCFSF:Uninvaded | 4.5 | 2.4 | 0.0821 |
| P.radiataCFSF:P.radiataSAF | 1.6 | 24.0 | 0.3974 |
| P.radiataCFSF:Uninvaded | 2.9 | 2.5 | 0.2052 |
| P.radiataSAF:Uninvaded | 3.6 | 2.6 | 0.1252 |

Restioid richness

```
> i7
```

| | n | means | variances |
|----------|----|-------|-----------|
| Burned | 18 | 0.72 | 0.80 |
| Unburned | 27 | 0.52 | 0.41 |

| | t | df | p |
|-----------------|------|----|------|
| Burned:Unburned | 0.83 | 29 | 0.41 |

```
> ii7
```

| | n | means | variances |
|------|----|-------|-----------|
| CFSF | 33 | 0.58 | 0.63 |
| SAF | 12 | 0.67 | 0.42 |

| | t | df | p |
|----------|------|----|-----|
| CFSF:SAF | 0.39 | 24 | 0.7 |

```
> iii7
```

| | n | means | variances |
|------------|----|-------|-----------|
| Reference | 3 | 1.33 | 0.33 |
| A. saligna | 15 | 0.27 | 0.64 |
| P. radiata | 27 | 0.70 | 0.45 |

| | t | df | p |
|-----------------------|-----|------|------|
| Reference:A. saligna | 2.7 | 3.7 | 0.12 |
| Reference:P. radiata | 1.8 | 2.6 | 0.34 |
| A. saligna:P. radiata | 1.8 | 25.0 | 0.19 |

```
> iv7 acacia
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 1.33 | 0.33 |
| b | 3 | 0.00 | 0.00 |
| c | 12 | 0.33 | 0.79 |

| | t | df | p |
|-----|-----|------|------|
| a:b | 4.0 | 2.0 | 0.10 |
| a:c | 2.4 | 4.8 | 0.14 |
| b:c | 1.3 | 11.0 | 0.42 |

```
> iv7 pine
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 1.33 | 0.33 |
| b | 6 | 0.67 | 0.27 |
| c | 3 | 0.00 | 0.00 |
| d | 18 | 0.83 | 0.50 |

| | t | df | p |
|--|---|----|---|
|--|---|----|---|

```

a:b 1.69  3.7 0.43840
a:c 4.00  2.0 0.13821
a:d 1.34  3.1 0.59935
b:c 3.16  5.0 0.08559
b:d 0.62 11.8 0.92362
c:d 5.00 17.0 0.00058
> v7

```

```

      n means variances
A.salignaCFSF 15 0.27  0.64
P.radiataCFSF 15 0.73  0.50
P.radiataSAF  12 0.67  0.42
Uninvaded     3 1.33  0.33

```

```

      t  df  p
A.salignaCFSF:P.radiataCFSF 1.70 27.6 0.34
A.salignaCFSF:P.radiataSAF  1.43 25.0 0.49
A.salignaCFSF:Uninvaded     2.72  3.7 0.17
P.radiataCFSF:P.radiataSAF  0.25 24.4 0.99
P.radiataCFSF:Uninvaded     1.58  3.3 0.49
P.radiataSAF:Uninvaded     1.74  3.4 0.43

```

Indigenous perennial grass richness

```
> i8
```

```

      n means variances
Burned  18  3.4  2.0
Unburned 27  2.7  1.9

```

```

      t df  p
Burned:Unburned 1.7 36 0.1

```

```
> ii8
```

```

      n means variances
CFSF  33  2.7  1.6
SAF   12  3.6  2.8

```

```

      t df  p
CFSF:SAF 1.6 16 0.13

```

```
> iii8
```

```

      n means variances
Reference  3  3.3  2.3
A. saligna 15  2.9  2.0
P. radiata 27  3.0  2.2

```

```

      t  df  p
Reference:A. saligna 0.49  2.7 0.88
Reference:P. radiata 0.40  2.4 0.92
A. saligna:P. radiata 0.21 30.3 0.98

```

```
> iv8 pine
```

```

      n means variances
a  3  3.3  2.33
b  6  3.7  2.67
c  3  2.7  0.33
d 18  2.8  2.30

```

```

      t  df  p
a:b 0.30 4.4 0.99
a:c 0.71 2.6 0.89
a:d 0.58 2.7 0.93
b:c 1.34 6.8 0.57
b:d 1.18 8.1 0.66
c:d 0.23 8.0 1.00

```

```
> iv8 acacia
```

```

      n means variances
a  3  3.3  2.3
b  3  3.0  1.0

```

```
c 12 2.8 2.3
```

```
      t  df  p
a:b 0.32 3.4 0.95
a:c 0.51 3.1 0.87
b:c 0.23 4.7 0.97
```

```
> v8
```

```
      n means variances
A.salignaCFSF 15 2.9 2.0
P.radiataCFSF 15 2.5 1.3
P.radiataSAF 12 3.6 2.8
Uninvaded 3 3.3 2.3
```

```
      t  df  p
A.salignaCFSF:P.radiataCFSF 0.86 26.7 0.83
A.salignaCFSF:P.radiataSAF 1.18 21.5 0.64
A.salignaCFSF:Uninvaded 0.49 2.7 0.96
P.radiataCFSF:P.radiataSAF 1.98 18.5 0.23
P.radiataCFSF:Uninvaded 0.93 2.5 0.79
P.radiataSAF:Uninvaded 0.25 3.3 0.99
```

Non-ericoid shrub richness

```
> i9
```

```
      n means variances
Burned 18 1.8 1.8
Unburned 27 1.4 1.2
```

```
      t  df  p
Burned:Unburned 1.2 31 0.23
```

```
> ii9
```

```
      n means variances
CFSF 33 1.5 1.1
SAF 12 1.6 2.4
```

```
      t  df  p
CFSF:SAF 0.078 15 0.94
```

```
> iii9
```

```
      n means variances
Reference 3 1.3 0.33
A. saligna 15 1.1 1.35
P. radiata 27 1.9 1.44
```

```
      t  df  p
Reference:A. saligna 0.59 6.0 0.83
Reference:P. radiata 1.28 4.3 0.47
A. saligna:P. radiata 2.07 29.8 0.11
```

```
> iv9 pine
```

```
      n means variances
a 3 1.3 0.33
b 6 1.7 3.47
c 3 1.7 4.33
d 18 1.9 0.64
```

```
      t  df  p
a:b 0.40 6.5 0.98
a:c 0.27 2.3 0.99
a:d 1.59 3.5 0.48
b:c 0.00 3.7 1.00
b:d 0.35 5.6 0.98
c:d 0.23 2.1 0.99
```

```
> iv9 acacia
```

```
      n means variances
a 3 1.3 0.33
b 3 0.0 0.00
```

c 12 1.3 1.33

| | t | df | p |
|-----|---|------|--------|
| a:b | 4 | 2.0 | 0.1024 |
| a:c | 0 | 6.8 | 1.0000 |
| b:c | 4 | 11.0 | 0.0054 |

> v9

| | n | means | variances |
|---------------|----|-------|-----------|
| A.salignaCFSF | 15 | 1.1 | 1.35 |
| P.radiataCFSF | 15 | 2.1 | 0.64 |
| P.radiataSAF | 12 | 1.6 | 2.45 |
| Uninvaded | 3 | 1.3 | 0.33 |

| | t | df | p |
|-----------------------------|------|------|-------|
| A.salignaCFSF:P.radiataCFSF | 2.75 | 24.8 | 0.051 |
| A.salignaCFSF:P.radiataSAF | 0.95 | 19.8 | 0.777 |
| A.salignaCFSF:Uninvaded | 0.59 | 6.0 | 0.930 |
| P.radiataCFSF:P.radiataSAF | 0.97 | 15.5 | 0.766 |
| P.radiataCFSF:Uninvaded | 1.87 | 3.7 | 0.371 |
| P.radiataSAF:Uninvaded | 0.45 | 10.0 | 0.969 |

Perennial indigenous species richness

> i10

| | n | means | variances |
|----------|----|-------|-----------|
| Burned | 18 | 16 | 44 |
| Unburned | 27 | 13 | 31 |

| | t | df | p |
|-----------------|-----|----|-------|
| Burned:Unburned | 1.9 | 32 | 0.067 |

> ii10

| | n | means | variances |
|------|----|-------|-----------|
| CFSF | 33 | 14 | 50 |
| SAF | 12 | 15 | 10 |

| | t | df | p |
|----------|------|----|------|
| CFSF:SAF | 0.26 | 41 | 0.79 |

> iii10

| | n | means | variances |
|------------|----|-------|-----------|
| Reference | 3 | 17.3 | 37 |
| A. saligna | 15 | 9.5 | 42 |
| P. radiata | 27 | 16.6 | 20 |

| | t | df | p |
|-----------------------|-----|------|--------|
| Reference:A. saligna | 2.0 | 3.0 | 0.2602 |
| Reference:P. radiata | 0.2 | 2.2 | 0.9775 |
| A. saligna:P. radiata | 3.7 | 21.5 | 0.0032 |

> iv10 acacia

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 17.3 | 37 |
| b | 3 | 11.3 | 16 |
| c | 12 | 9.1 | 50 |

| | t | df | p |
|-----|------|-----|------|
| a:b | 1.42 | 3.5 | 0.43 |
| a:c | 2.03 | 3.5 | 0.24 |
| b:c | 0.73 | 5.6 | 0.76 |

> iv10 pine

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 17 | 37.3 |
| b | 6 | 17 | 7.0 |
| c | 3 | 13 | 2.3 |
| d | 18 | 17 | 26.2 |

| | t | df | p |
|--|---|----|---|
|--|---|----|---|

```

a:b 0.136  2.4 1.00
a:c 1.100  2.2 0.72
a:d 0.075  2.5 1.00
b:c 2.514  6.6 0.15
b:d 0.137 17.4 1.00
c:d 2.492 11.7 0.11

```

```
> v10
```

| | n | means | variances |
|---------------|----|-------|-----------|
| A.salignaCFSF | 15 | 9.5 | 42 |
| P.radiataCFSF | 15 | 18.2 | 23 |
| P.radiataSAF | 12 | 14.6 | 10 |
| Uninvaded | 3 | 17.3 | 37 |

| | t | df | p |
|-----------------------------|------|------|--------|
| A.salignaCFSF:P.radiataCFSF | 4.15 | 25.8 | 0.0017 |
| A.salignaCFSF:P.radiataSAF | 2.64 | 21.2 | 0.0672 |
| A.salignaCFSF:Uninvaded | 2.00 | 3.0 | 0.3552 |
| P.radiataCFSF:P.radiataSAF | 2.35 | 24.3 | 0.1152 |
| P.radiataCFSF:Uninvaded | 0.23 | 2.5 | 0.9946 |
| P.radiataSAF:Uninvaded | 0.75 | 2.3 | 0.8699 |

Indigenous cover

```
> i11
```

| | n | means | variances |
|----------|----|-------|-----------|
| Burned | 18 | 1.2 | 0.031 |
| Unburned | 27 | 1.1 | 0.084 |

| | t | df | p |
|-----------------|-----|----|-------|
| Burned:Unburned | 1.7 | 43 | 0.093 |

```
> ii11
```

| | n | means | variances |
|------|----|-------|-----------|
| CFSF | 33 | 1.1 | 0.069 |
| SAF | 12 | 1.3 | 0.012 |

| | t | df | p |
|----------|-----|----|-------|
| CFSF:SAF | 4.4 | 42 | 7e-05 |

```
> iii11
```

| | n | means | variances |
|------------|----|-------|-----------|
| Reference | 3 | 1.47 | 0.0097 |
| A. saligna | 15 | 0.93 | 0.0670 |
| P. radiata | 27 | 1.21 | 0.0299 |

| | t | df | p |
|-----------------------|-----|------|---------|
| Reference:A. saligna | 6.1 | 8.9 | 0.00046 |
| Reference:P. radiata | 3.9 | 3.6 | 0.04636 |
| A. saligna:P. radiata | 3.8 | 21.1 | 0.00278 |

```
> iv 11 pine
```

| | n | means | variances |
|---|----|-------|-----------|
| a | 3 | 1.5 | 0.0097 |
| b | 6 | 1.3 | 0.0118 |
| c | 3 | 1.2 | 0.0199 |
| d | 18 | 1.2 | 0.0319 |

| | t | df | p |
|-----|------|------|-------|
| a:b | 1.74 | 4.5 | 0.404 |
| a:c | 2.49 | 3.6 | 0.214 |
| a:d | 4.24 | 4.6 | 0.034 |
| b:c | 1.32 | 3.2 | 0.609 |
| b:d | 2.86 | 14.6 | 0.053 |
| c:d | 0.57 | 3.2 | 0.935 |

```
> iv acacia
```

```

n means variances
a 3 1.47 0.0097
b 3 0.57 0.0022
c 12 1.02 0.0407

```

```

t df p
a:b 14.3 2.9 1.9e-03
a:c 5.5 7.0 2.2e-03
b:c 7.0 12.9 2.7e-05

```

```
> v11
```

```

n means variances
A.salignaCFSF 15 0.93 0.0670
P.radiataCFSF 15 1.13 0.0296
P.radiataSAF 12 1.32 0.0123
Uninvaded 3 1.47 0.0097

```

```

t df p
A.salignaCFSF:P.radiataCFSF 2.5 24.3 0.08110
A.salignaCFSF:P.radiataSAF 5.2 19.8 0.00023
A.salignaCFSF:Uninvaded 6.1 8.9 0.00082
P.radiataCFSF:P.radiataSAF 3.4 24.1 0.01240
P.radiataCFSF:Uninvaded 4.7 4.9 0.02078
P.radiataSAF:Uninvaded 2.3 3.4 0.25271

```

Alien cover

```
> i12
```

```

n means variances
Burned 18 0.36 0.031
Unburned 27 0.48 0.085

```

```

t df p
Burned:Unburned 1.7 43 0.09

```

```
> ii12
```

```

n means variances
CFSF 33 0.50 0.069
SAF 12 0.25 0.012

```

```

t df p
CFSF:SAF 4.4 42 6.4e-05

```

```
> iii12
```

```

n means variances
Reference 3 0.10 0.010
A. saligna 15 0.64 0.068
P. radiata 27 0.36 0.030

```

```

t df p
Reference:A. saligna 6.1 8.7 0.00053
Reference:P. radiata 3.9 3.5 0.04854
A. saligna:P. radiata 3.8 21.0 0.00294

```

```
> iv12 acacia
```

```

n means variances
a 3 0.10 0.0101
b 3 1.00 0.0023
c 12 0.55 0.0417

```

```

t df p
a:b 14.0 2.9 0.00210
a:c 5.5 6.9 0.00244
b:c 6.9 12.9 0.00003

```

```
> iv12 pine
```

```

n means variances

```

```
a 3 0.10 0.010
b 6 0.23 0.011
c 3 0.35 0.020
d 18 0.40 0.032
```

```
      t  df  p
a:b 1.77 4.3 0.392
a:c 2.46 3.6 0.219
a:d 4.21 4.5 0.036
b:c 1.28 3.2 0.627
b:d 2.87 14.9 0.052
c:d 0.59 3.2 0.930
```

> vi12

```
      n means variances
A.salignaCFSF 15 0.64 0.068
P.radiataCFSF 15 0.44 0.029
P.radiataSAF 12 0.25 0.012
Uninvaded 3 0.10 0.010
```

```
      t  df  p
A.salignaCFSF:P.radiataCFSF 2.5 24.2 0.08536
A.salignaCFSF:P.radiataSAF 5.2 19.7 0.00023
A.salignaCFSF:Uninvaded 6.1 8.7 0.00095
P.radiataCFSF:P.radiataSAF 3.4 24.1 0.01065
P.radiataCFSF:Uninvaded 4.7 4.8 0.02228
P.radiataSAF:Uninvaded 2.3 3.3 0.25894
```

> vi12 Alien herbaceous cover

```
      n means variances
A.saligna 15 26 557
P.radiata 20 12 166
Uninvaded 3 1 1
```

```
      t df  p
A.saligna:P.radiata 2.1 20 0.1248
A.saligna:Uninvaded 4.0 14 0.0033
P.radiata:Uninvaded 3.7 20 0.0042
```

> vi12 Alien woody cover

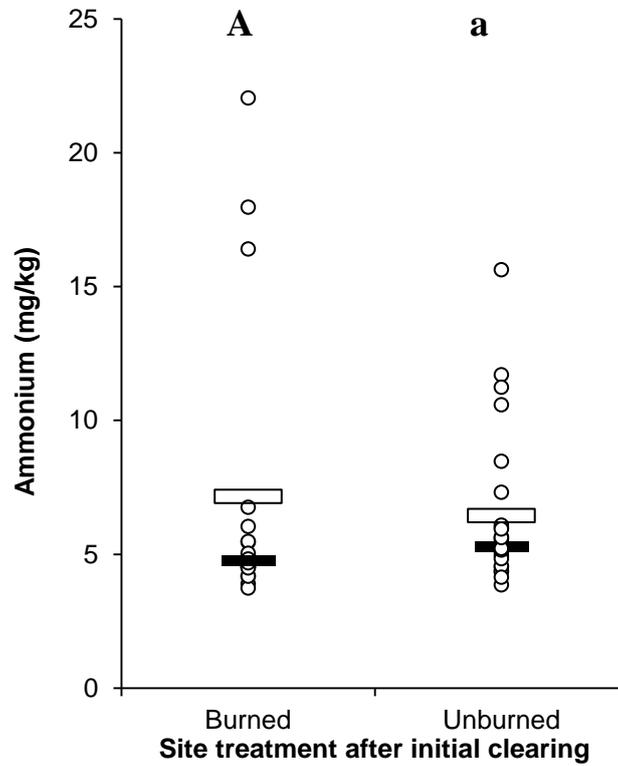
```
      n means variances
A.saligna 15 3.93 15.50
P.radiata 20 0.40 0.67
Uninvaded 3 0.33 0.33
```

```
      t  df  p
A.saligna:P.radiata 3.42 14.9 0.01
A.saligna:Uninvaded 3.37 15.9 0.01
P.radiata:Uninvaded 0.18 3.4 0.98
```

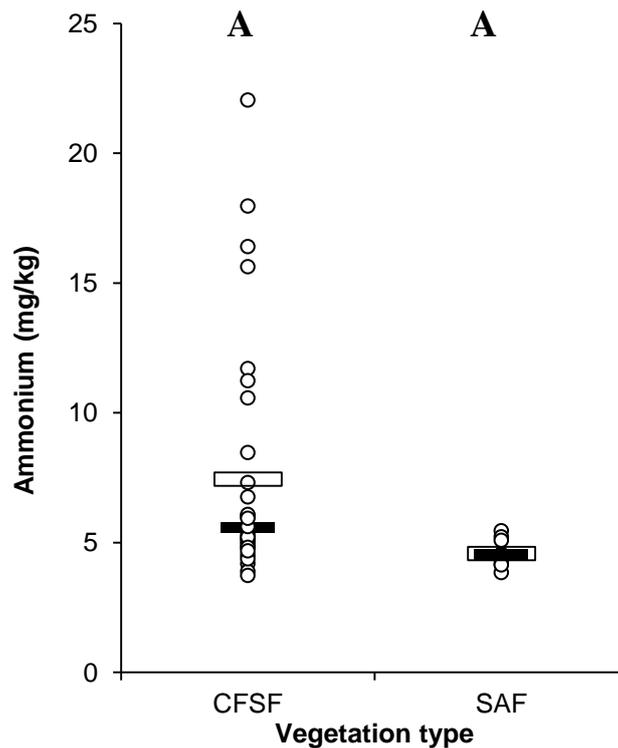
Appendix 4C

Relationship between abiotic functional indicators as response variables 1) Ammonium 2) pH 3) EC 4) Available Phosphorus 5) Litter and i) Site treatment after initial clearing (Burned or Unburned) ii) Vegetation type (Cape Flat Sand Fynbos, CFSF, or Swartland Alluvium Fynbos, SAF) iii) Dominant Invasive species (Uninvaded, *A. saligna*, *P. radiata*) and the iv) Number of cycles of invasion (Uninvaded, One, Two or Three), separated by species: *A. saligna* and *P. radiata*. Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).

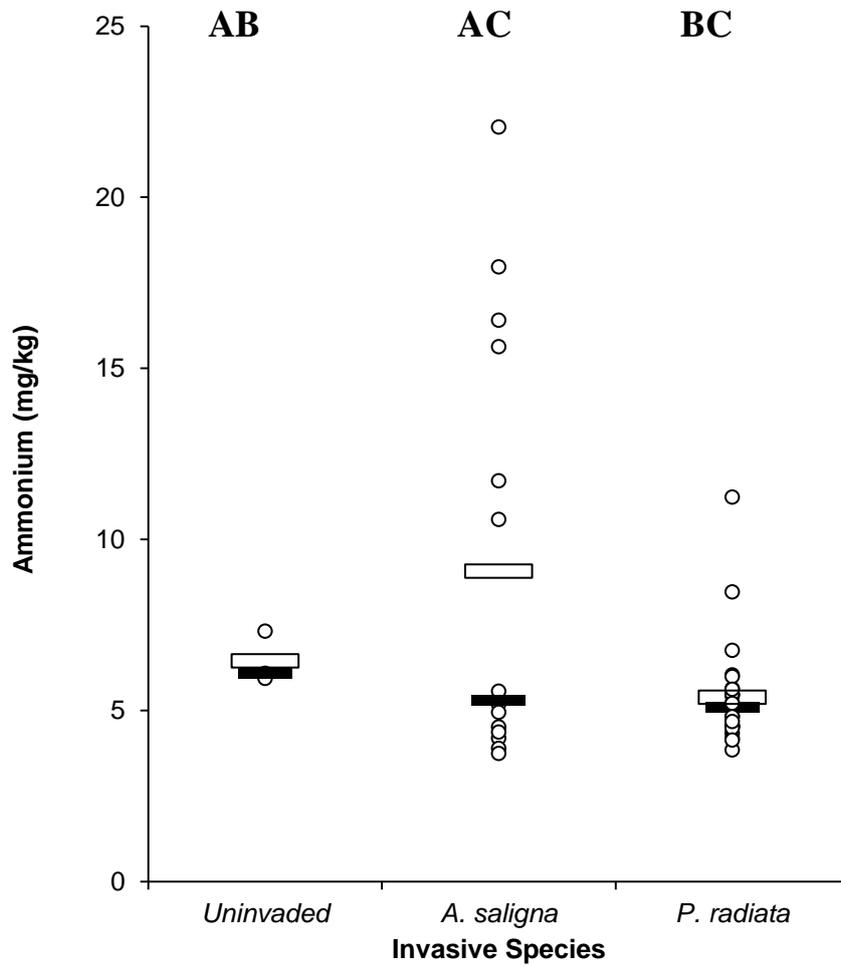
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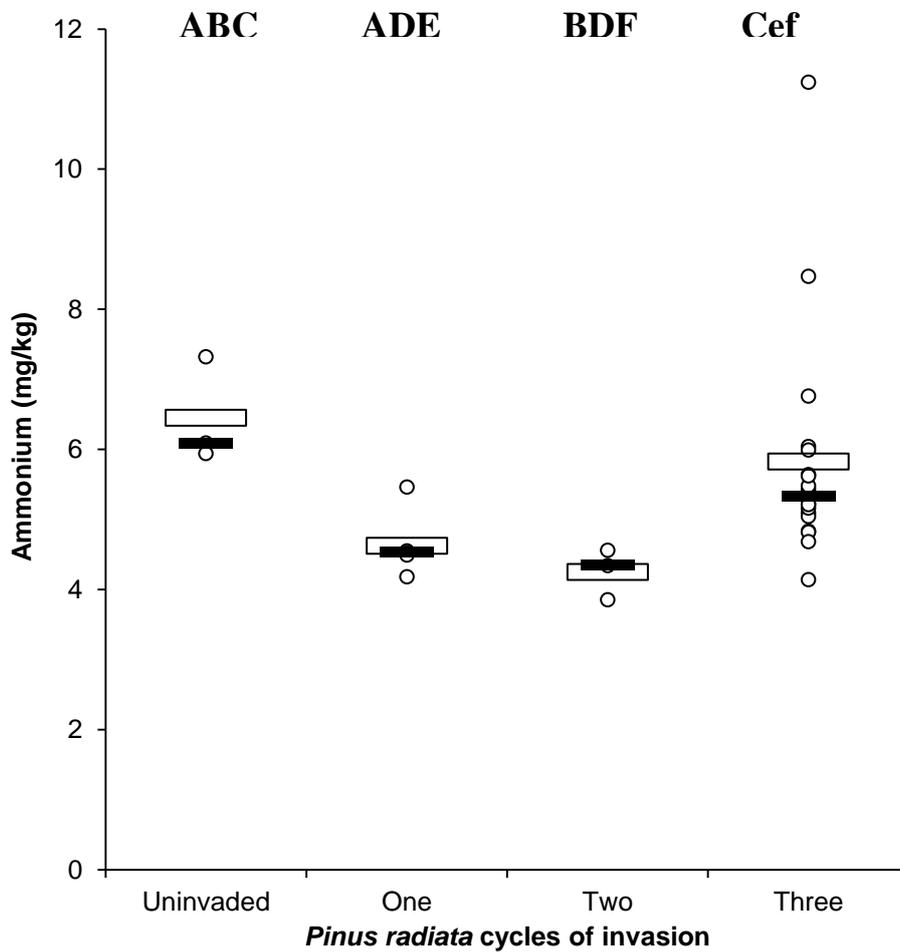
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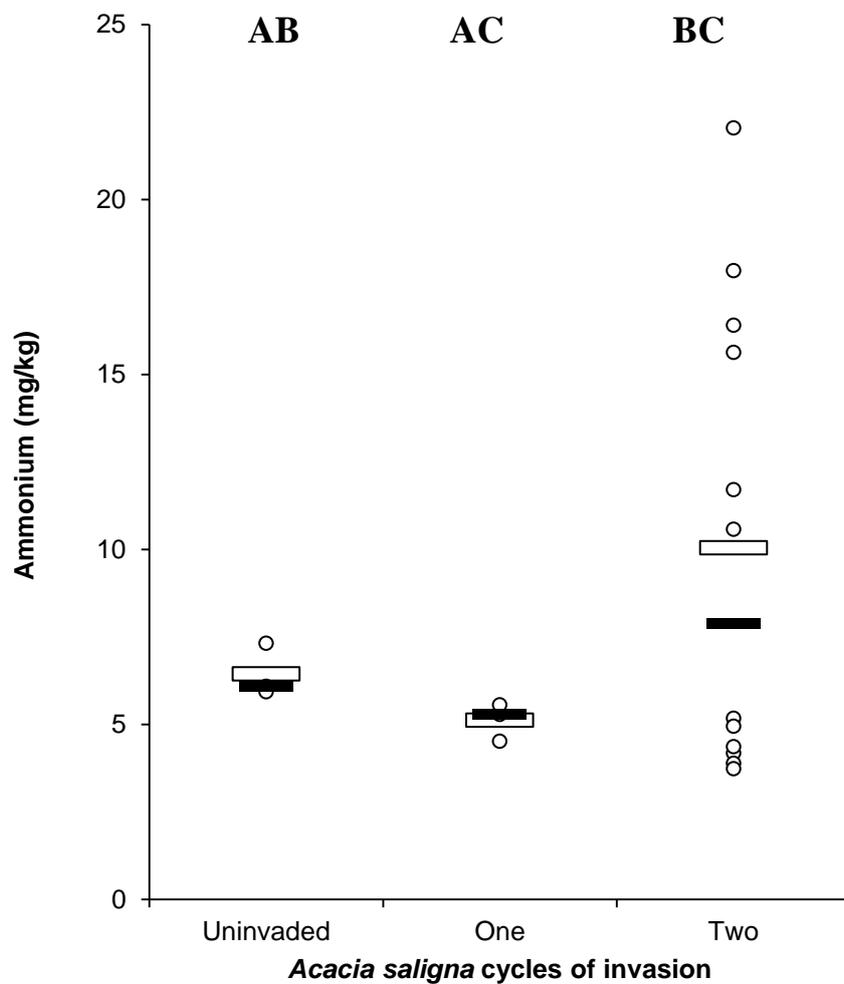
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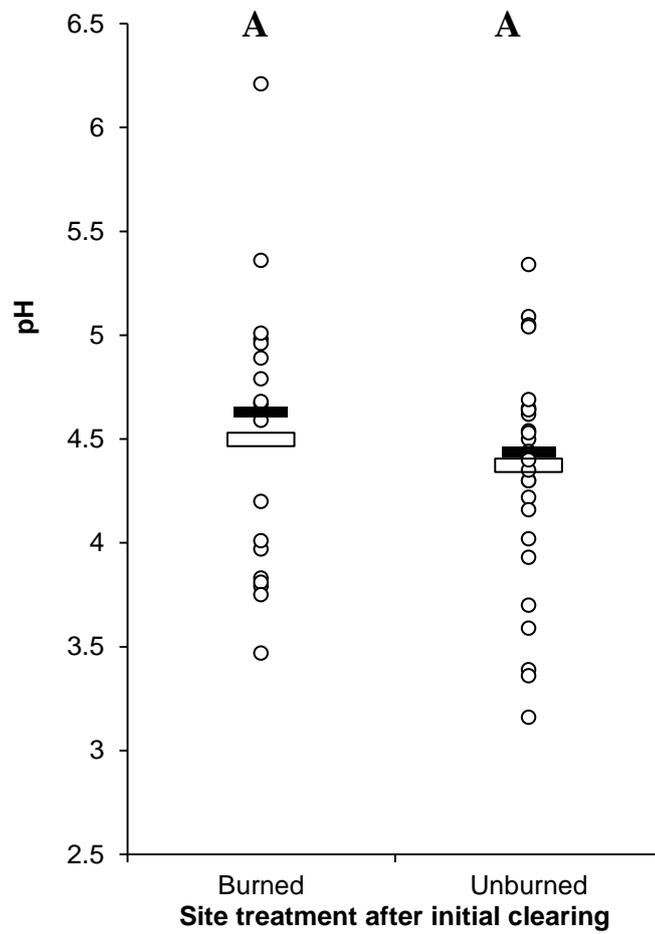
1)iv *P. radiata*



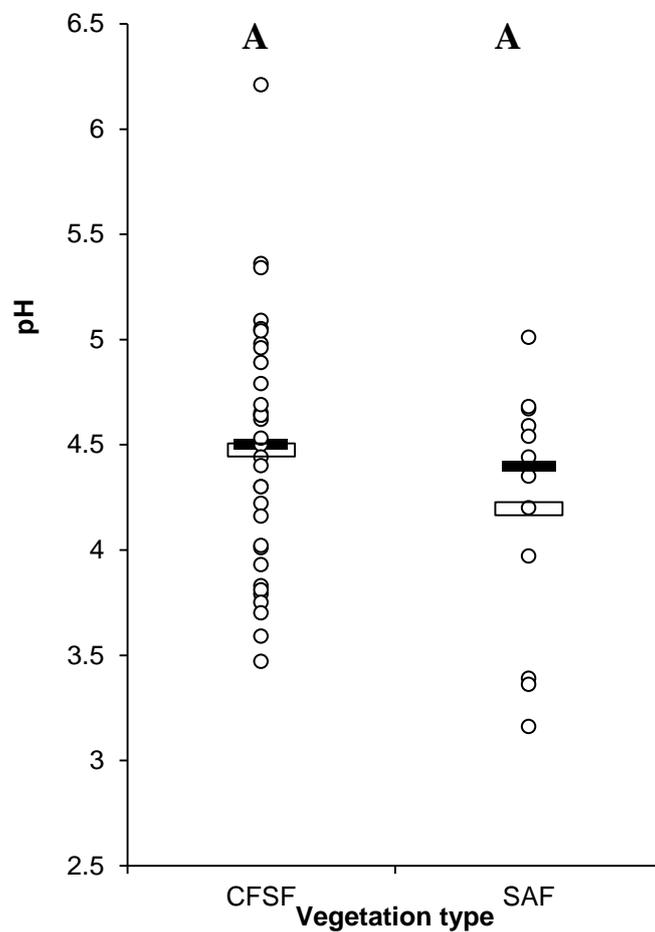
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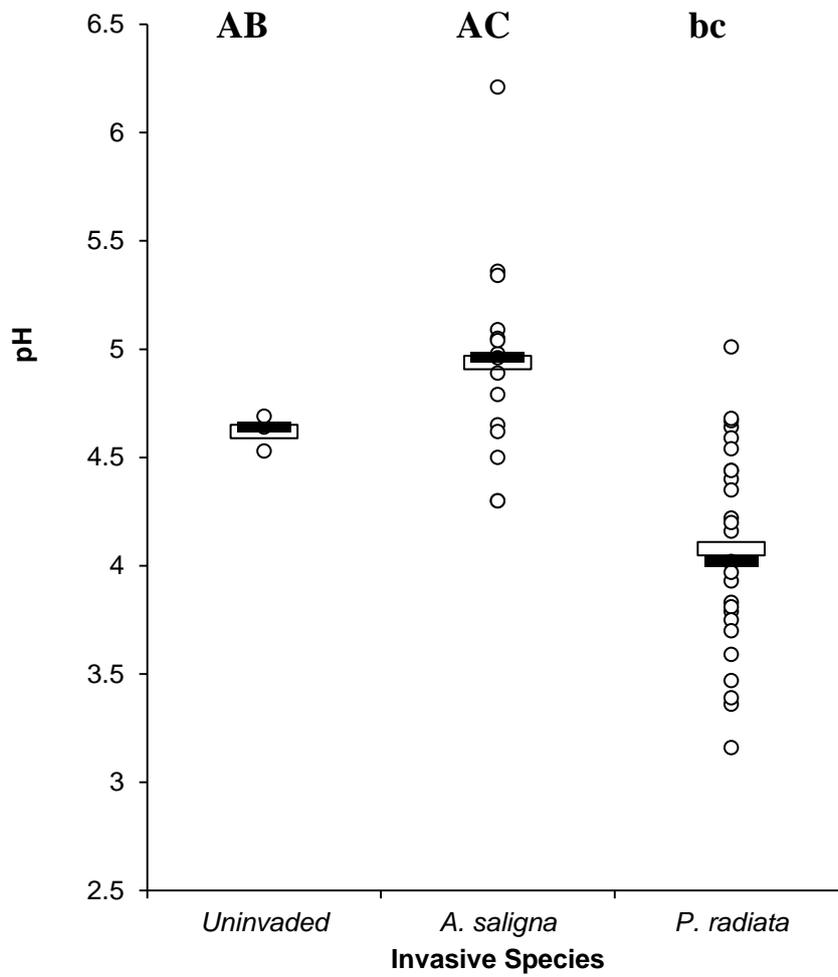
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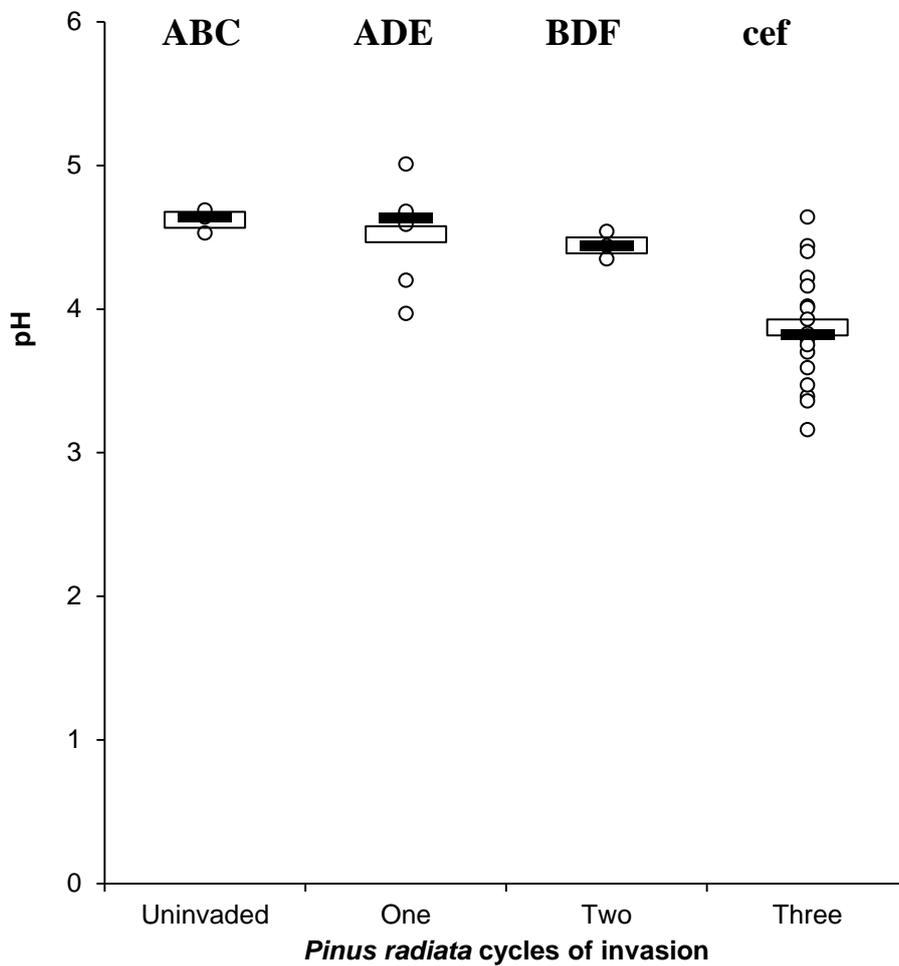
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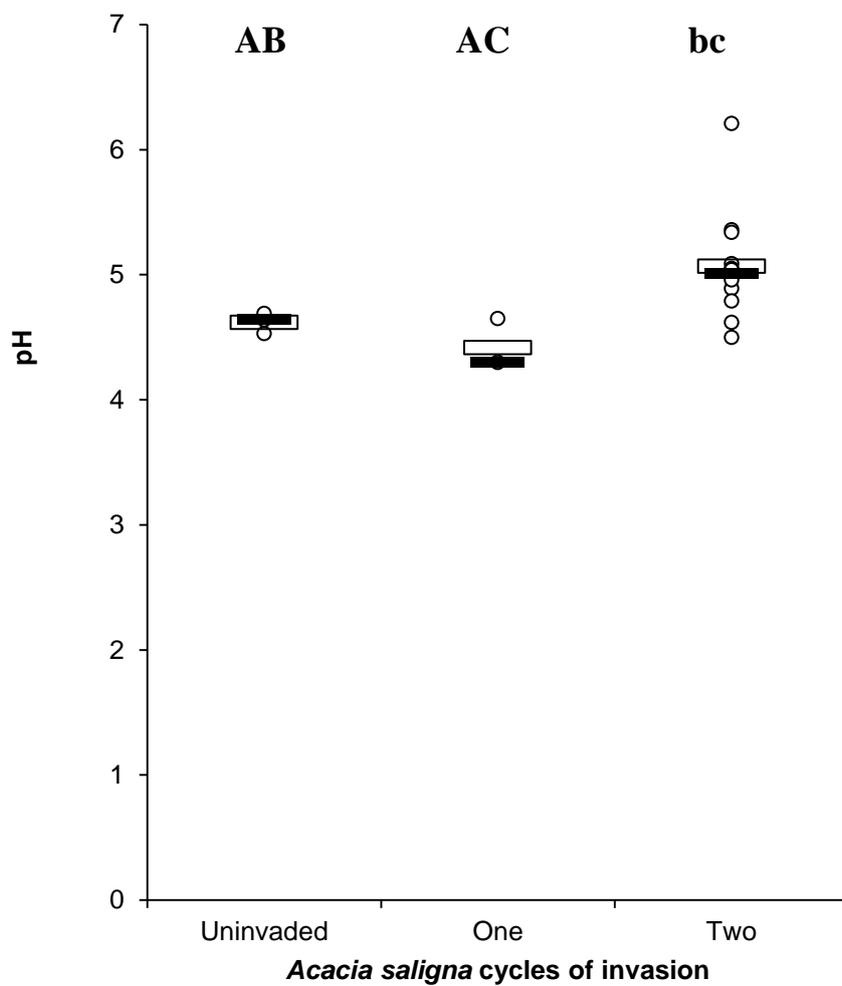
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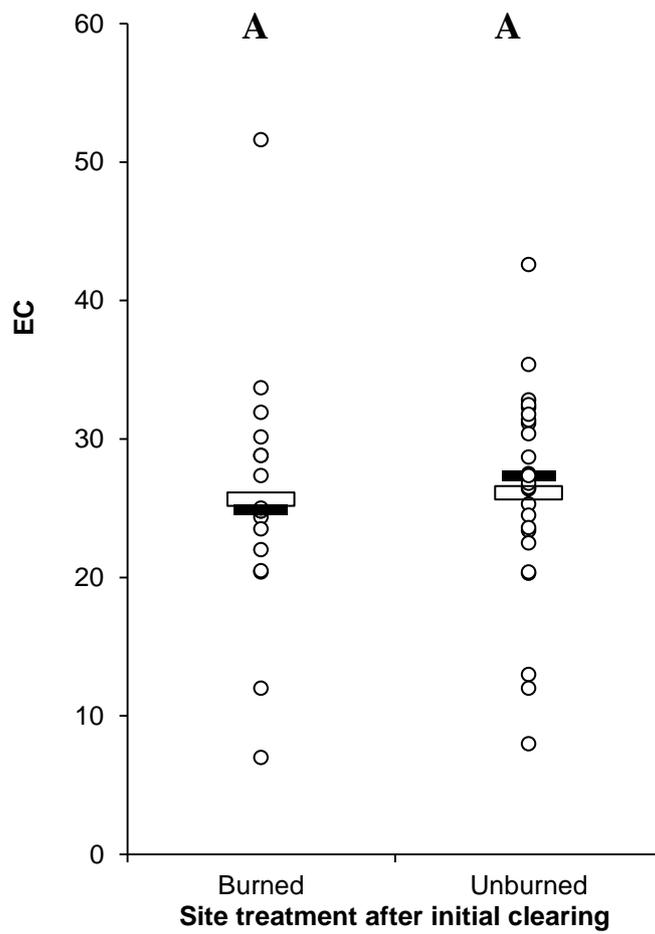
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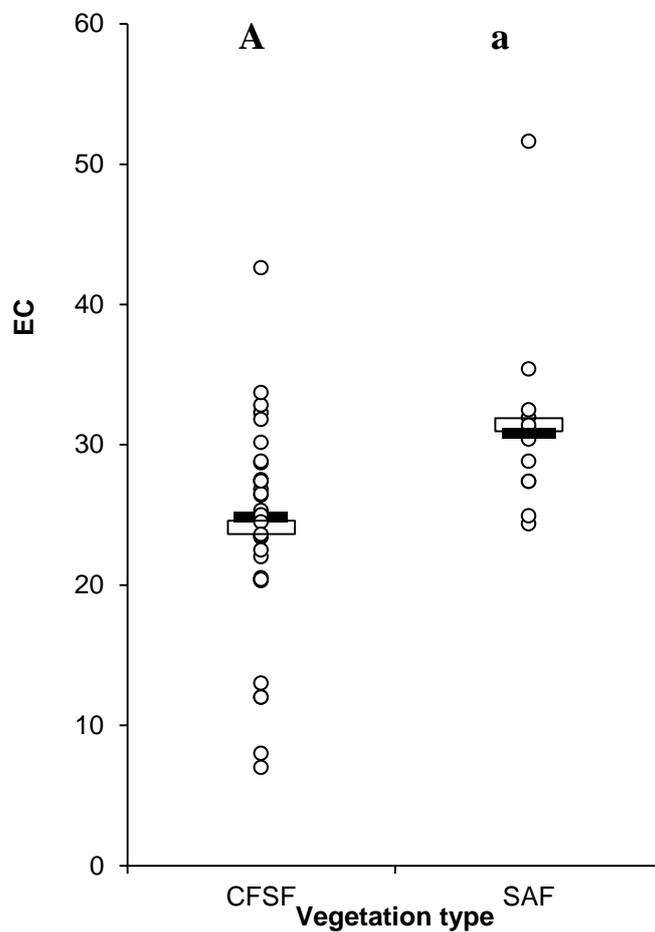
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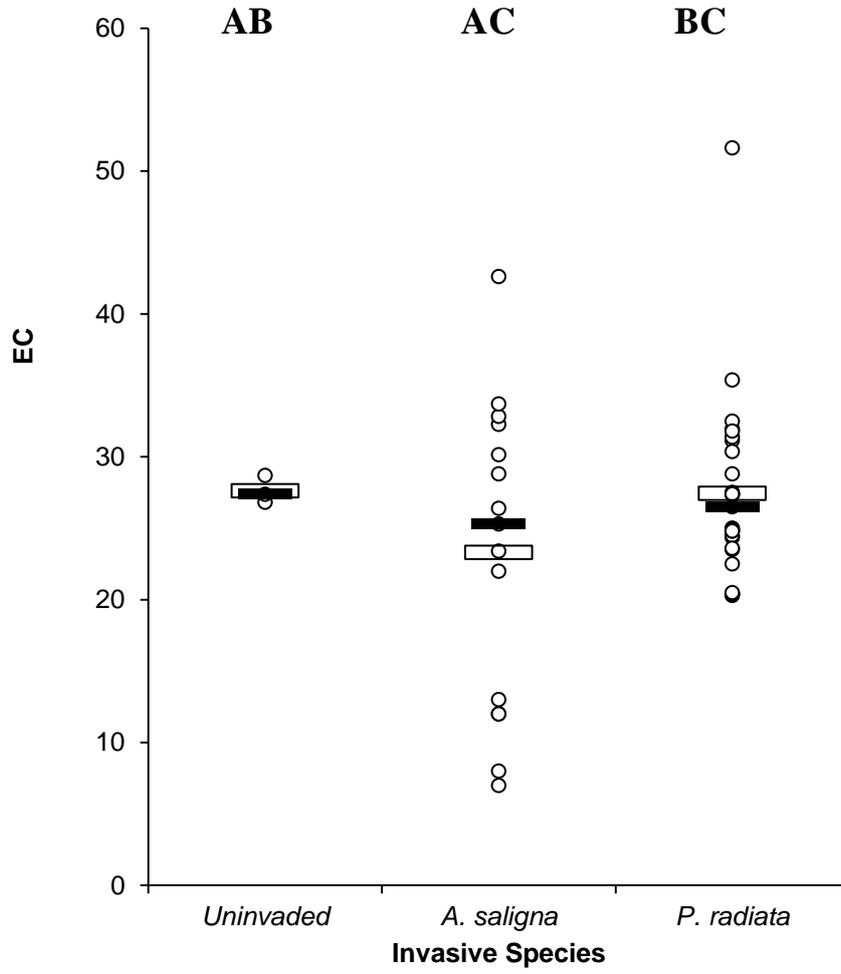
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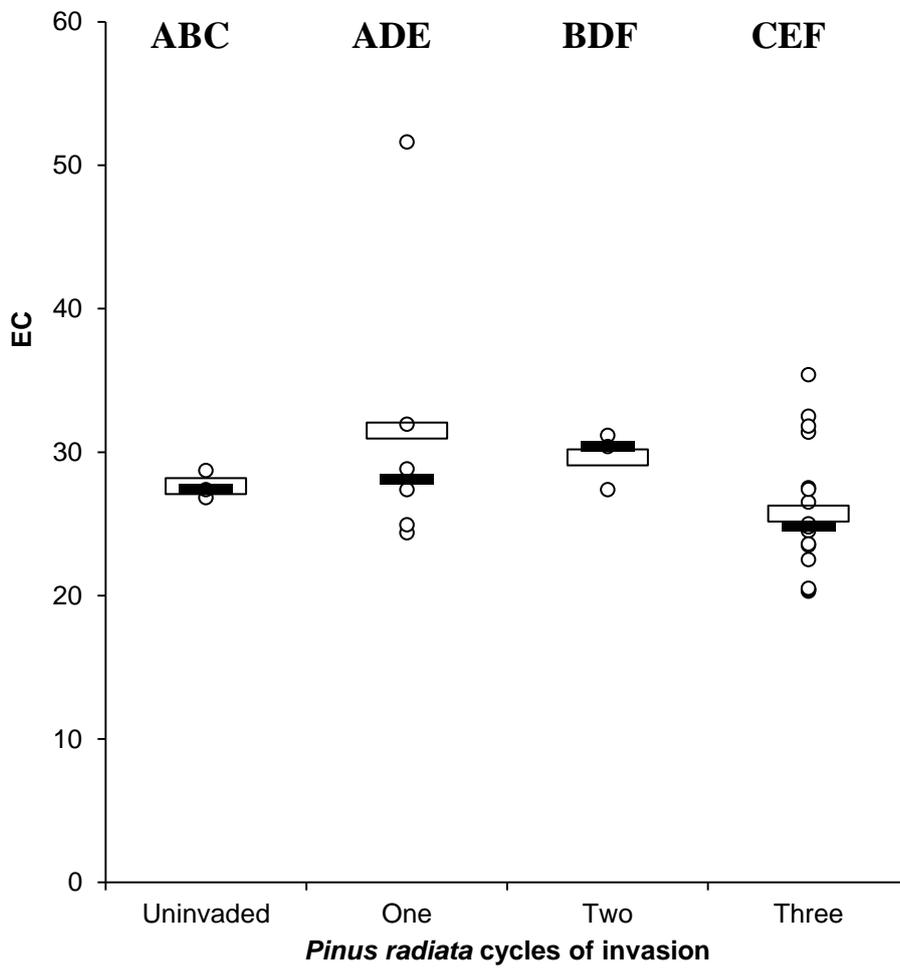
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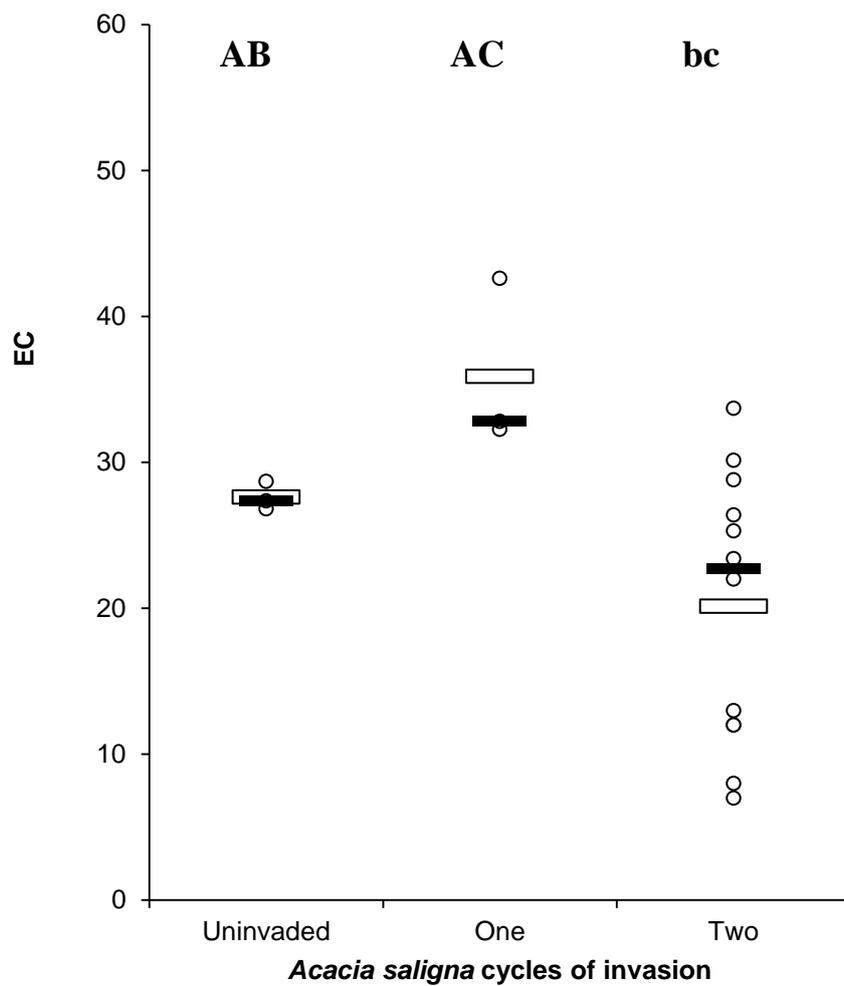
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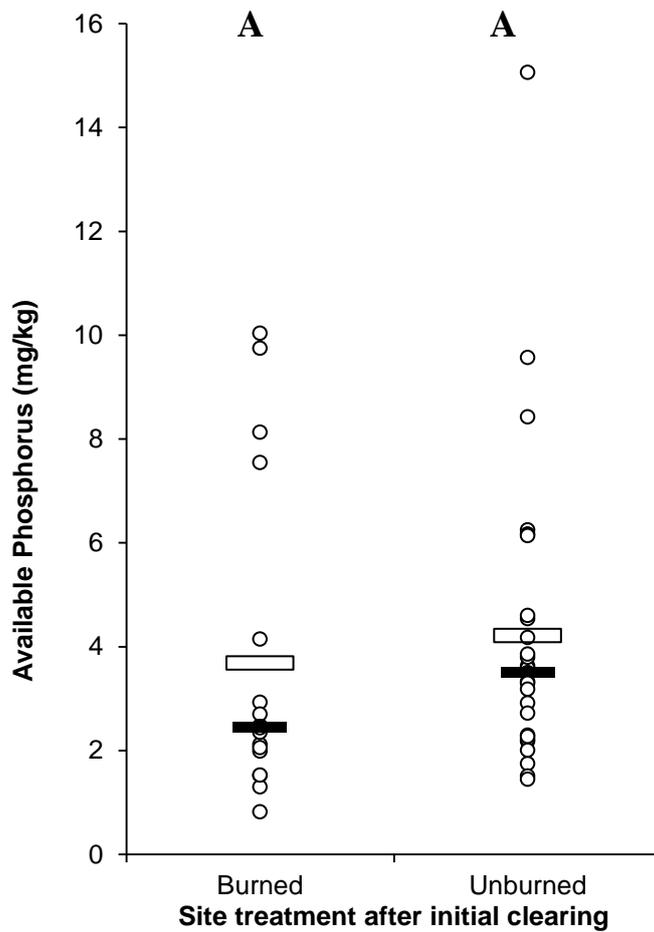
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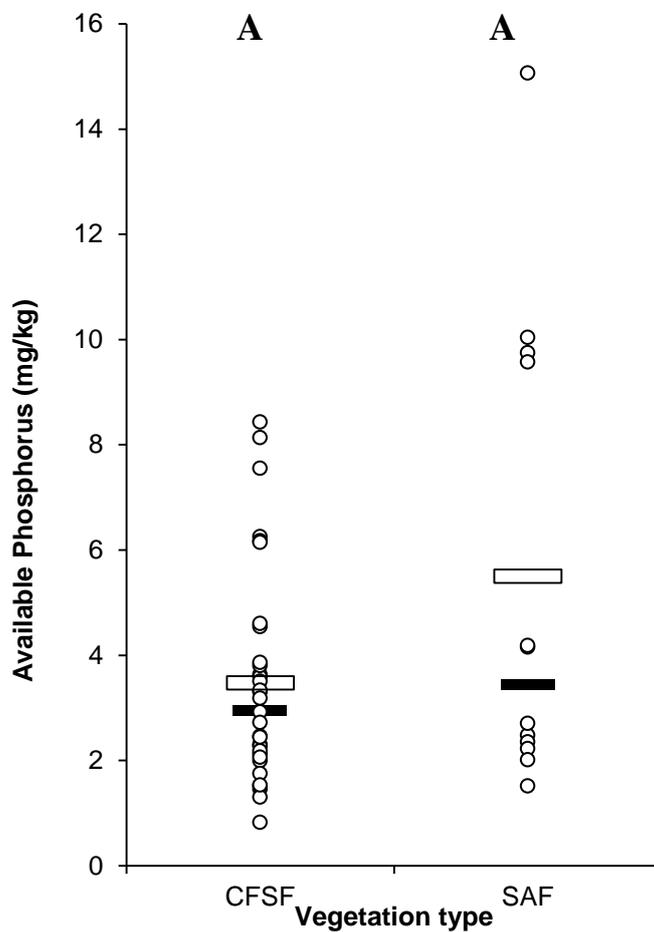
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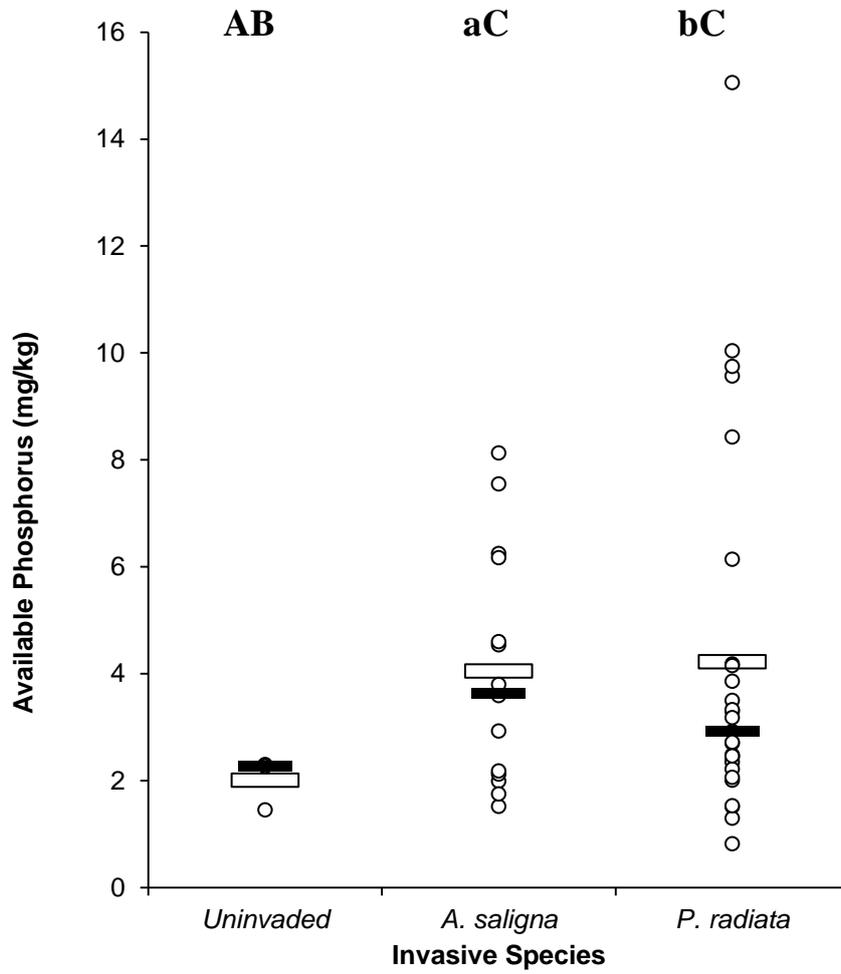
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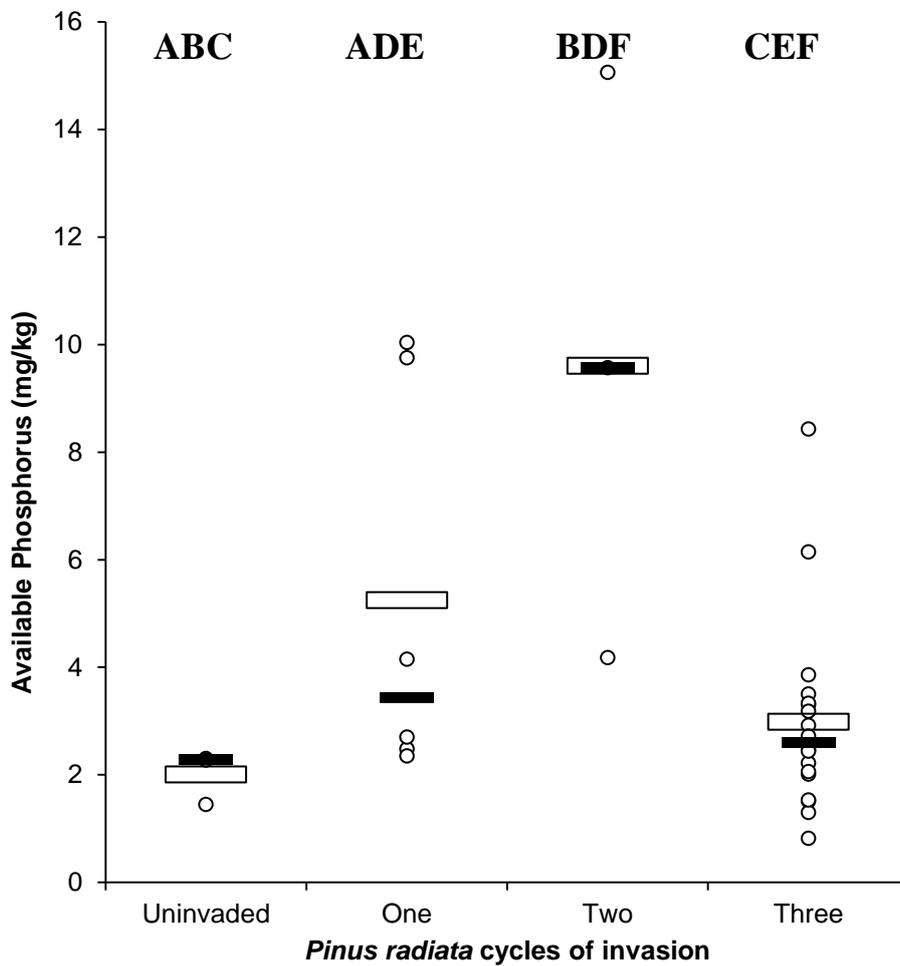
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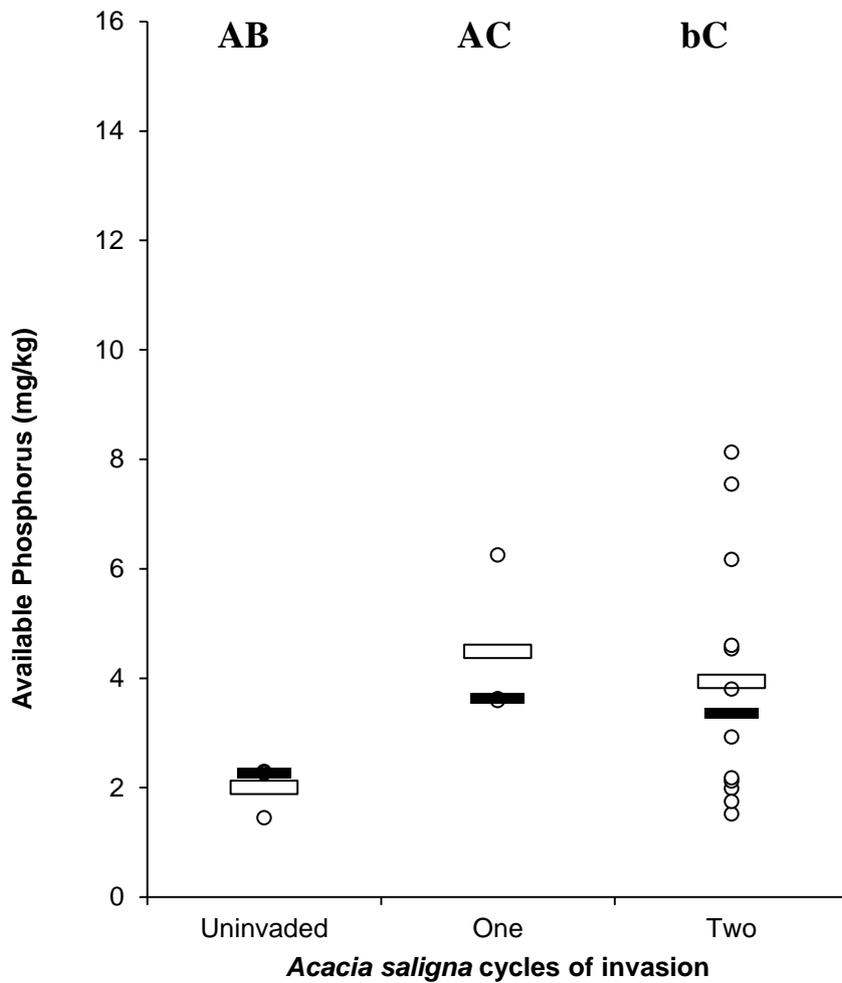
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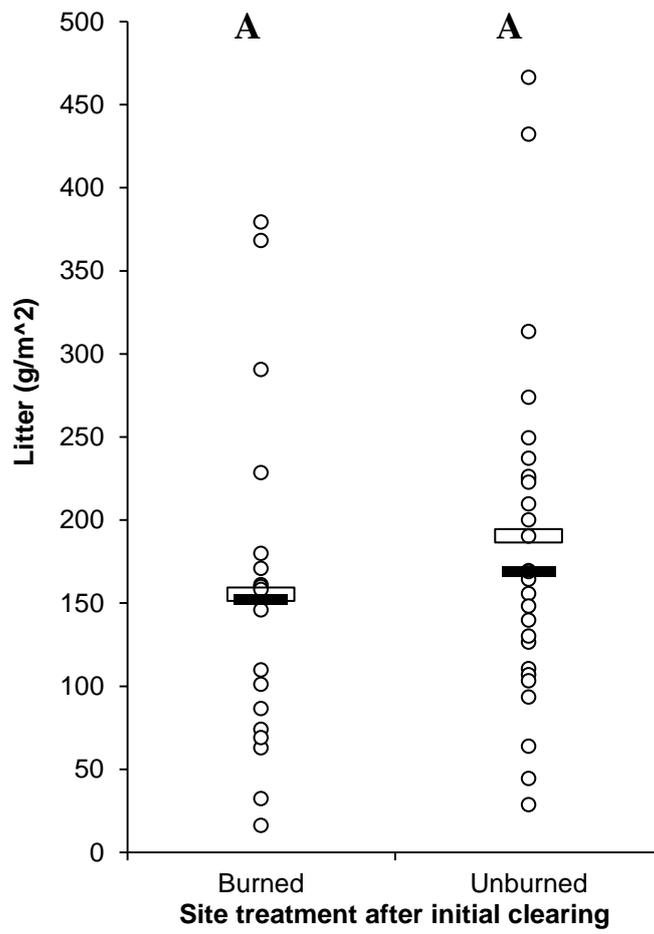
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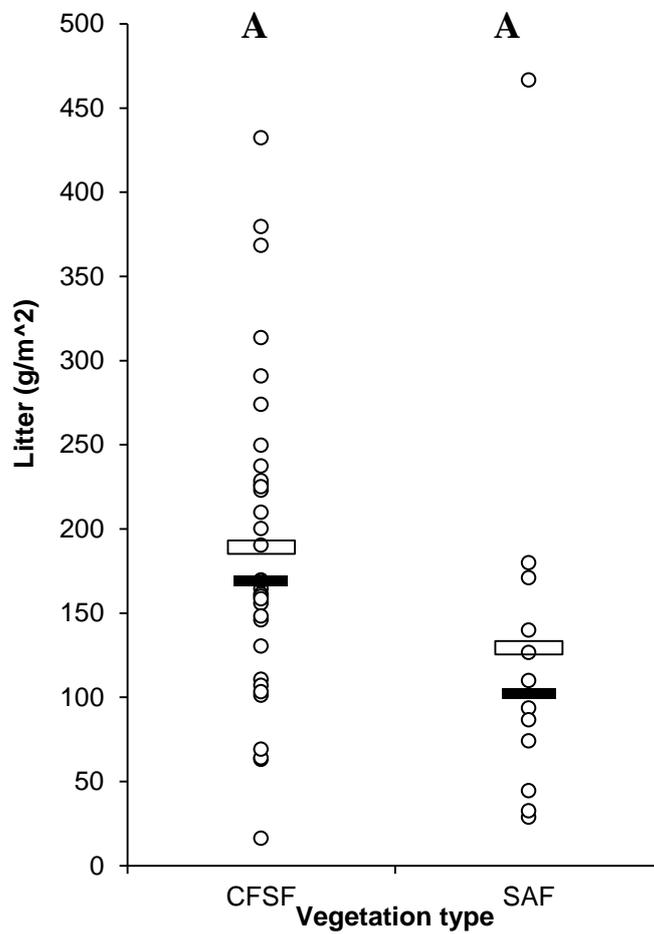
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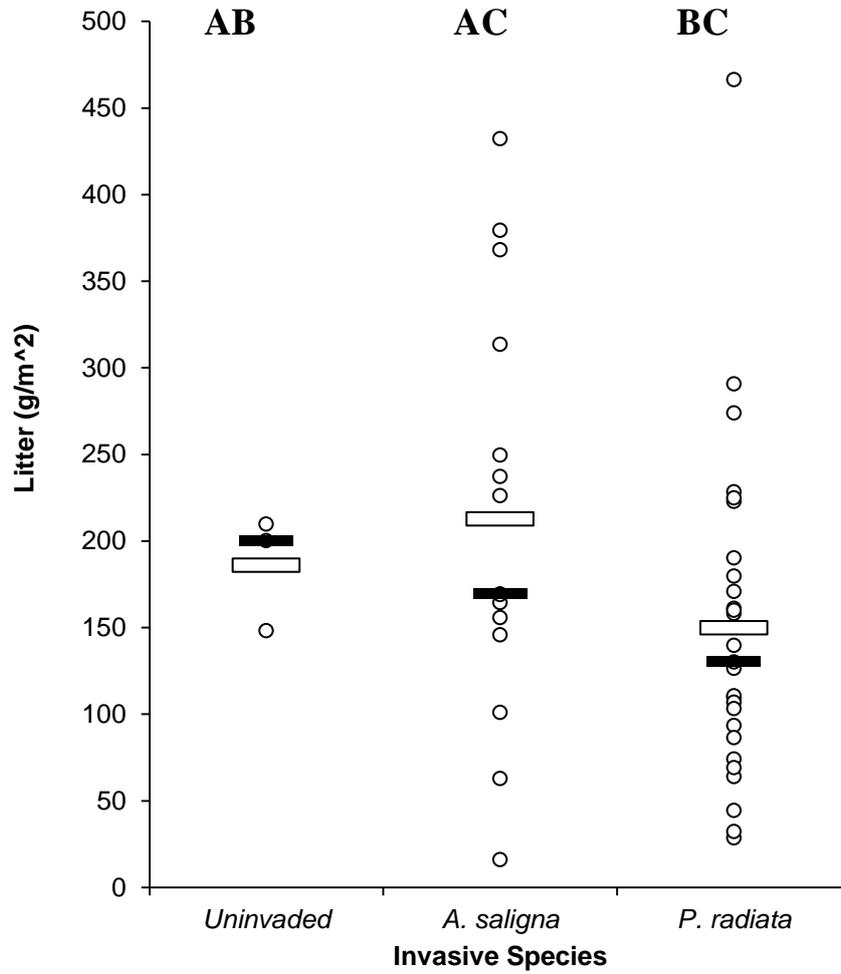
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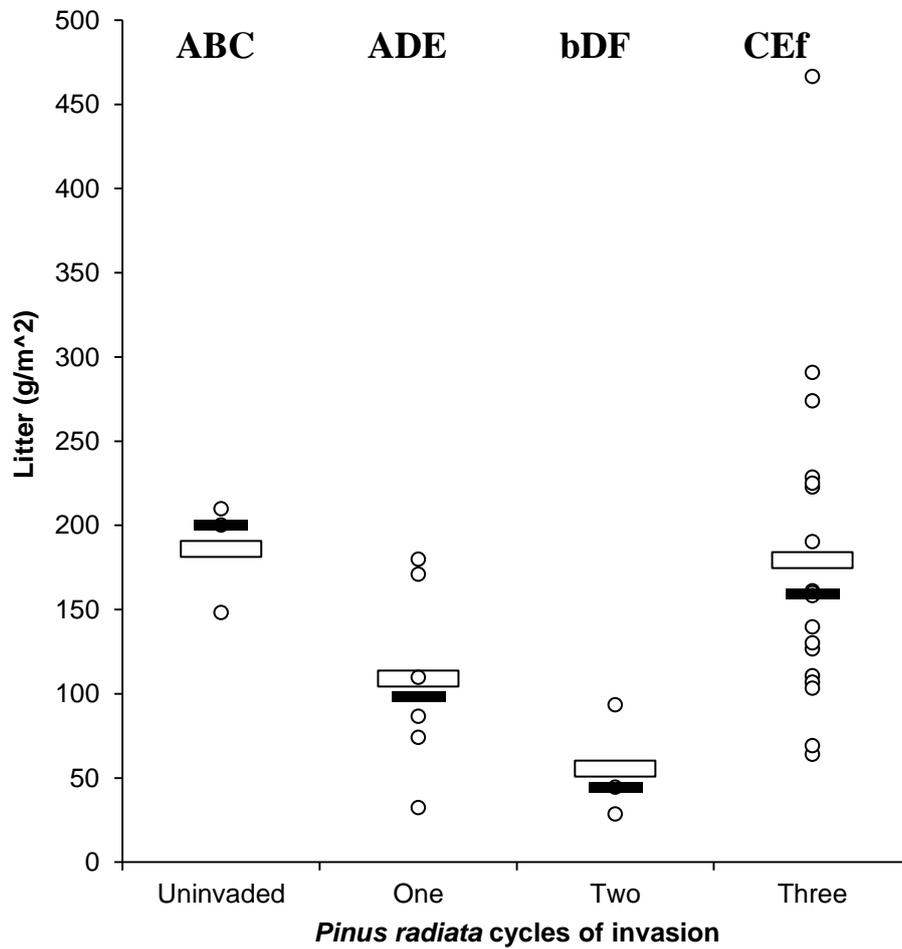
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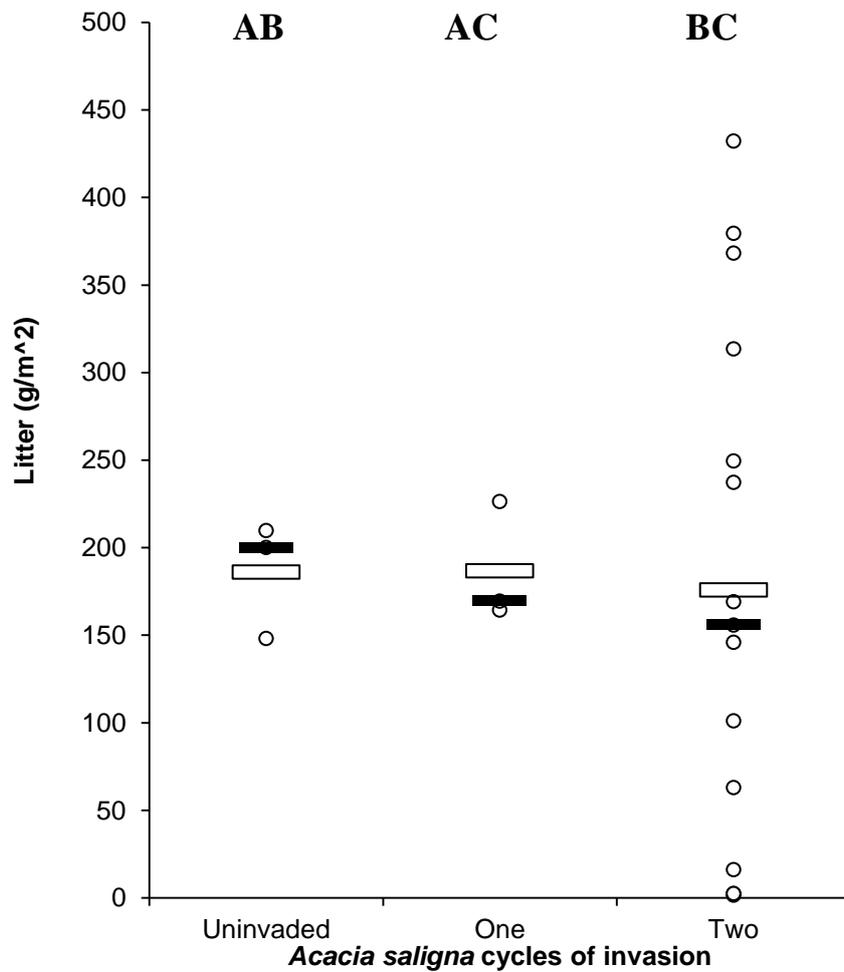
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5)iv *P. radiata*

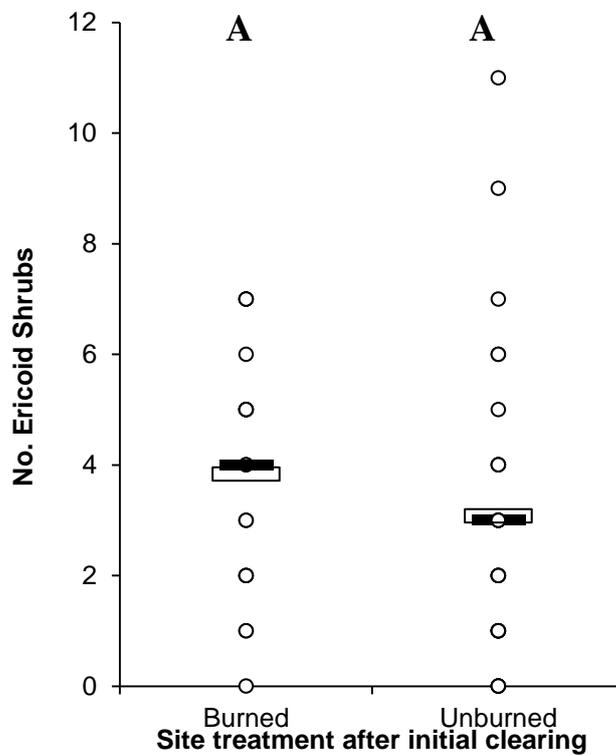


5)iv *A. saligna*

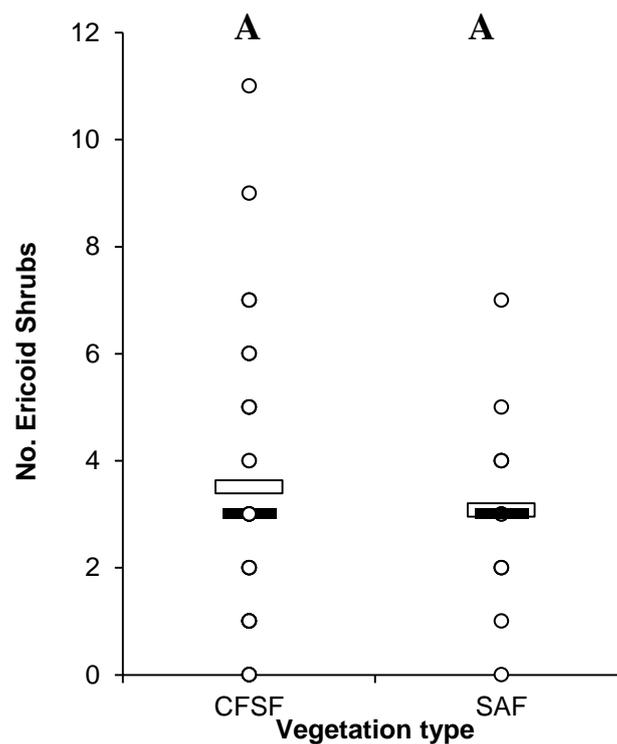


Relationship between biotic functional indicators as response variables No. of 6) Ericoid Shrubs, 7) Restioids 8) Indigenous Perennial Grasses 9) Non-Ericoid Shrubs and i) Site treatment after initial clearing (Burned or Unburned) ii) Vegetation type (Cape Flat Sand Fynbos, CFSF, or Swartland Alluvium Fynbos, SAF) iii) Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*) and the iv) Number of cycles of invasion (Uninvaded, One, Two or Three), separated by species: *A. saligna* and *P. radiata*. Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).

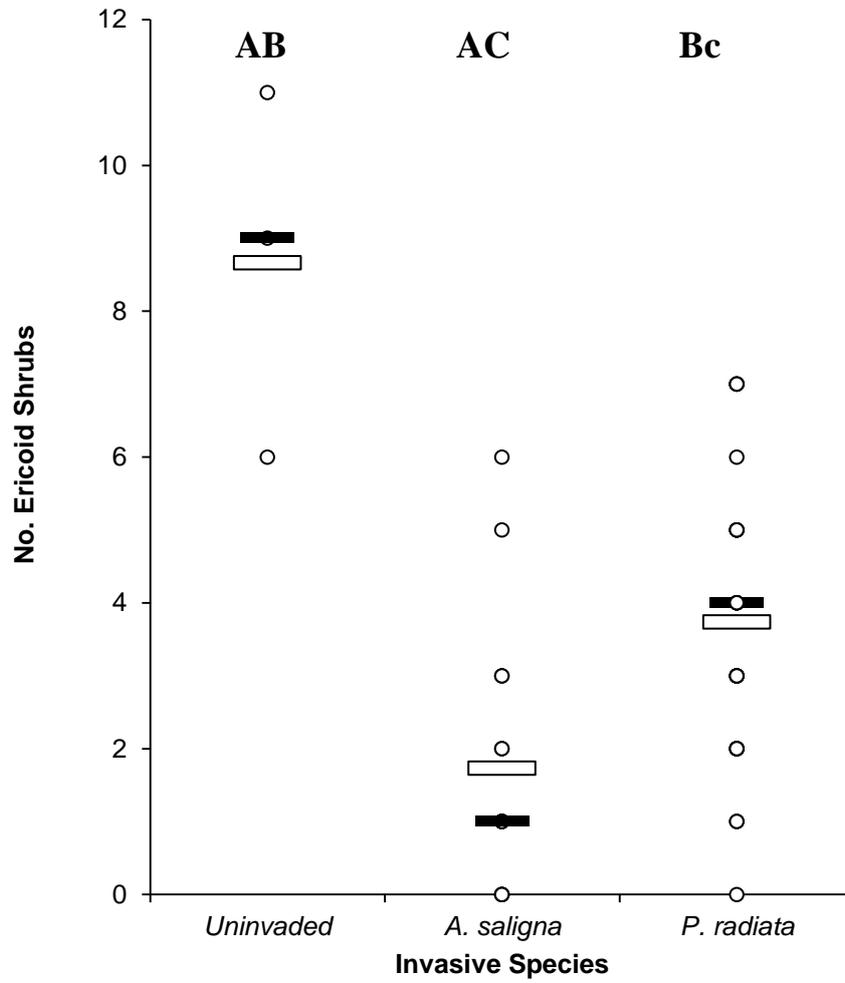
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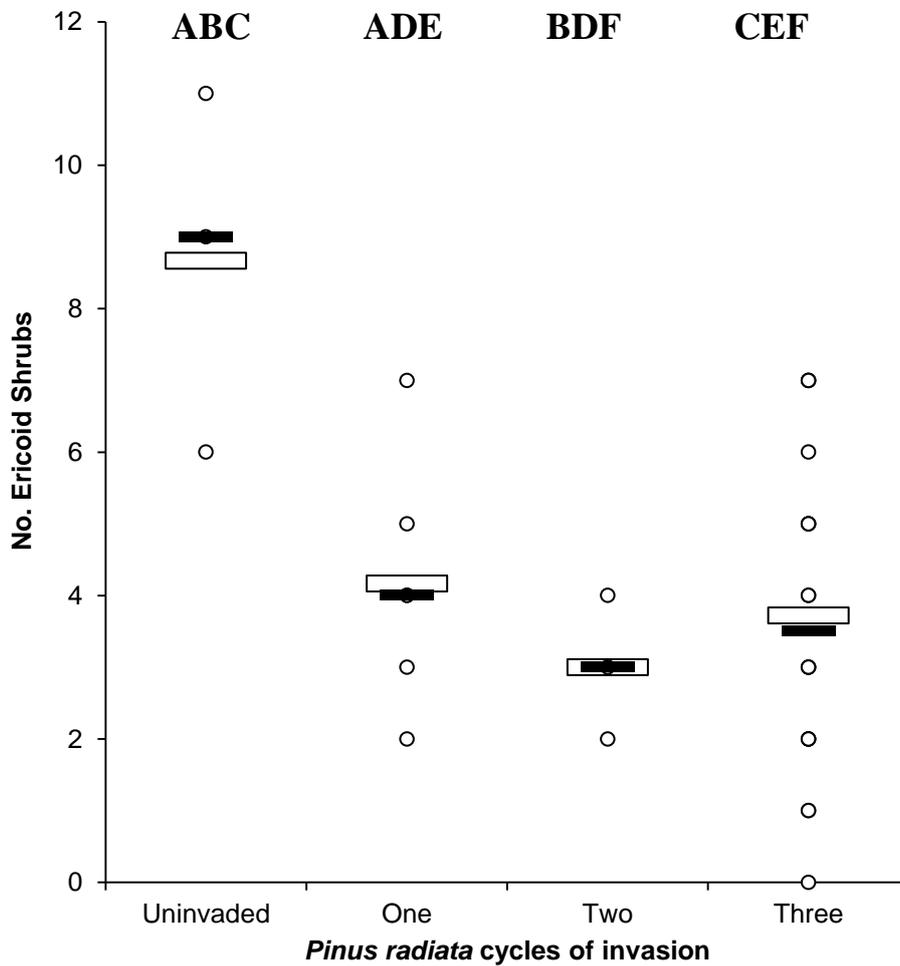
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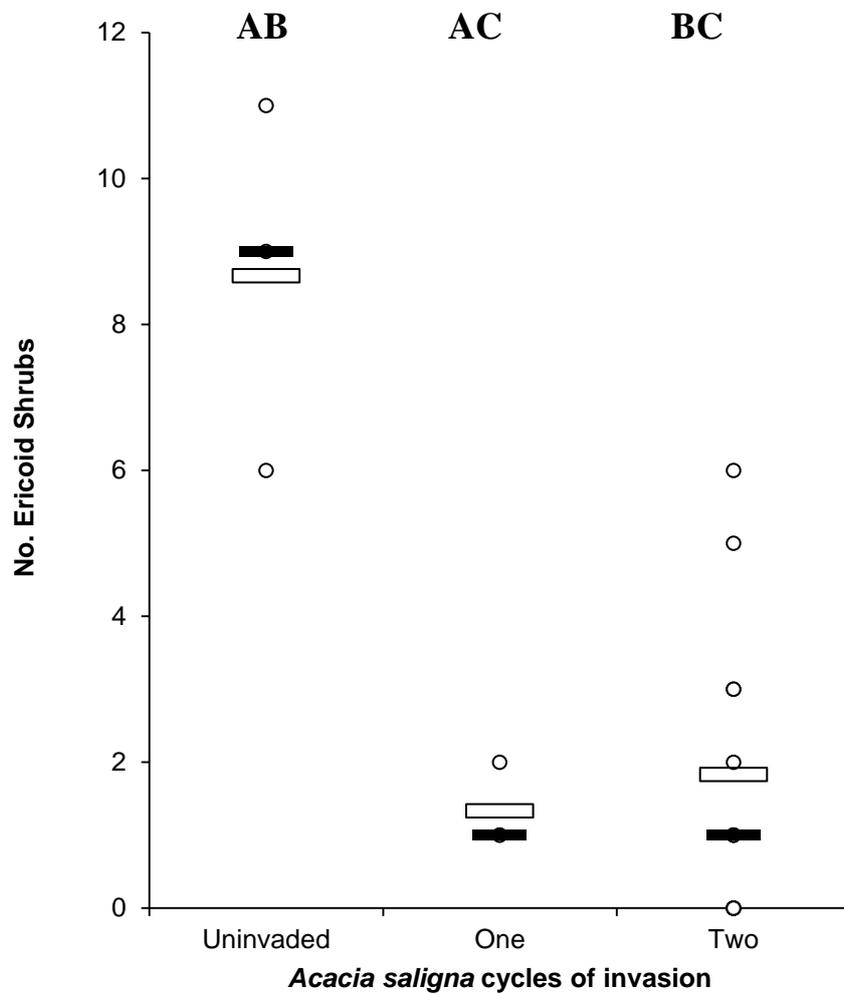
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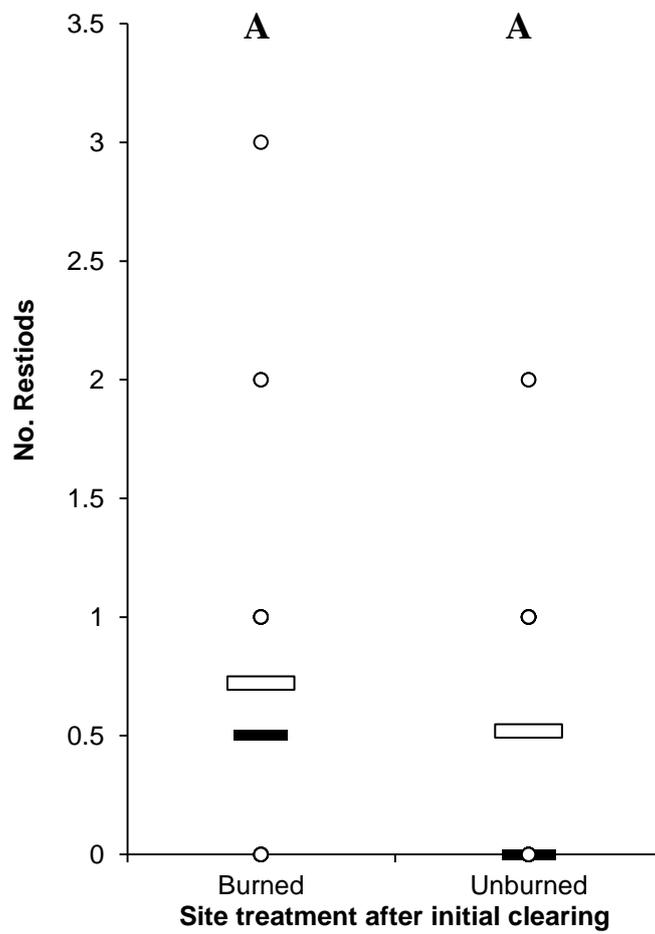
6)iv *P. radiata*



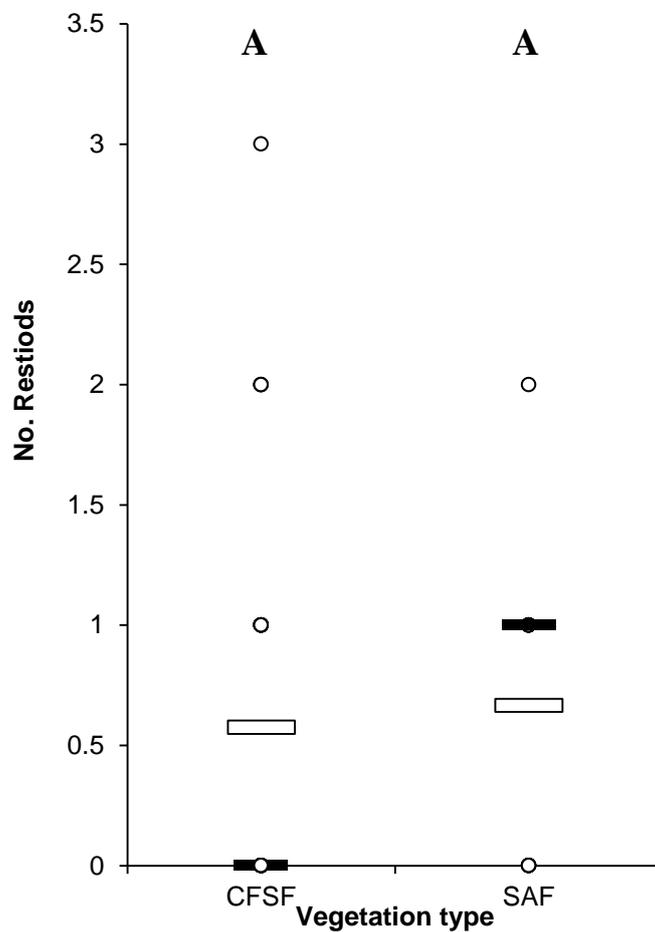
6)iv *A. saligna*



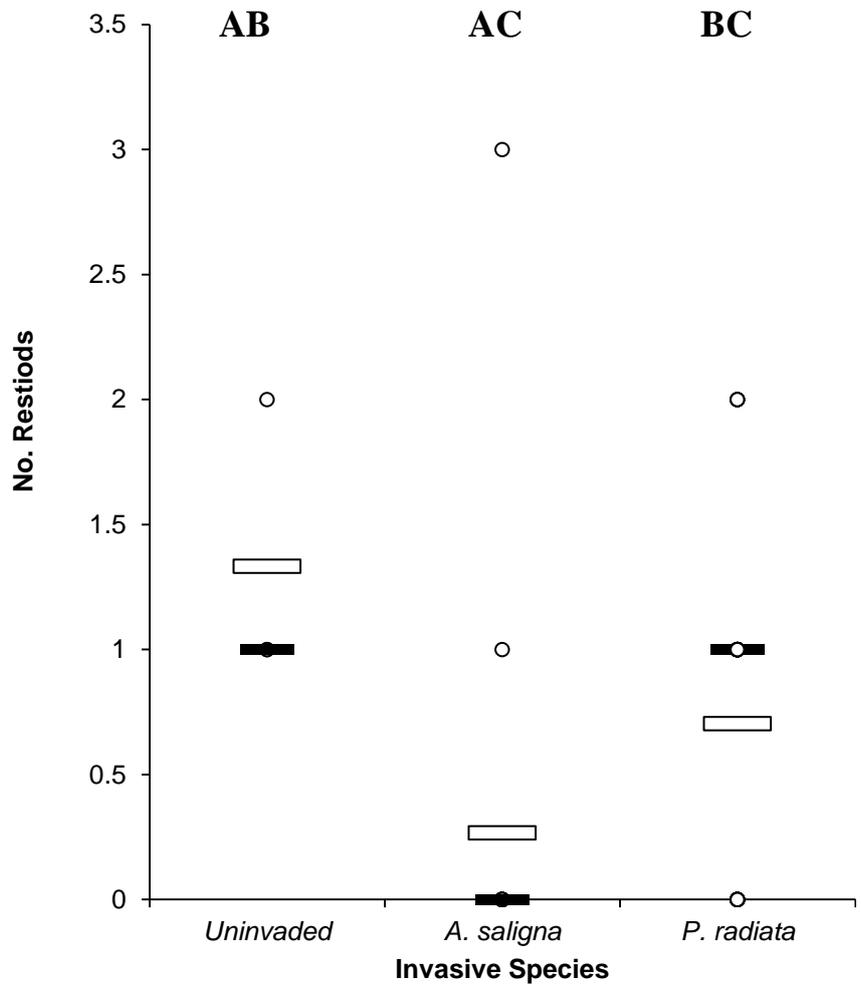
7)i



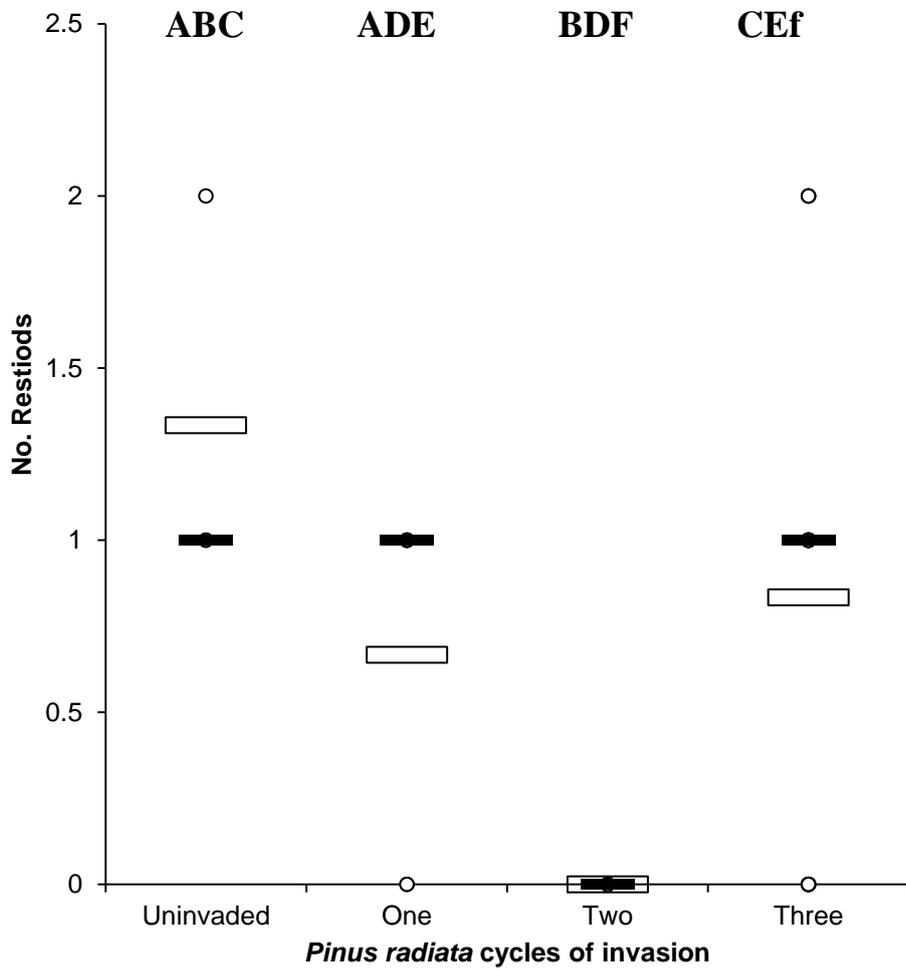
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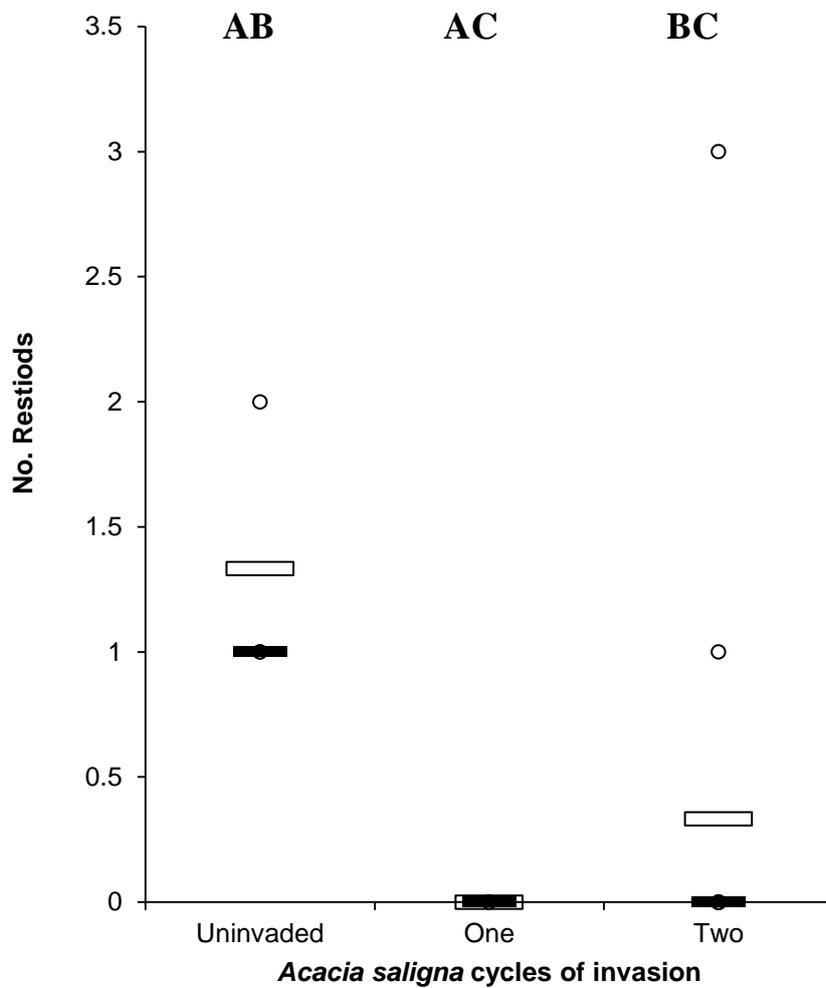
7)iii



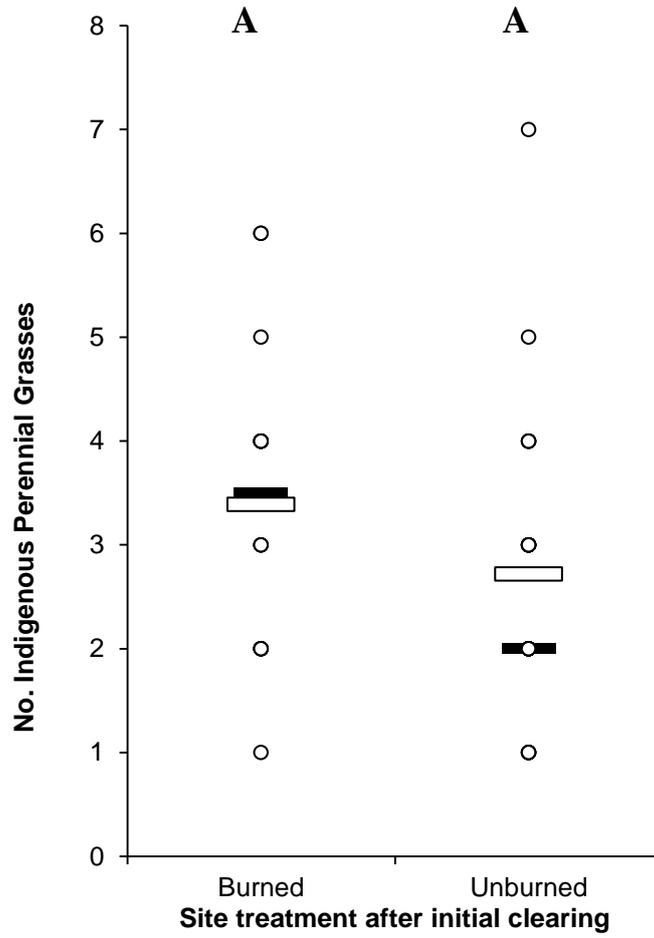
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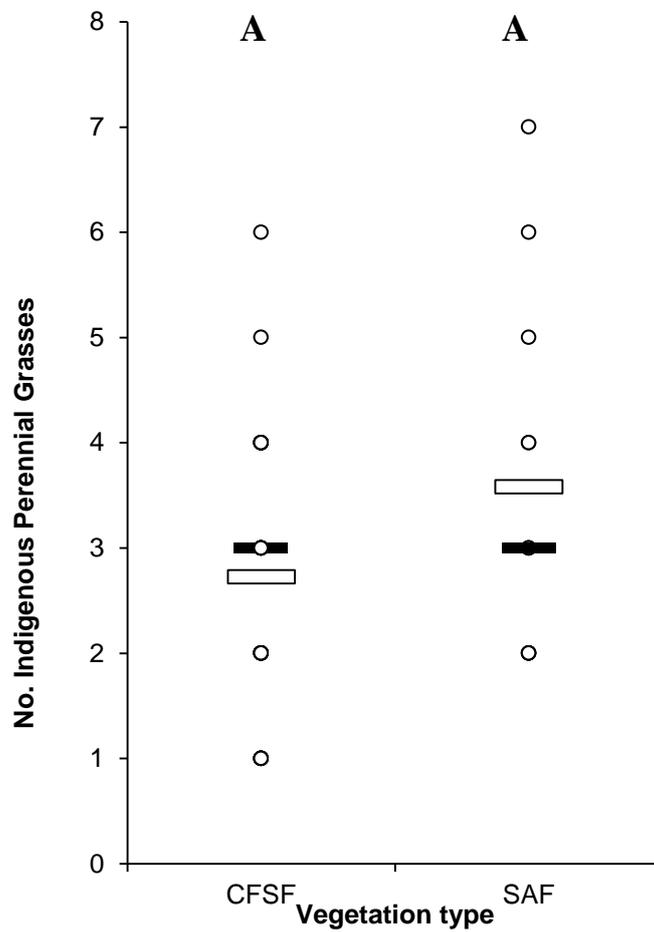
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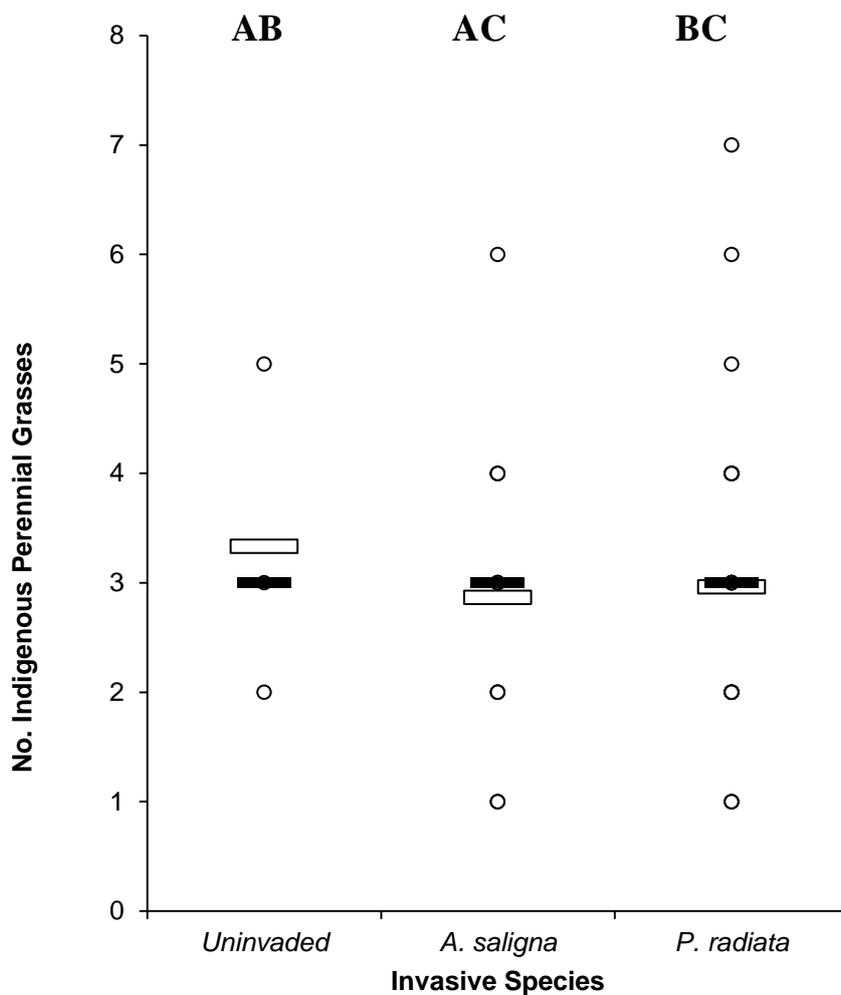
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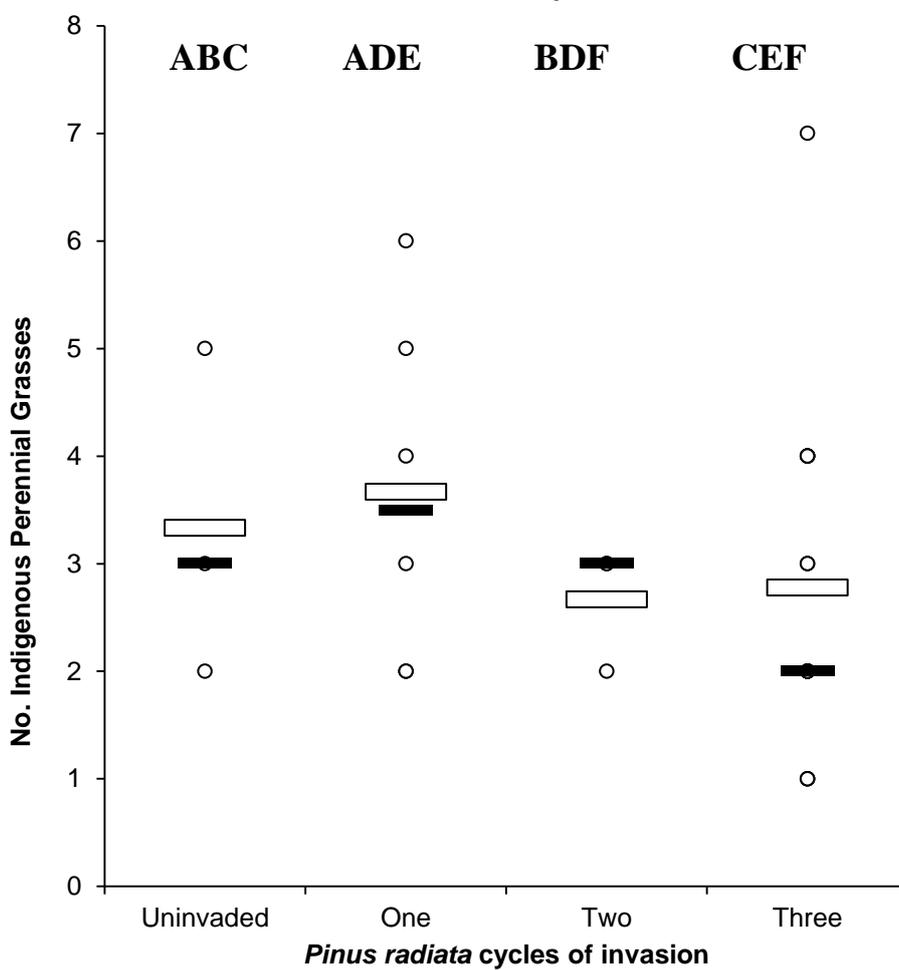
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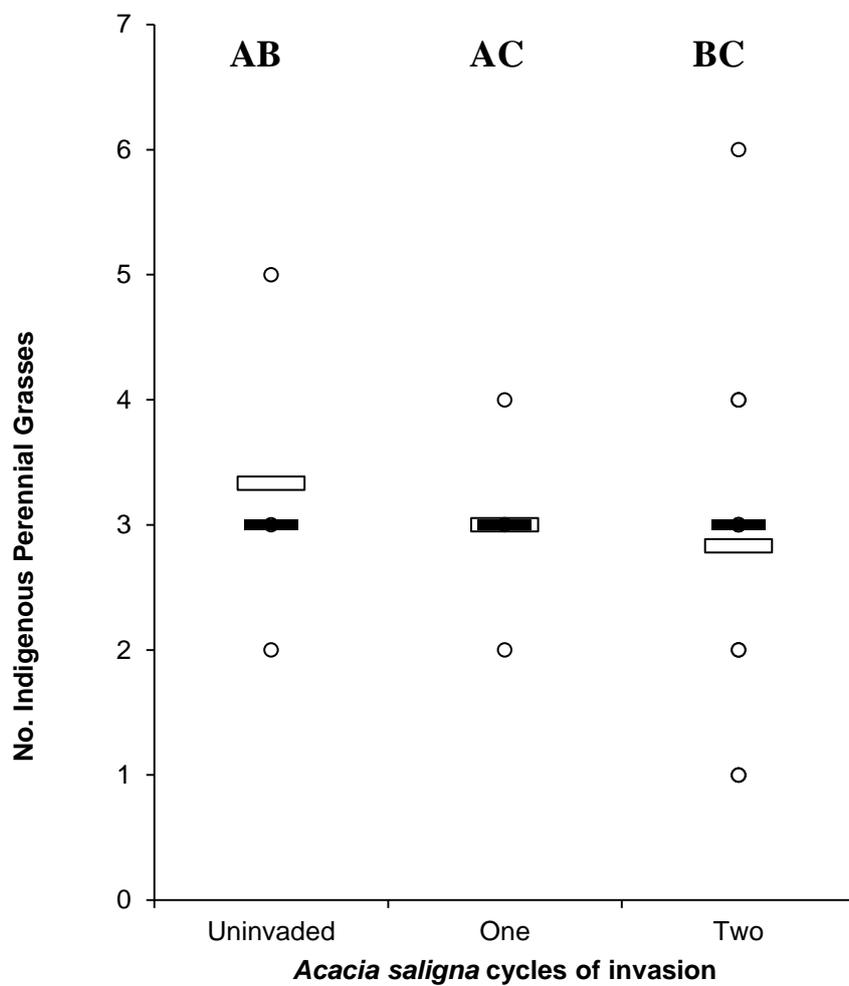
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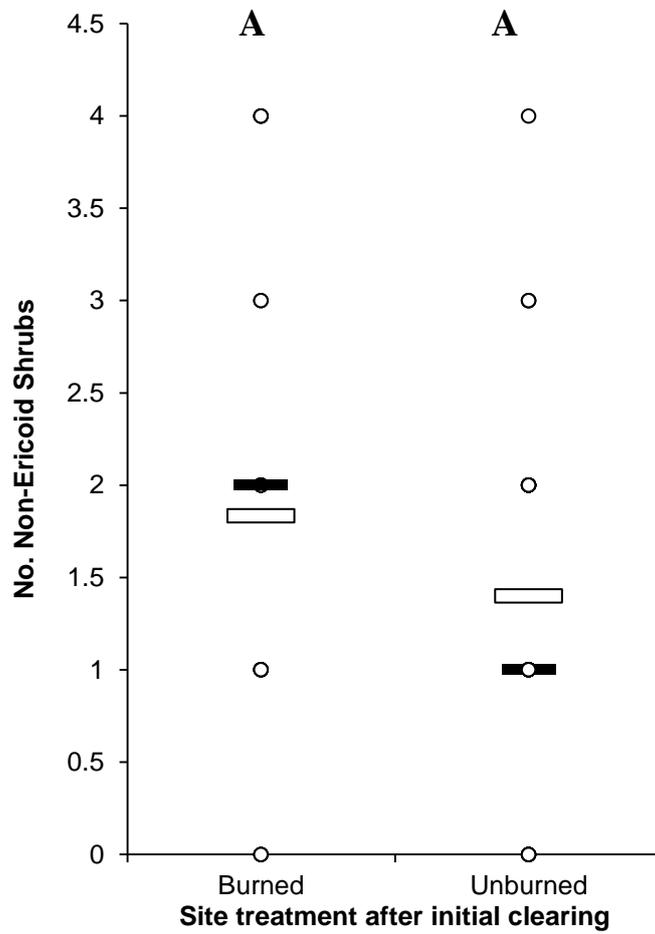
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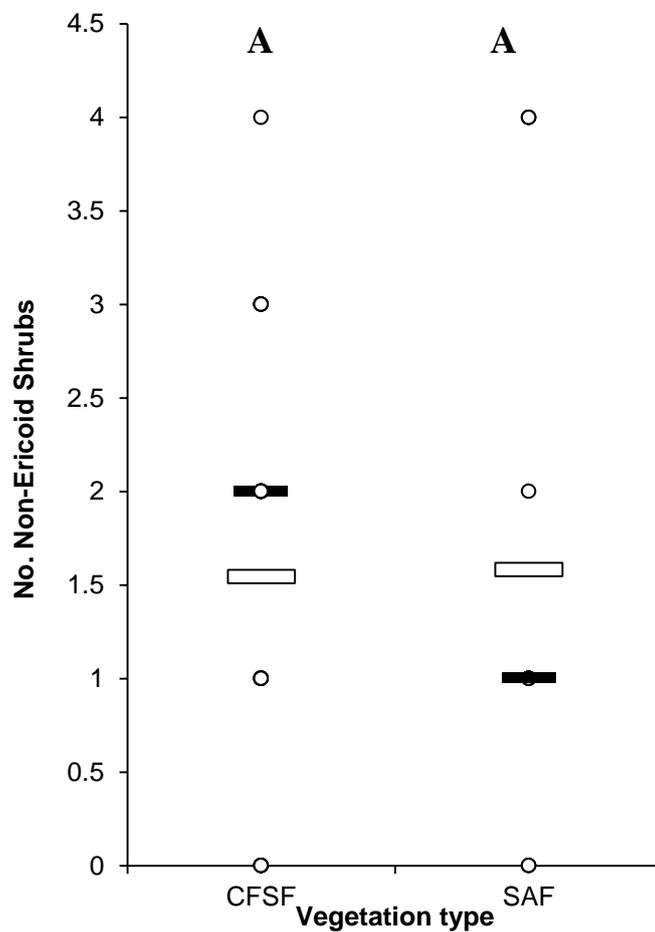
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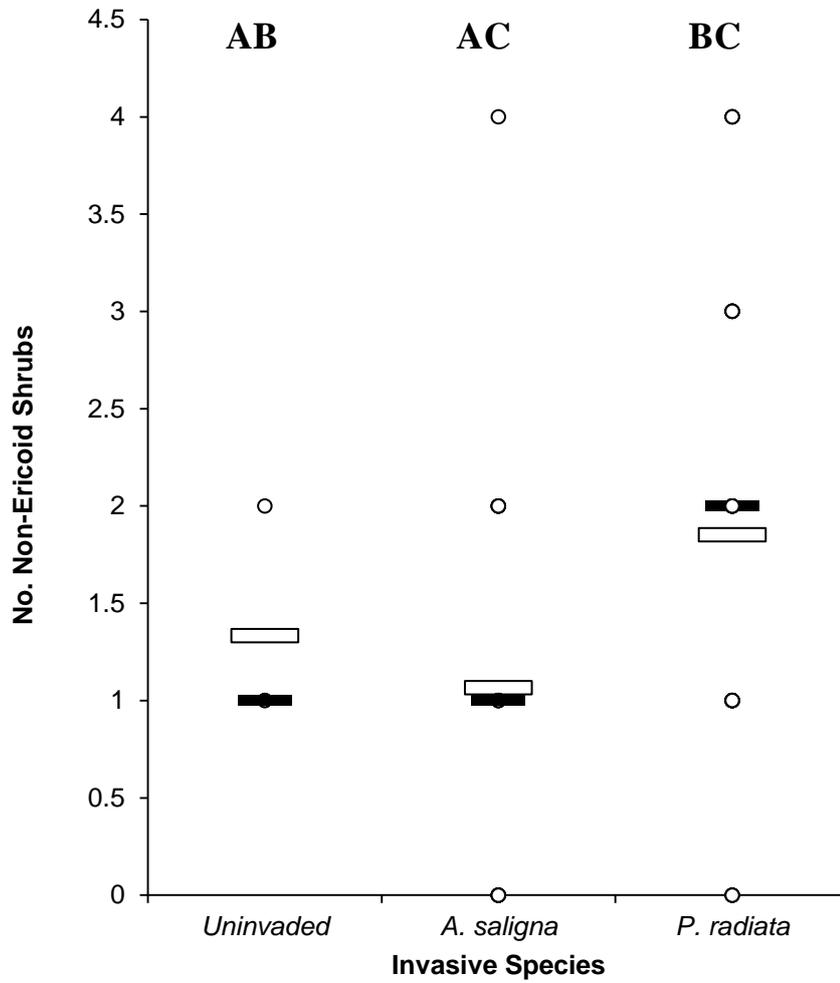
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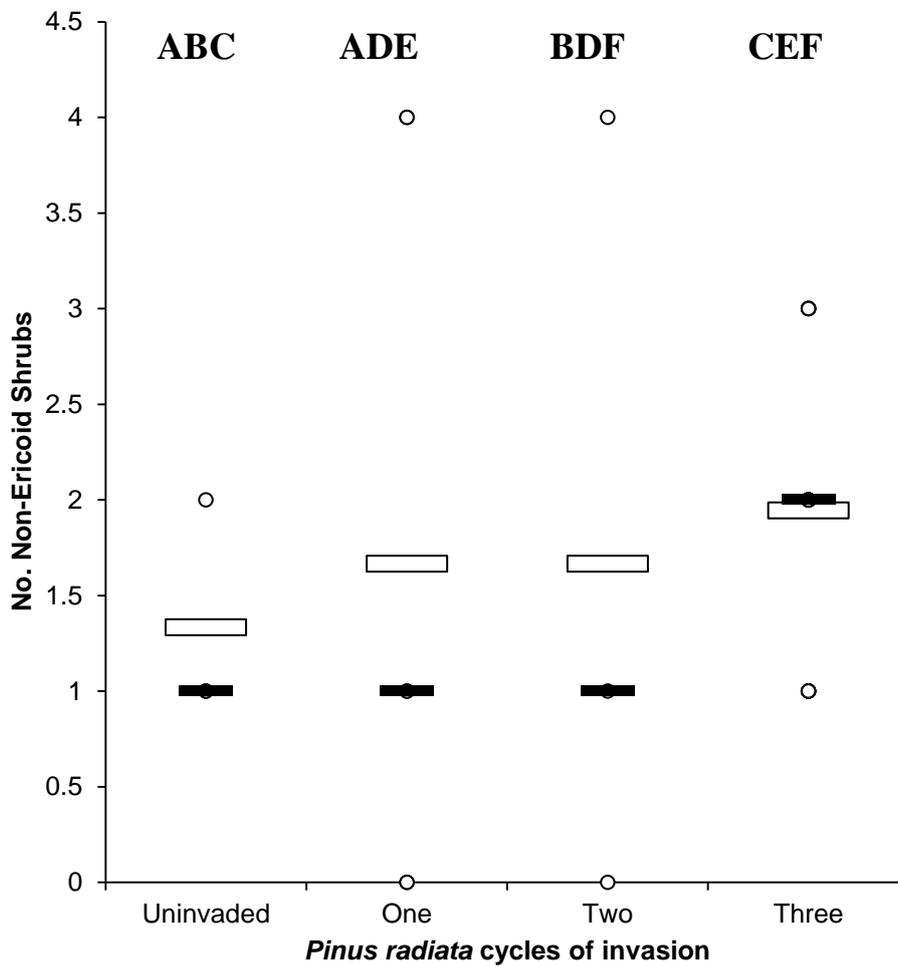
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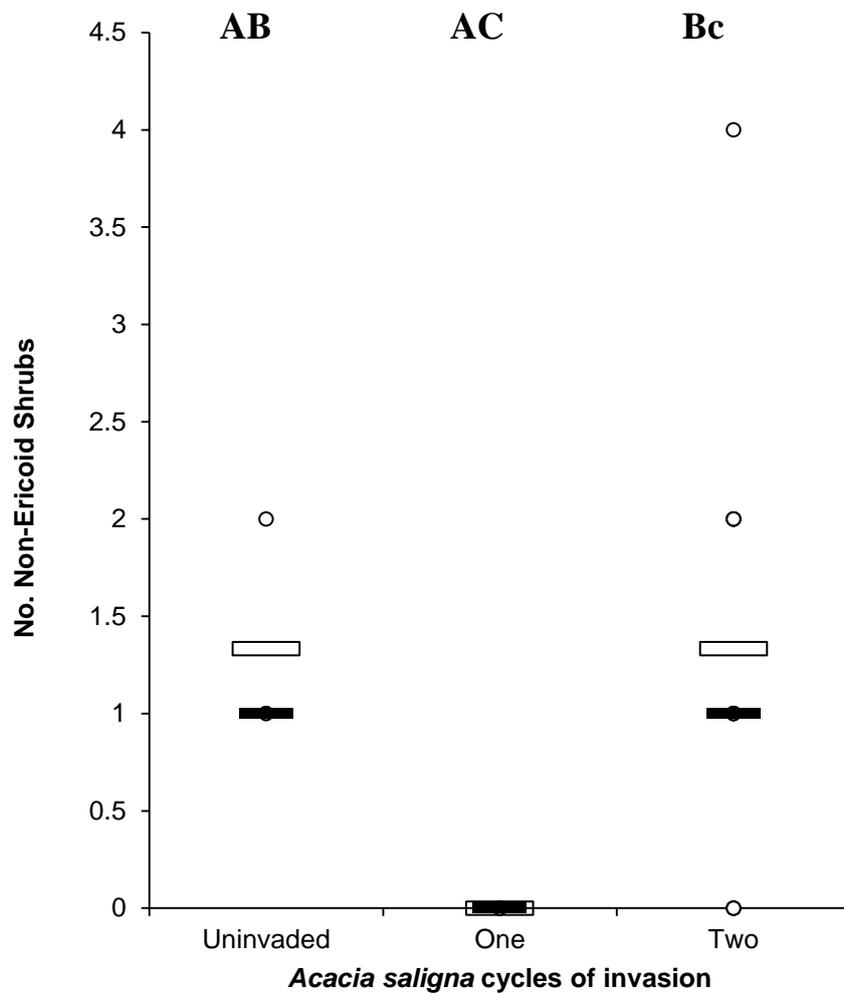
9) iii



9)iv *P. radiata*

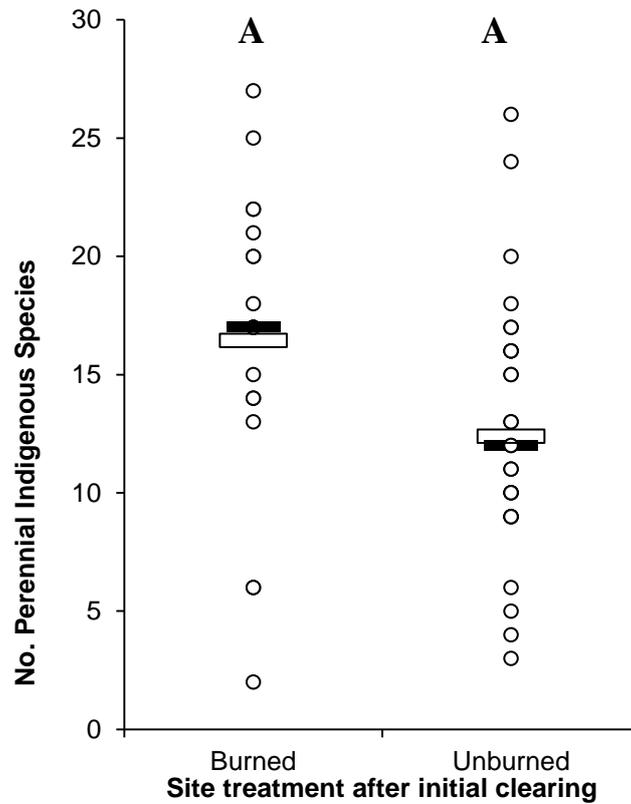


9)iv *A. saligna*

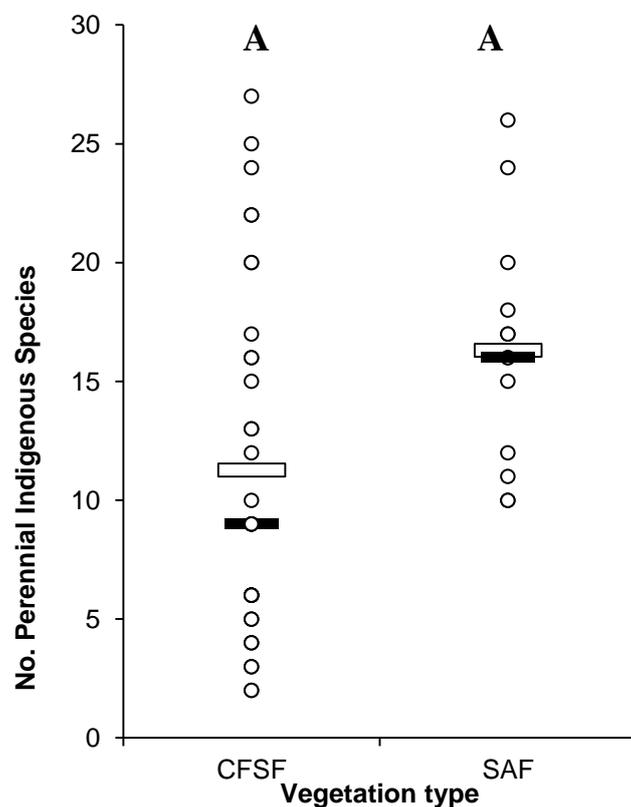


Relationship between the biodiversity indicator 10) No. of Perennial Indigenous Species and i) Site treatment after initial clearing (Burned or Unburned) ii) Vegetation type (Cape Flat Sand Fynbos, CFSF, or Swartland Alluvium Fynbos, SAF) iii) Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*) and the iv) Number of cycles of invasion (Uninvaded, One, Two or Three), separated by species: *A. saligna* and *P. radiata*. Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variable is represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).

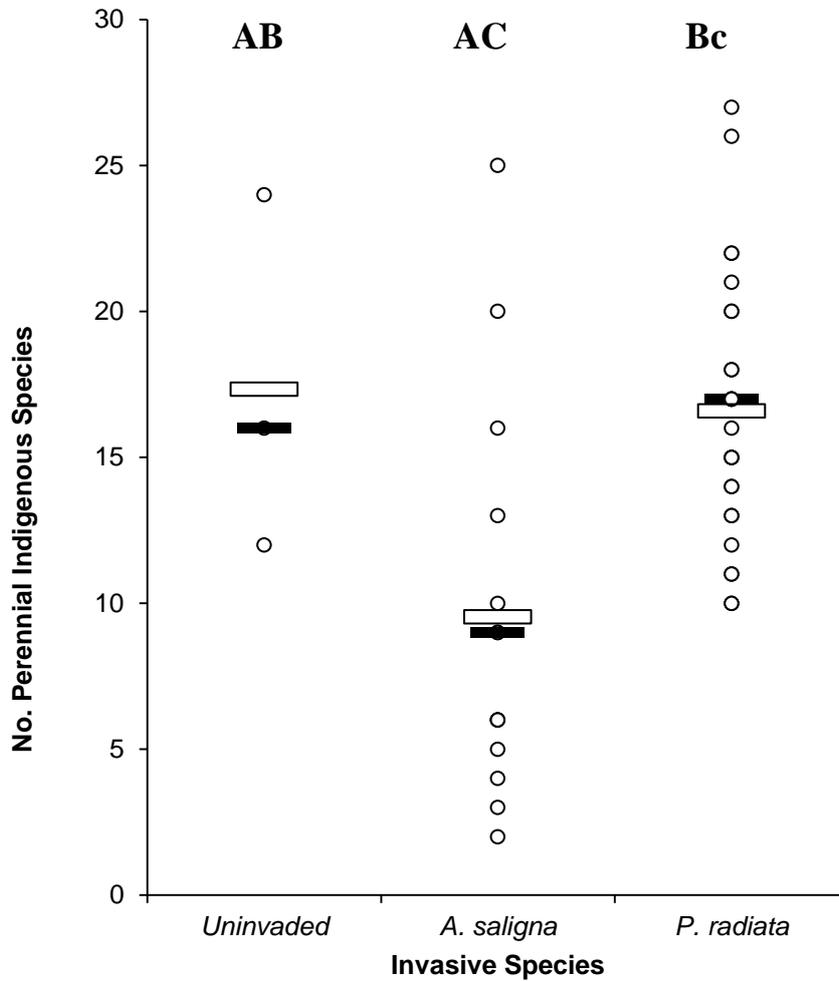
10) i



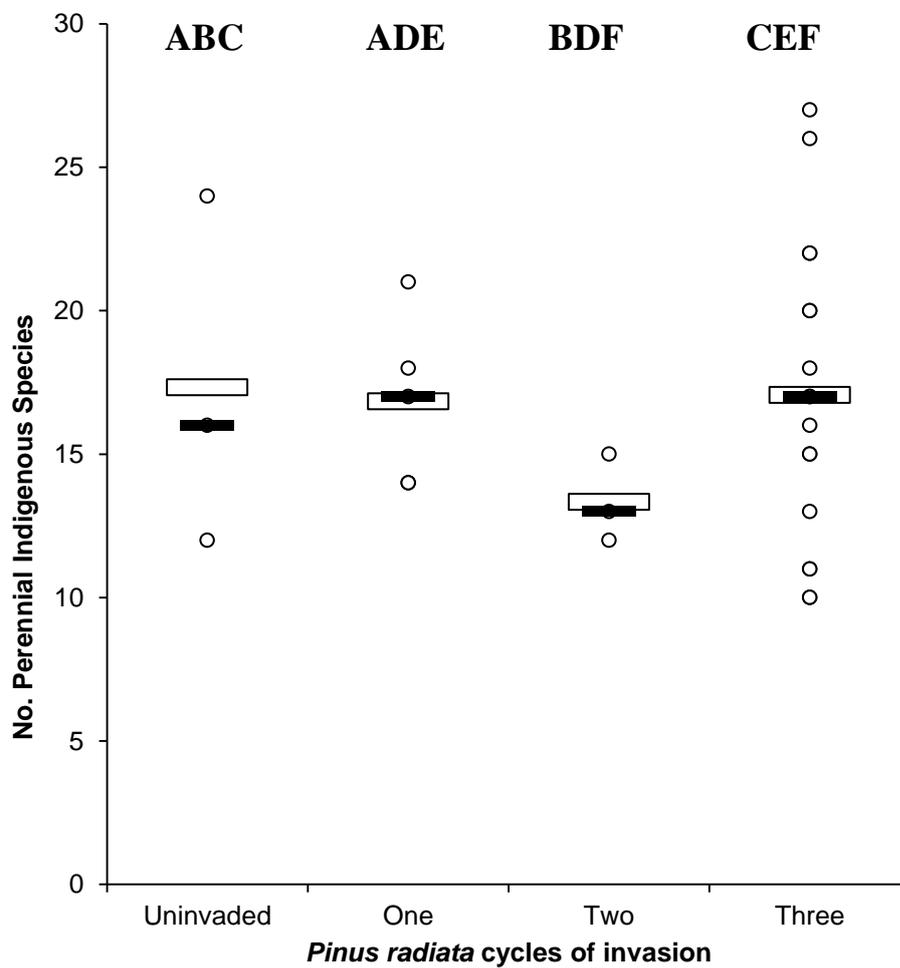
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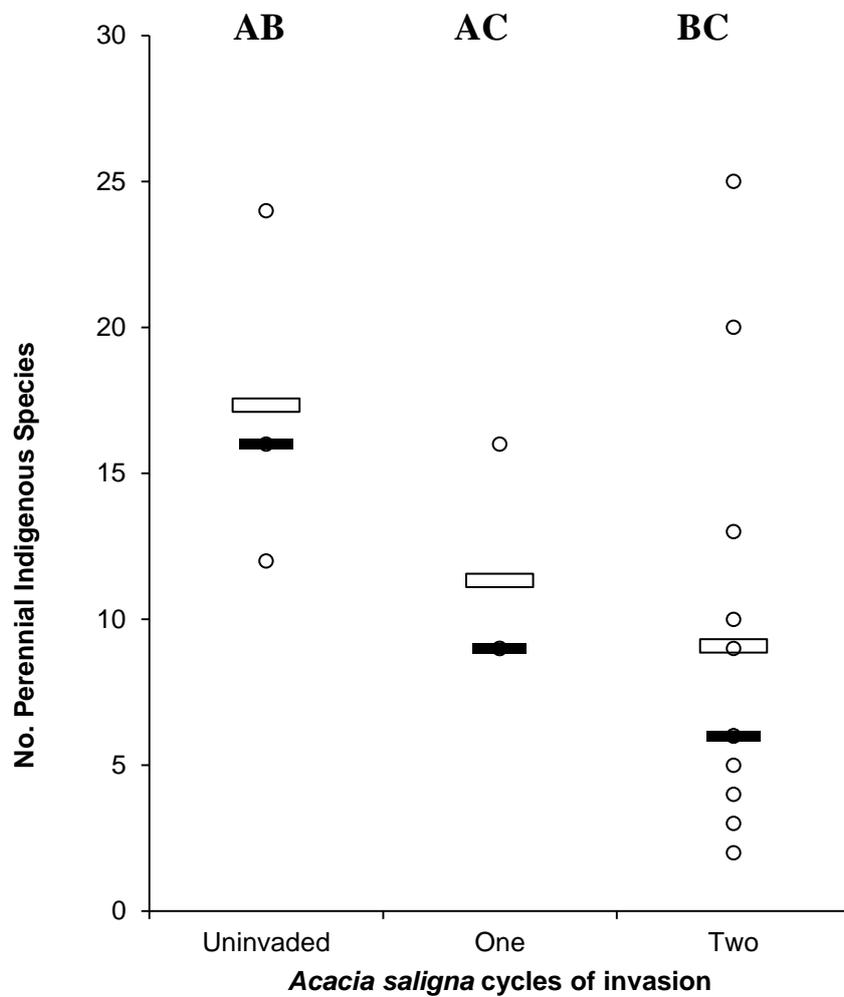
10) iii



10) iv *P. radiata*

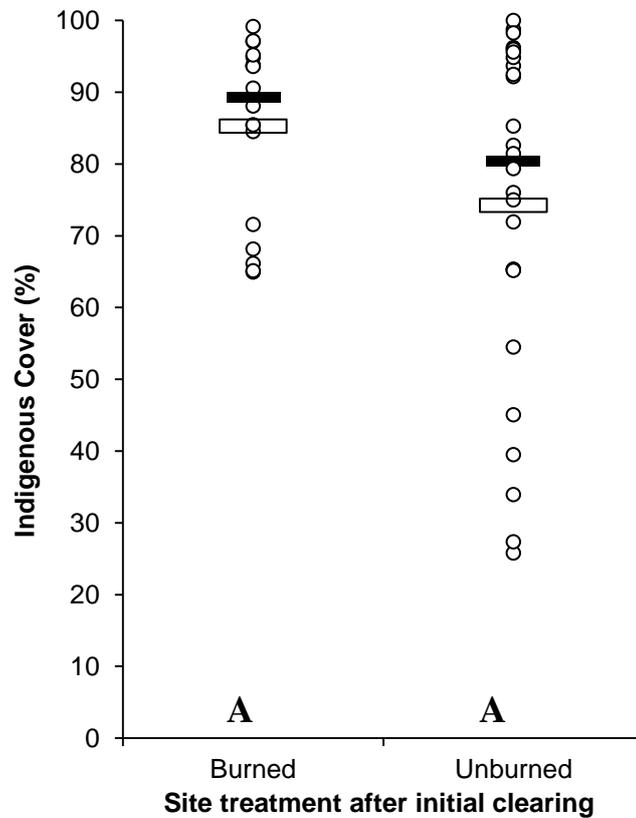


10)iv *A. saligna*

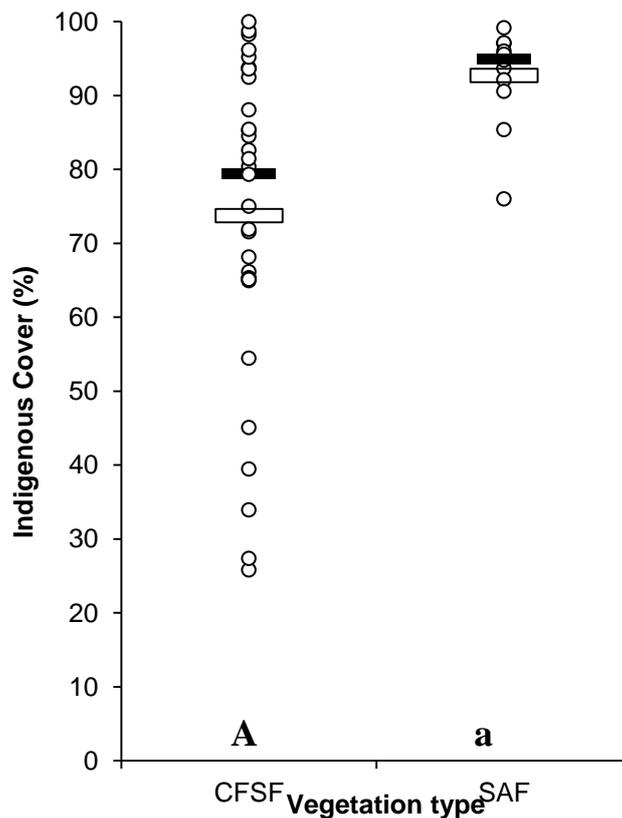


Relationship between biotic structural indicators as response variables 11) Indigenous Cover 12) Alien Cover and i) Site treatment after initial clearing (Burned or Unburned) ii) Vegetation type (Cape Flat Sand Fynbos, CFSF, or Swartland Alluvium Fynbos, SAF) iii) Dominant Invasive Species (Uninvaded, *A. saligna*, *P. radiata*) and the iv) Number of cycles of invasion (Uninvaded, One, Two or Three). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See **Appendix 4B** for corresponding statistics. Letters denote comparisons made between groups, where lower case letters denote significant differences ($p < 0.05$).

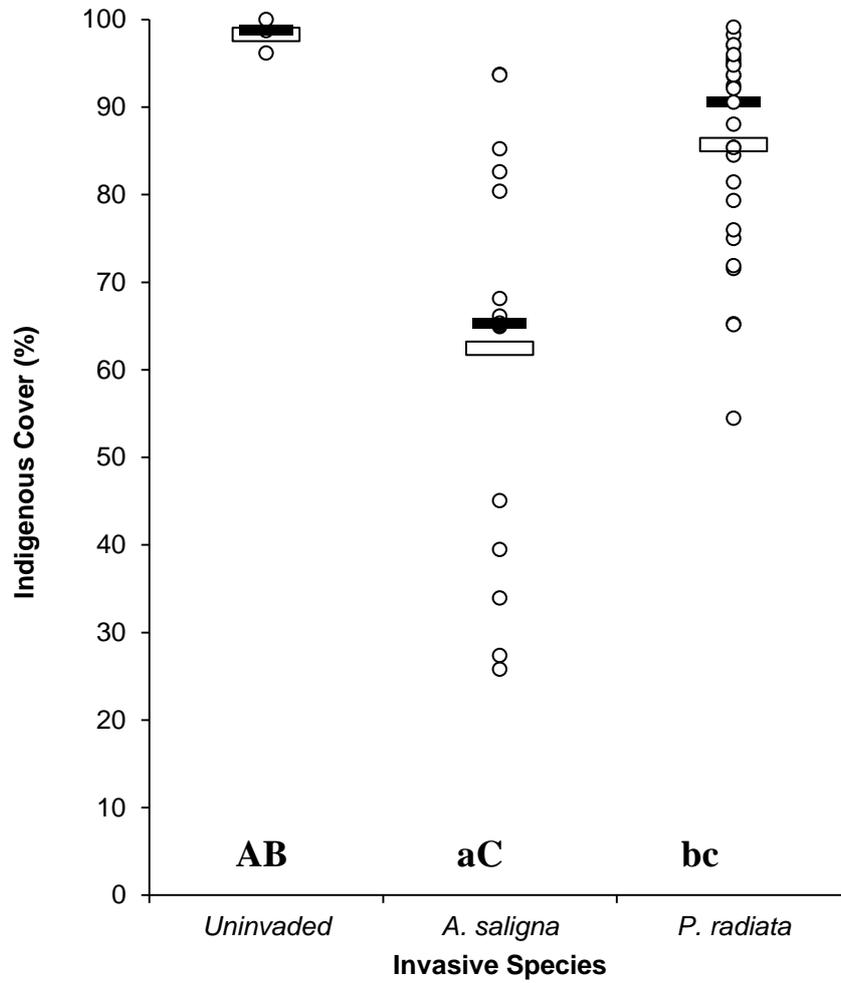
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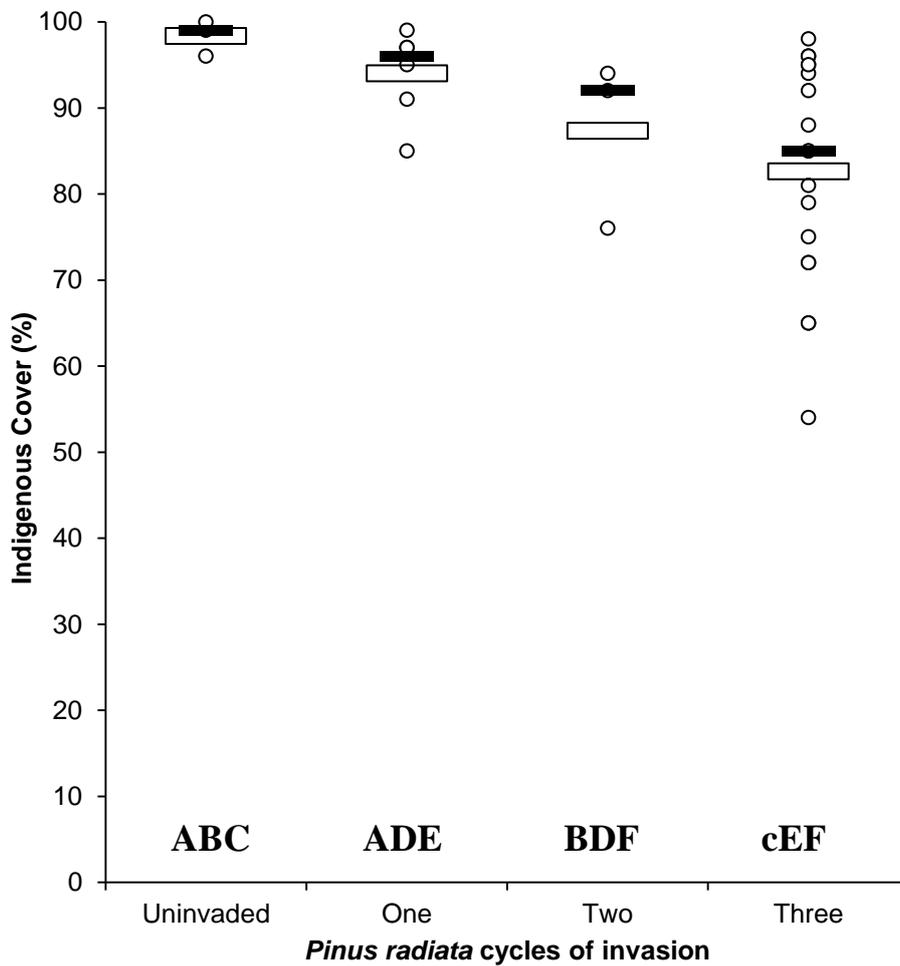
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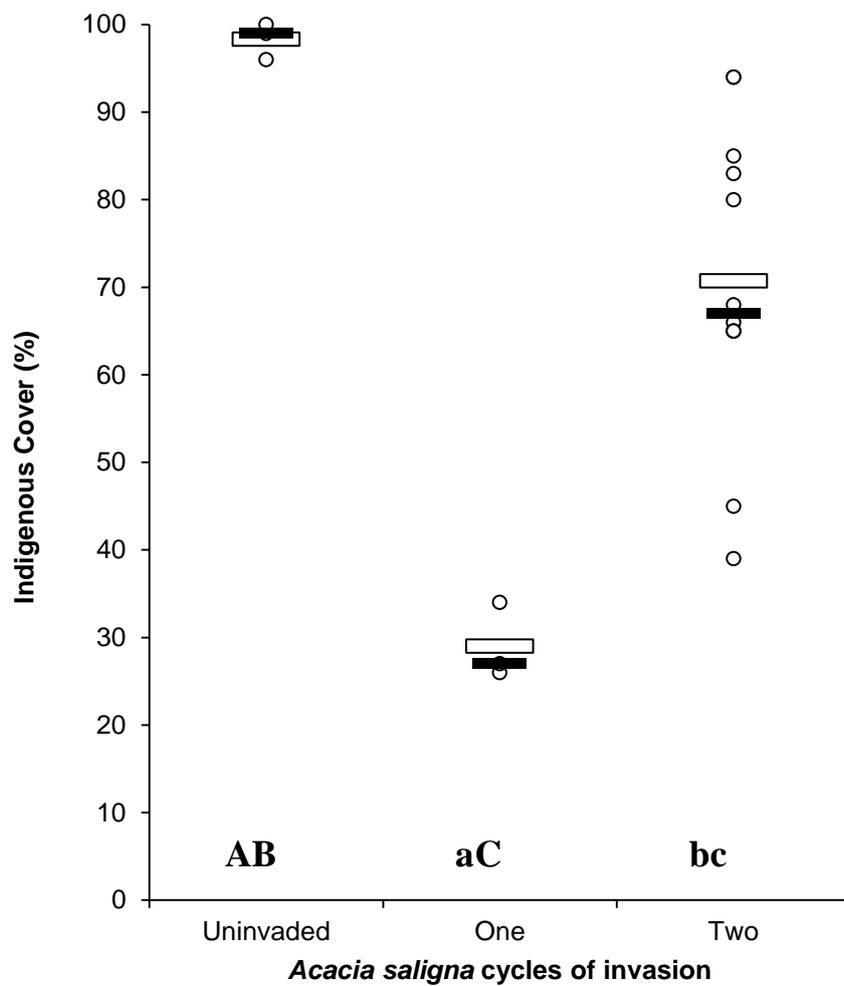
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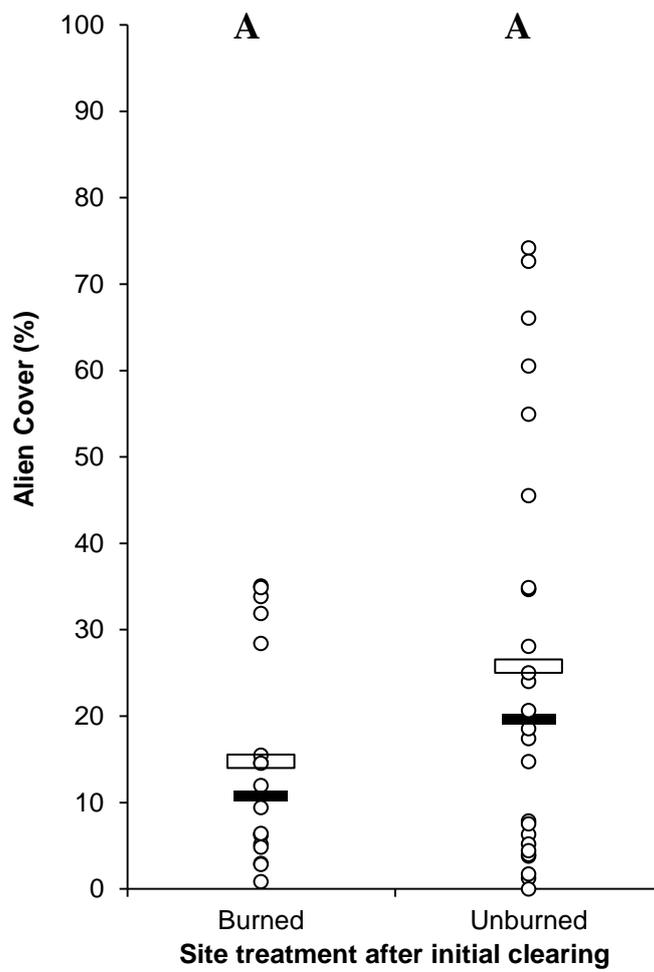
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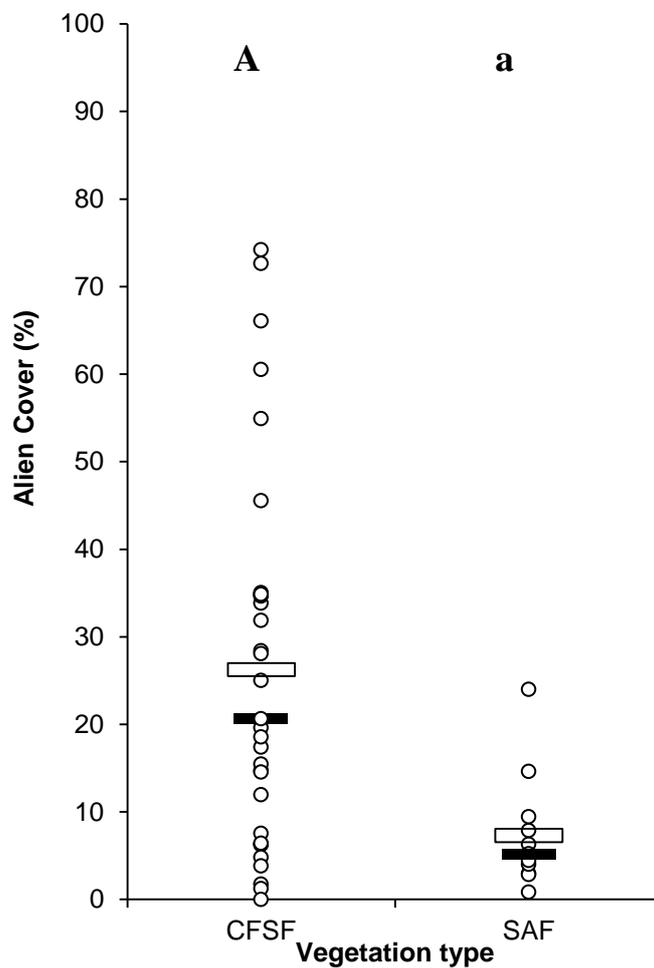
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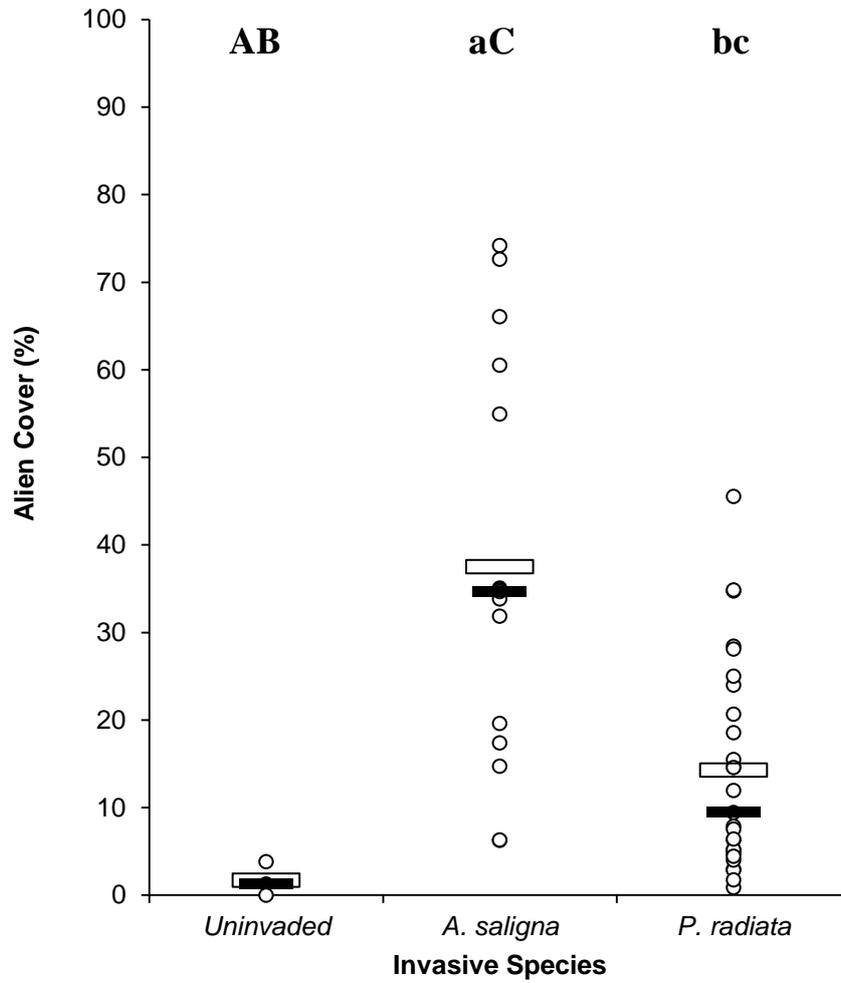
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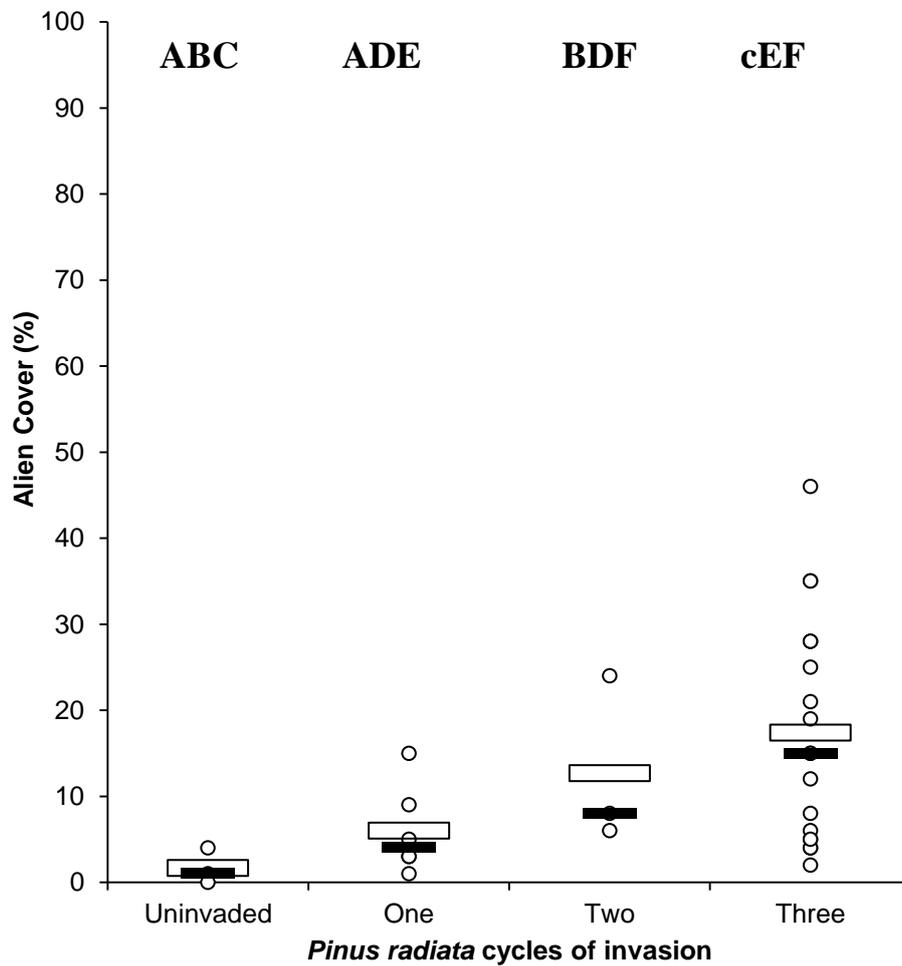
12)ii



12)iii



12)iv *P. radiata*



12)iv *A. saligna*

